

**ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE**

**FAKULTA LESNICKÁ A DŘEVAŘSKÁ**

**Katedra Pěstování lesů**



**Česká zemědělská  
univerzita v Praze**

Disertační práce

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Autor:

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Název disertační práce:

**Pěstební analýza strukturně diferencovaných borových porostů**

***Silvicultural analysis of structurally differentiated pine stands***

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**Obor:** Pěstování lesa

**Ročník:** IV.

**Katedra:** Katedra pěstování lesů

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**Zahájení studia:** 5. 10. 2018

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Jakub Brichta

## ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE

Fakulta lesnická a dřevařská

### ZADÁNÍ DISERTAČNÍ PRÁCE

|                         |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
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| Autor práce:            | Ing. Jakub Brichta                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Studijní program:       | Lesní inženýrství                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Obor:                   | Pěstování lesa                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Vedoucí práce:          | doc. Ing. Lukáš Bílek, Ph.D.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Garantující pracoviště: | Katedra pěstování lesů                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Jazyk práce:            | Čeština                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Název práce:            | <b>Pěstební analýza strukturně diferencovaných borových porostů</b>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| Název anglicky:         | <b>Silvicultural analysis of structurally differentiated pine stands</b>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Cíle práce:             | <p>Cílem disertační práce bude:</p> <ul style="list-style-type: none"><li>• na základě literární rešerše popsat současný stav poznání ohledně způsobů pěstování borových porostů a možnosti adaptace borového hospodářství na klimatickou změnu,</li><li>• stanovit přírůstový a produkční potenciál borovice lesní v závislosti na pěstebním zásahu, smíšení, stanovišti, věku, případně parametrech jednotlivých stromů,</li><li>• odvodit přírůst strukturně diferencovaných porostů a jeho srovnání s vybranými klimatickými charakteristikami,</li><li>• odvodit vztah mezi strukturujícími pěstebními zásahy a úspěšností přirozené obnovy borovice lesní,</li><li>• posoudit vliv poškození zvěří na zdravotní stav a stabilitu lesních porostů a jednotlivých stromů.</li></ul>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Metodika:               | <p><b>Výběr ploch</b></p> <p>Terénní měření bude probíhat na plochách založených v rámci diplomové práce a na trvalých zkušných plochách založených v letech 2015 až 2018 v rámci řešení projektu QJ1520037 (Zvyšování adaptability borového hospodářství v podmínkách České republiky). V průběhu doktorského studia pak budou stávající plochy doplněny i o nové vhodné objekty. V současné době se trvalé zkušné plochy nacházejí na území LČR, s. p., a to Lesní správy (LS) Choceň, LS Nasavrky, LS Plasy, LS Třeboň, na území VLS ČR, s. p. (Divize Mimoň) a na území Městských lesů Doksy, s.r.o. Plochy tak reprezentují hlavní oblasti borového hospodářství v podmínkách ČR. Jedná se zejména o přírodní lesní oblasti (PLO) 17 (Polabí), PLO 6 (Západočeská pahorkatina), PLO 15 (Jihočeské pánve) a PLO 18 (Severočeská pískovcová plošina a Český ráj). Zároveň studijní lokality pokrývají oblasti, kde se uplatňují pěstební postupy směřující ke strukturalizaci mateřských porostů a iniciaci přirozené obnovy. Alternativně budou další plochy založeny v zahraničí v oblastech se zastoupením borových porostů.</p> <p><b>Sběr dat</b></p> <p>Vedle klasických dendrometrických postupů bude na těchto plochách využita technologie FieldMap (jmenovitě pak bude měřeno: přesná poloha jednotlivých bodů /jedinců mateřského porostu i poloha jedinců přirozené obnovy/ a dendrometrické charakteristiky stromů v porostu /výčetní tloušťka, výška, korunová projekce, kvalitativní charakteristiky/). Alternativně bude pro přesné měření pozice jedinců obnovy využita metoda RTK v síti GPS. Na plochách bude probíhat odběr vzorků pro dendrochronologické analýzy tak, aby bylo možné analyzovat přírůst jedinců a jeho vztah k průběhu klimatu. Světelné podmínky budou odvozeny prostřednictvím charakteristik zápoje, alternativně s využitím metod DPZ.</p> |

#### Zpracování dat

Dendrochronologické datování bude provedeno v dendrochronologické laboratoři Katedry pěstování lesů za využití posuvného měřicího stolu LINTAB RINNTECH a datovacího softwaru TSAP Win. Další analýzy budou provedeny pomocí softwaru DendroClim. Statistické analýzy budou provedeny v programech Statistica a R.

#### Harmonogram řešení:

2018–2022: Studium odborné literatury

2018–2019: Práce na odborné publikaci kategorie Jscopus (Vliv uvolnění na tloušťkový přírůst výstavků borovice lesní)

2019 – 2020: Mapování vlivu těžebního zásahu a přípravy půdy na úspěšnost přirozené obnovy borovice lesní, analýza zdravotního stavu a stability mateřského prostu

2019 – 2020: Práce na odborné publikaci kategorie Jimp (Vliv těžebního zásahu a přípravy půdy na úspěšnost přirozené obnovy borovice lesní)

2019–2020: Mapování porostní struktury v podmínkách maloplošného podroostního hospodaření, odběr vzorků pro dendrochronologické analýzy

2019–2020: Zpracování vzorků v dendrochronologické laboratoři

2020–2021: Práce na odborné publikaci kategorie Jimp (Produkční charakteristiky strukturně diferencovaných borových porostů)

2021 –2022: Syntéza poznatků a formulace výsledků výzkumu, doporučení pro lesnickou vědu a praxi

Doporučený rozsah práce: 100 normostran

Klíčová slova: borovice lesní, tloušťkový přírůst, přirozená obnova, struktura porostu, stabilita

#### Doporučené zdroje informací:

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Předseda oborové rady

Elektronicky schváleno: 29. 9. 2024

**prof. Ing. Róbert Marušák, PhD.**

Děkan



### **Prohlášení**

Prohlašuji, že jsem disertační práci na téma „*Pěstební analýza strukturně diferencovaných borových porostů*“ vypracoval samostatně na základě konzultací se školitelem, za využití vlastních výsledků, podpořených dostupnými literárními prameny, které jsou v práci náležitě citovány. Souhlasím s tím, aby tato práce byla zveřejněna v souladu s § 47b Zákona č. 111/1998 Sb., o vysokých školách.

Dne 30. 9. 2024, v Praze.

Ing. Jakub Brichta

## **Poděkování**

Tímto upřímně děkuji všem kolegům z Katedry pěstování lesů FLD ČZU v Praze za spolupráci v realizaci metodologie níže popsaného výzkumu, stejně jako při zpracování a interpretaci jeho výsledků. Vážím si také příležitosti podílet se na výzkumech projektech založených ještě v době před započítím aktivit disertační práce. Zvláštní dík patří školiteli doc. Ing. Lukáši Bílkovi, Ph.D. za přátelské a profesionální jednání v provedení mé osoby akademickou prací. Konkrétní vyjádření vděku je určeno také Ing. Zdeňku Vackovi, Ph.D. za významnou pomoc mimo jiné při revidování odborných publikací. V neposlední řadě je nutné poděkovat také všem ostatním zaměstnavatelům, kteří mi umožnili výzkumné aktivity doplnit o praktické zkušenosti z oblasti lesního hospodářství a předně lesní pedagogiky a práce s veřejností. Děkuji rodině a přátelům za podporu. Třebaže se závěry předložené disertační práce nejví jako zcela zásadní pro fungování lidské společnosti, věřím, že její dokončení může být zároveň satisfakcí nejen pro mne samého, ale také pro všechny výše zmíněné.

## **Abstrakt:**

Disertační práce je zaměřena na rozbor pěstebních možností a limitů borovice lesní (*Pinus sylvestris* L.), v kontextu globální klimatické změny a měnících se požadavků na lesní hospodářství. Mezi hlavní cíle předložené disertační práce patří: detailní rešerše informací o daném taxonu; zjištění vlivu strukturujících pěstebních zásahů na iniciaci a dimenze přirozené obnovy pod mateřským porostem; popis produkce a struktury heterogenních borových porostů; posouzení vlivu vybraných abiotických a biotických faktorů na vitalitu borových porostů.

Výzkum byl prováděn v lesních komplexech Evropy s významným zastoupením borovice lesní. Měření struktury dospělých porostů probíhalo v heterogenních borových porostech, se zájmovou plochou 0,125-0,50 ha, kde proběhl také sběr dendrochronologických vzorků. Přirozená obnova borovice lesní byla inventarizována na experimentální ploše s různými variantami hustoty mateřského porostu a přípravy půdy. Hodnocení vlivu loupání zvěří proběhlo v probírkových porostech borovice lesní. Získaná data o struktuře a produkci lesních porostů byla dále analyzována prostřednictvím běžných softwarů (R, STATISTICA 13, CANOCO 5, SIBYLA Triquetra 10, PointPro 2.1), dendrochronologické vzorky byly vyhodnoceny skrze software TSAP Win, klimatická data pak byla porovnávána s letokruhovými sériemi v programu DendroClim 2002.

Stěžejními výsledky disertační práce jsou konkrétní doporučení pro uplatnění clonných postupů na vybraných stanovištích; z dendroklimatologických dat napříč Evropou vyplývá, že radiální růst borovice lesní postupně ztrácí přirozenou cyklicitu, kdy jsou klimatické extrémy s radiálním přírůstem stále více korelovány. Bylo potvrzeno, že přírůst borovice lesní je více ovlivněn teplotou než dostupností srážek. Ve středních polohách byly smíšené porosty borovice lesní a smrku ztepilého (*Picea abies* L. Karst) z hlediska stability i produkce vyhodnoceny jako vhodnější ve srovnání s nesmíšenými porosty obou dřevin. Byla potvrzena nutnost adaptace (změna stávajících pěstebních postupů) borového hospodářství na nové klimatické podmínky, jejímiž hlavními principy jsou strukturalizace borových porostů a podpora porostních směsí, kde to stanovištní podmínky umožňují.

## **Klíčová slova:**

borovice lesní; klimatická změna; strukturní diferenciacie; podroostní hospodaření

## **Abstract:**

The dissertation is focused on the analysis of the growing possibilities and limits of Scots pine (*Pinus sylvestris* L.), in the context of global climate change and changing requirements for forest management. The main goals of the submitted dissertation include: detailed research of information about the given taxon; determination of the effect of structuring treatments interventions on the initiation and dimensions of natural regeneration under the mature stand; description of the production and structure of heterogeneous pine stands; assessment of the influence of selected abiotic and biotic factors on the vitality of pine stands.

The research was carried out in forest complexes of Europe with a significant presence of Scots pine. The measurement of the structure of mature stands took place in heterogeneous pine stands, with an area of interest of 0.125-0.50 ha, where dendrochronological samples were also collected. The natural regeneration of Scots pine was inventoried on an experimental plot with different variants of the density of the parent stand and soil preparation. The evaluation of the effect of bark stripping took place in thinning stands of Scots pine. The obtained data on the structure and production of forest stands were further analyzed using standard software (R, STATISTICA 13, CANOCO 5, SIBYLA Triquetra 10, PointPro 2.1), dendrochronological samples were evaluated using the TSAP Win software, and the climatic data were then compared with the tree-ring series in the program DendroClim 2002.

The main results of the dissertation are specific recommendations for the application of aperture procedures at selected sites; dendroclimatological data across Europe show that the radial growth of Scots pine is gradually losing its natural cyclicity, when climatic extremes are increasingly correlated with radial growth. Scots pine growth has been confirmed to be more influenced by temperature than rainfall availability. In the middle locations, mixed stands of Scots pine and Norway spruce (*Picea abies* L. Karst) were evaluated as more suitable in terms of stability and production compared to mixed stands of both tree species. The necessity of adaptation (change of existing silviculture methods) of Scots pine management to new climatic conditions was confirmed, the main principles of which are the structuring of pine stands and the support of stand mixtures where the habitat conditions allow.

## **Key words:**

Scots pine; climate change; structural differentiation; shelterwood management



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## 1. ÚVOD

Středoevropské lesní hospodářství aktuálně prochází řadou technologických, ale také ideologických proměn. Nejen v mnoha oblastech České republiky jsme tak již druhé desetiletí svědky častého kolapsu lesních porostů, které se projevuje lokálně na úrovni lesního porostu i v rádech celých lesních hospodářských celků. Jedná se tak zejména o porosty smrkové a borové, kdy jejich předčasný rozpad můžeme mimo jiné přisuzovat způsobu jejich založení. Úspěšně založené jehličnaté porosty se tak dnes v odlišných klimatických podmínkách jeví jako labilní vůči celé řadě přírodních faktorů. Neuspokojivý stav lesů a predikce klimatu pro středně až dlouhodobý časový horizont lesníky nutí přehodnocovat a mnohdy výrazně měnit vžité pěstební a hospodářské postupy. K postupné adaptaci lesních ekosystémů nám jistě chybí ještě mnoho praktických informací, minimálně se však na základě zkušeností z několika posledních dekád o adaptaci a zachování lesní krajiny můžeme pokusit.

Velkou výzvou pro středoevropské lesníky je mimo jiné adaptace lesních porostů na stanovištích, kde často ani není možná náhrada stávající dřevinné skladby. Typickým příkladem takových stanovišť jsou přirozená borová stanoviště, kterým dominuje borovice lesní (*Pinus sylvestris* L.). Borovice lesní je na území České republiky tradiční dřevinou, je zde dokonce ve větší míře dokládána již od preboreálu (HORSÁK & CHYTRÝ 2010). Nelze opomenout ani zásadní hospodářský význam borovice lesní, nejen pro její rychlý růst a kvalitní dřevní hmotu, ale předně díky schopnosti prosperovat na široké škále stanovišť. Dalším hospodářským pozitivem této dřeviny je také její výrazná ekologická amplituda. Areál borovice lesní se tak rovnoměrně rozprostírá po celé ploše území ČR, velmi důležitou roli tato dřevina plní zejména na místech, kde jiné taxony nejsou schopny odrůstat. Na chudých suchem ohrožených až extrémních stanovištích je pěstování borovice často jedinou možností pro vytváření ucelených lesních porostů, a to i v rámci adaptace na změny klimatu. Ačkoli je borovice aktuálně na řadě lokalit velmi negativně ovlivňována suchem, stále patří mezi nejvíce zastoupené dřeviny v naší krajině, to samé platí také pro její rozšíření v měřítku celé Evropy a Asie. Ve světle klimatických změn je tedy třeba zvýšit povědomí o alternativních pěstebních postupech v borových porostech, a to nejen na území ČR. Náročným, ale o to důležitějším úkolem bude také připravit nově založené lesní porosty na klimatické podmínky, které se během jejich existence budou pravděpodobně výrazně měnit. Možnosti, jak zvýšit adaptabilitu a stabilitu borových porostů jsou různé, stále častěji se tak jedná o postupné odklánění se od

holosečného způsobu hospodaření, nýbrž směrem k podrobnému hospodaření až k využívání výběrných principů. Jako aktuální se dnes již nejeví ani pěstování homogenních borových porostů, a to jak s ohledem na prostorovou, věkovou, tak druhovou diverzitu. Mnoho literárních pramenů ze současnosti se v tomto kontextu shoduje ve vysokém potenciálu využívání či napodobování přirozených procesů. Alternativní obnovní postupy pěstování borových porostů jsou však již známé a běžně využívané, a to ve Skandinávských zemích (LUNDGVIST et al. 2019; HYPPÖNEN et al. 2013), v Německu (DRÖSSLER et al. 2017; SPATHELF et al. 2015), Polsku (BIELAK et al. 2014; ALEKSANDROWICZ-TRZCIŃSKA et al. 2017) i v České republice (BÍLEK et al. 2017).

V současné době již neplatí paušální spojování borovice výlučně s holou sečí. I přes výrazné nároky borovice na sluneční záření (SLAVÍKOVÁ 1986; LINDER 1997; MUSIL 2003; VACEK et al. 2007; HEIKE 2008; HORSÁK a CHYTRÝ 2010), ji dnes můžeme pěstovat několika způsoby.

Předložená disertační práce je souborem 7 publikovaných odborných článků, které jsou v celém svém rozsahu součástí kapitoly 5. Výsledky. Disertační práce rovněž obsahuje popis cílů a rozbor problematiky ve formě literární rešerše (kapitoly 2 a 3), jednotlív popis metodologie výzkumu uvedených prací (kapitola 4), obsažených v této práci. Součástí disertační práce jsou také souhrnná diskuse, závěr a seznam použité literatury (kapitoly 6 až 7).

Oborné publikace, které jsou součástí výsledkové kapitoly, jsou následující:

1. VACEK, S.; VACEK, Z.; BÍLEK, L.; REMEŠ, J.; HŮNOVÁ, I.; BULUŠEK, D.; KRÁL, J.; BRICHTA, J. (2019). *Stand dynamics in natural Scots pine forests as a model for adaptation management?* Dendrobiology, 82, 24–42.

2. BRICHTA, J., BÍLEK, L., LINDA, R., & VÍTÁMVÁS, J. (2020). *Does shelterwood regeneration on natural Scots pine sites under changing environmental conditions represent a viable alternative to traditional clear-cut management?* Central European Forestry Journal, 66(2), 104-115.

3. CUKOR, J., VACEK, Z., LINDA, R., VACEK, S., ŠIMŮNEK, V., MACHÁČEK, Z., BRICHTA, J., PROKŮPKOVÁ, A. (2022). *Scots pine (Pinus sylvestris L.) demonstrates a high resistance against bark stripping damage.* Forest Ecology and Management, 513, 120182.

4. BRICHTA, J., VACEK, S., VACEK, Z., CUKOR, J., MIKESKA, M., BÍLEK, L., ŠIMŮNEK, V., BRABEC, P. (2023). *Importance and potential of Scots pine (L.) in 21 century*. Central European Forestry Journal, 69(1), 3-20.
5. ŠLEGLOVÁ, K., BRICHTA, J., BÍLEK, L., & SUROVÝ, P. (2023). *Measuring the Canopy Architecture of Young Vegetation Using the Fastrak Polhemus 3D Digitizer*. Sensors, 24(1), 109.
6. BRABEC, P., BRICHTA, J., VACEK, Z., VACEK, S., ŠIMŮNEK, V., & HÁJEK, V. (2023). *Potential of mixed Picea abies (L.) Karst. and Pinus sylvestris L. forests in lowland areas of Central Bohemia*. Journal of Forest Science, 69(11), 470-484.
7. BRICHTA, J., ŠIMŮNEK, V., BÍLEK, L., VACEK, Z., GALLO, J., DROZDOWSKI, S., BRAVO-FERNÁNDEZ, J.A., MASON, B., ROIG GOMEZ, S., HÁJEK, V., VACEK, S., ŠTÍCHA, V., BRABEC, P., FUCHS, Z. (2024). *Effects of Climate Change on Scots Pine (Pinus sylvestris L.) Growth across Europe: Decrease of Tree-Ring Fluctuation and Amplification of Climate Stress*. Forests, 15(1), 91.

## 2. CÍLE PRÁCE

Předložená disertační práce byla vypracována v souladu s předem stanoveným zadáním. Cíle předložené práce byly sestaveny na základě potřeby prohloubit znalosti o reakci borovice lesní na měnící se klimatické podmínky, vymezit možnosti strukturalizace a clonných postupů borových porostů jako jednoho z nástrojů adaptace. Výčet konkrétních cílů práce je následující:

- na základě literární rešerše popsat současný stav poznání ohledně způsobů pěstování borových porostů a možnosti adaptace borového hospodářství na klimatickou změnu,
- stanovit přírůstový a produkční potenciál borovice lesní v závislosti na pěstebním zásahu, smíšení, stanovišti, věku, případně parametrech jednotlivých stromů,
- odvodit přírůst strukturně diferencovaných porostů a jeho srovnání s vybranými klimatickými charakteristikami,
- odvodit vztah mezi strukturujícími pěstebními zásahy a úspěšností přirozené obnovy borovice lesní,
- posoudit vliv poškození zvěří na zdravotní stav a stabilitu lesních porostů a jednotlivých stromů.

Přínosem zpracování disertační práce by mělo být vytvoření souhrnného materiálu o borovici lesní (*Pinus sylvestris* L.), předně pro potřeby studia daného taxonu, ale také s ohledem na aktualizaci již známých informací v kontextu klimatické změny. Praktický přínos realizace disertační práce spočívá v hospodářských doporučeních pro alternativní obnovní postupy na různých stanovištích, za využití clony mateřského porostu či smíšení s jinými dřevinami.

### 3. LITERÁRNÍ REŠERŠE

Následující kapitola je syntézou poznatků o borovici lesní (*Pinus sylvestris* L.) a jejích vybraných pěstebních charakteristikách. Syntéza daného je rovněž uvedena ve 4. publikaci (Brichta et al. 2023), jež je součástí kapitoly 5. Výsledky.

#### 3.1 Popis ekologických nároků, geografický vývoj taxonu a současný význam

Borovice lesní (*Pinus sylvestris* L.) je dřevinou s velmi širokým klimatickým a edafickým areálem (KELLY & CONNOLLY 2000; ÚRADNÍČEK et al. 2001; DURRANT et al. 2016; VACEK et al. 2016). Vzhledem k tomu, že nesnáší výrazné zastínění, je borovice lesní vytlačována z živinově bohatších stanovišť klimaxovými dřevinami (PRŮŠA 2001; MIKESKA et al. 2008). Rozsáhlé lesní porosty borovice lesní se typicky vyskytují na suchých a chudých písčitých půdách, v oblastech s pískovcovým podložím a na extrémních stanovištích s omezenou hloubkou půdy, jakož i na rašelinistích (KUČERA 1999; VACEK et al. 2017, 2021a; ŠOFLETEA et al. 2020). V Evropě se borovice lesní vyskytuje v nadmořských výškách od nížin po hory, a to v různých ekotypech (BÍLEK et al. 2017; HEBDA et al. 2017; ŁABISZAK et al. 2017; VACEK et al. 2022). Ekotypy borovice lesní vycházejí z populací, které se dochovaly z pozdní doby ledové ve formě izolovaných refugií ve střední Evropě (JANKOVSKÁ & POKORNÝ 2008; MIKESKA et al. 2008; TÓTH et al. 2017). Nejstarší borové lesy v České republice rostou na skalních výchozech, ve skalních útvarech, na hadcových a minerálně chudých a suchých písčích. Z hlediska vývoje jsou borové lesy na rašelinistích mladší (PLÍVA 1971; MIKESKA et al. 2008; POLENO et al. 2009). Přirozeným prostředím borových porostů mohou být nicméně oligotrofní stanoviště, stejně jako porosty bohaté na bylinnou vegetaci (ØYEN et al. 2006; MIKESKA et al. 2008; VACEK et al. 2022). Nutné je také dodat, že podle prostředí, kde se borovice dále vyvíjela, vznikla celá řada pionýrských i klimaxových populací (KAŇÁK 1999).

Historicky nejstarší akrofosilní důkazy a sedimentární záznamy dokazují přítomnost borovice lesní mezi 70 000 BP v Karpatské pánvi a 20 000 BP v Maďarské nížině (MAGYARI 2011; TÓTH et al. 2017). Současné autochtonní bory a borové doubravy však vznikly evolucí vegetace převážně během 10 000 let postglaciálu. Borovice lesní a bříza bělokorá (*Betula pendula* Roth.) byly nejčastějšími stromovými taxony ranného postglaciálu. Současný výskyt borovice lesní lze proto považovat za pozůstatek jejího původního areálu, tedy pozůstatek



ranného postglaciálu, zejména na takových stanovištích, které nebyly z edafických důvodů vhodné pro jiné dřeviny (STASZKIEWICZ 1968; JANKOVSKÁ & POKORNÝ 2008). I navzdory tomu, že se tato azonální společenstva od preboreálu postupně vyvíjela, zachovala se pouze na extrémních stanovištích s omezenou konkurencí jiných druhů dřevin. První porosty borovice s břízou se na tehdejší území střední Evropy objevily v období staršího holocénu – v preboreálu (HUSOVÁ 1999; MIKESKA et al. 2008). V boreálu se na uvedeném území začaly objevovat světlé borové lesy s příměsí lísky obecné (*Corylus avellana* L.). V období atlantiku, tedy klimatického optima, převládaly smíšené listnaté lesy s převahou dubu (*Quercus spp.*), ale zároveň se v chladnějších a vlhčích oblastech rychle rozšířil také smrk ztepilý (*Picea abies* [L.] Karst.). Přibližně před 6 200 až 4 000 lety se začal šířit buk lesní (*Fagus sylvatica* L.) a jedle bělokorá (*Abies alba* Mill.), zejména ve středních polohách (BOLTE et al. 2007; MIKESKA et al. 2008). Všechny tyto dřeviny postupně vytlačily borovici na místa, kde jí nemohly konkurovat. V epiatlantiku byla vytvořena přirozená zonace klimaxové vegetace, a borovice tak ustoupila do stanovišť extrémního a azonálního charakteru (chudé písky, skály, rašeliniště). Na extrémních stanovištích, které byly nepřístupné pro již aktivní antropogenní činnost, se nakonec vytvořila společenstva podobná těm současným (HUSOVÁ 1999; POLENO et al. 2007; MIKESKA et al. 2008). Otázkou však zůstává, jaká je role borovice lesní ve 21. století, kdy změna klimatu mění zastoupení lesních dřevin a jejich růstové optimum (FALK & HEMPELMANN 2013; DYDERSKI et al. 2018; KLOPČIČ et al. 2022)?

V současné době borovice lesní disponuje největším areálem ze všech popsaných borovic. Rozšíření borovice lesní zahrnuje především mírné a chladnější pásy velké části Evropy a Asie (tato oblast je jinak známá jako Eurasie). V Evropě se borové porosty objevují od severního Portugalska a Skotska po Dálný východ mezi 37°–70,5° severní šířky. Centrem rozšíření tohoto taxonu je pak Sibiř. Méně se borovice lesní vyskytuje v okolí Středozemního moře. Nejsevernější výskyt tohoto druhu v Evropě je v Laponsku (ÚRADNÍČEK et al. 2001; MUSIL & HAMERNÍK 2007; DURRANT et al. 2016). Borovice lesní je typická jak pro oblasti Skandinávie, severozápadní Sibiře, celé střední a východní Evropy, ale vyskytuje se také v oblasti Kavkazu a Zakavkazska. Objevuje se také v severním Mongolsku, SV Číně a JV Sibiři (BUSINSKÝ 2008). V oblasti severní Evropy a Asie dosahuje až polární hranice lesa (OLEKSYN et al. 2002). Mimo svůj hlavní euroasijský areál se však borovice lesní druhotně rozšířila i v Severní Americe, kde se pěstuje především na plantážích (POLENO 1990; ÚRADNÍČEK et al. 2001; MUSIL

& HAMERNÍK 2007; SCHILDLER et al. 2010). V Polsku je borovice lesní dokonce hlavní hospodářskou dřevinou, která pokrývá 58 % lesní plochy (DGLP 2021). V České republice zaujímá borovice lesní 16,0 % lesní plochy (MZE 2022).

### **3.2 Základní principy přírodě blízkého hospodaření v lesích**

Základním aspektem efektivity udržitelného, přírodě blízkého hospodaření s lesem je snaha o pochopení přírodních procesů a vazeb mezi určitými dřevinami a jejich prostředím (WOZIWODA et al. 2018). Jemnější hospodaření v lesích dnes nachází mnoho pojmenování a mnoho rozdílných způsobů či pojetí. Jedná se například o: ekologické lesnictví (SEYMOUR & HUNTER 1999; EVANS 2006; FRANKLIN et al. 2007; MITCHELL et al. 2009), konzervační lesnictví (MINCKLER 1974), ekosystémový management (CLARK et al. 1991), ekologicky založené lesnictví (KOTAR 1997) či již zmíněné přírodě blízké lesní hospodaření (VACEK & PODRÁZSKÝ 2006; O'HARA 2015). Přírodě blízké lesnictví (PBL) je způsob hospodaření s lesem, který z praktického hlediska odmítá jakákoli schémata či dogmata (především ve fázi stadia obnovy lesa), a využívá tak biologických sil lesního ekosystému při uplatňování vědeckých poznatků i praktických zkušeností (VACEK & PODRÁZSKÝ 2006). Hovoříme-li o přírodě blízkém lesnictví, je nutné také dodat, že se jedná o hospodaření, o proces šetrného využívání lesa za účelem vytváření dřevní suroviny (FSC 2011). Nejedná se tedy o ponechávání lesních porostů zcela přirozenému vývoji, kdy dřevní surovina není využívána pro hospodářské účely. Přírodě blízké hospodaření je tak často ekologizováno ve stav maximálního možného a účelného využívání přírodních sil a biologické automatizace pro dosažení stanovených hospodářských cílů, mimo jiné i úspory přidaných vkladů do lesní výroby (ČAPEK 1994).

Jelikož lesní ekosystémy aktuálně čelí výrazným klimatickým extrémům (IPCC 2023), úkolem lesních hospodářů tedy zpravidla není zachování těchto porostů v původní podobě, nýbrž jejich přetváření vedoucí k vyšší adaptabilitě na rychle se měnící klimatické podmínky (O'HARA et al. 2015). Souvislosti zde nacházíme také ve spojení s druhovou (PRETZSCH et al. 2015; NOVÁK et al. 2021; BRABEC et al. 2023), horizontální či vertikální diferenciací porostu (**Obr. 1**; SCHÜTZ 2002; VACEK et al. 2018), kdy heterogenní porost může být nástrojem, a zároveň efektem přírodě blízkého pěstování lesů. Dalším důležitým aspektem PBL je udržování jejich polyfunkčnosti (ŠÍŠÁK et al. 2013; BÍLEK et al. 2017). Principy přírodě blízkého

hospodaření nejčastěji vedou k maloplošnému obhospodařování lesů (KERN et al. 2017; KŘÍSTEK et al. 2018), které je charakteristické zejména pro stín snášející dřeviny. Takovému hospodaření se světlomilnými dřevinami, jako je dub a borovice, je nicméně doposud věnováno jen málo pozornosti.



**Obr. 1** Přírodě blízký strukturně diferencovaný borový porost, Třeboň 2019. Foto: Jakub Brichta

### 3.3 Strukturní diferenciacie lesních porostů

Struktura lesa je současně výsledkem i nástrojem pěstování lesů, kvantifikovaná především hustotou porostu, jeho zásobou, vertikální strukturou, kruhovou základnou porostu, horizontálním rozložením stromů v porostu, heterogenitou prostorového uspořádání stromů, objemem mrtvého dřeva nebo kategorizací jedinců v tloušťkových třídách (POMMERING 2002; PUETTMANN et al. 2008; SILVER et al. 2013). V obecné rovině strukturně diferencovaný porost popisujeme jako takový lesní porost, který je více či méně heterogenní, a to s ohledem na jeho prostorovou rozrůzněnost ve vodorovném směru (horizontálně diferencovaný), či na jeho výškové rozrůznění v korunové vrstvě (vertikálně diferencovaný) (SCHÜTZ 2002). Struktura porostu výrazně ovlivňuje většinu proměnných v lesním ekosystému, ale v souvislosti s obnovou lesa a pěstováním různých dřevin ovlivňuje zejména vznik, odrůstání a kvalitu přirozené obnovy, jak u dřevin stín snášejících (GAYER 1886; POLENO et al. 2009; BÍLEK et al.

2011; ČAVLOVIĆ et al. 2014), tak i dřevin světlomilných (BÍLEK et al. 2017; DRÖSSLER et al. 2017; ALEKSANDROWICZ-TRZCIŃSKA al. 2017; LUNDQVIST et al. 2019; BRICHTA et al. 2020).

Ačkoli od strukturně diferencovaných porostů obecně očekáváme vyšší stabilitu a lepší adaptabilitu na měnící se klimatické podmínky (MONTERO et al. 2001; ŻURKOWSKI 2006; GIUGGIOLA et al. 2013; ALEKSANDROWICZ-TRZCIŃSKA et al. 2017; AMEZTEGUI et al. 2017), nebyly v minulosti pěstební systémy vedoucí ke strukturně diferencovaným borovým porostům příliš rozšířeny, a to i přesto, že jsou přírodě bližší způsoby lesního hospodaření známy už od konce 19. st. (GAYER 1886). O lese tloušťkově, věkově a výškově diferencovaném s minimem pěstebním zásahů, nakonec pojednávala práce MÖLLER & MÖLLER (1922), která takový les označila jako „Dauerwald“ – les trvale tvořivý. Skutečnost nevyužívání dalších způsobů hospodaření v borových porostech lze odůvodnit zejména nedostatečnou informovaností lesnické veřejnosti pro zdánlivou nevhodnost podrostního hospodaření s výrazně světlomilnou dřevinou, jakou borovice lesní. Zároveň je však nutné dodat, že borovici se na holé ploše daří odrůstat (SLAVÍKOVÁ 1986; LINDER 1997; MUSIL 2003; HEIKE 2008; HORSÁK a CHYTRÝ 2010; VACEK et al. 2007).

Jako účinné adaptační opatření proti klimatickým extrémům a dalším abiotickým a biotickým činitelům, je obecně přijímána snaha o věkovou rozrůzněnost porostů, které lze dosáhnout především maloplošnými clonnými postupy či dokonce přestavbou lesa věkových tříd na lesy výběrné. Ačkoli je borovice lesní obecně považována za dřevinu výrazně světlomilnou s minimální tolerancí k zastínění (MUSIL 2003), se v posledních desetiletích vedle dnes již běžného výstavkového hospodaření (VACEK & PODRÁZSKÝ 2006; BRICHTA et al. 2019) ve větší míře uplatňuje i hospodářství podrostní (MONTERO et al. 2001; BARZDAJN & ZIENTARSKI 2007; GAUDIO et al. 2011; KOJOLA et al. 2012; SPATHELF & AMMER 2015; BÍLEK et al. 2017; BRICHTA et al. 2020). Je nutné zmínit studie z panství Bärenthoren (JAWORSKI 1995; ZAJĄCZKOWSKI 1996), odkud jsou informace o schopnosti borovice lesní vytvářet víceetážové porosty již dlouho známy. Analýzy hospodaření v panství Bärenthoren definují zdejší systém hospodaření ve strukturně diferencovaných borových porostech coby management v intencích 30 až 60leté obnovní doby s využitím pouze maloplošných sečí. Také mladší práce (EDWARDS & MASON 2004; ŻURKOWSKI 2006; BARZDAJN & ZIENTARSKI 2007; ANDRZEJCZYK 2008; LUNDQVIST et al. 2019) potvrzují, že ačkoli borovice lesní zpravidla vytváří výškově vyrovnané porosty, je schopna přirozeně vytvářet také porosty víceetážové. Tyto strukturně diferencované

borové porosty jsou však limitovány pouze na podmínky přirozených borových stanovišť, kde zpravidla nebývá vysoká konkurence ostatních dřevin (ANDRZEJCZYK 2008). V kontextu adaptace stávajících borových porostů na změny klimatických podmínek, ale také směrem ekonomické úspory, můžeme v tomto případě strukturní diferenciaci porostu zahájit prostřednictvím přirozené obnovy pod mateřským porostem (BELAND et al. 2000; BRICHTA et al. 2020; HUTH et al. 2022). Snížení zakmenění mateřského porostu pomocí několika clonných sečí (BRICHTA et al. 2020) může být dobrým výchozím bodem pro přeměnu homogenního borového porostu na porost strukturně diferencovaný. Následné pěstování takových porostů by mělo být prováděno za udržování podprůměrné zásoby porostu. V případě práce ANDRZEJCZYK (2008) je hranice zásoby porostu v tomto kontextu stanovena na 150–170 m<sup>3</sup>/ha, ANDRZEJCZYK (2008) dále doporučuje provádět výchovné zásahy v 10letých intervalech.

#### ***3.4.1 Podrovní hospodaření a přirozená obnova***

Pomocí přirozené obnovy lze borové porosty obnovovat různými způsoby, jedná se o holosečné hospodaření s různou velikostí a orientací seče, kotlíkovou seč, velkoplošný i maloplošný clonný obnovní způsob, až s uplatněním skupinovitého či jednotlivého výběru (BÍLEK et al. 2017). Který ze zmíněných postupů pro obnovu borového porostu využít obecně udávají terénní podmínky a dostupnost lesní mechanizace či převažující funkce lesa, nicméně také požadavky dotčených vlastníků a správců lesa na krajinný ráz dané lokality. Rozhodujícími prvky pro výběr určité varianty obnovy, které jsou však často opomíjeny, jsou podmínky prostředí (ŠINDELÁŘ 2004). Jedná se tak o základní ekologické charakteristiky stanoviště: nadmořskou výšku, dostupnost vláhy, obsah živin v půdě, charakter podloží, druhové a věkové složení okolních porostů atd.

V některých případech je v kombinaci s přirozenou obnovou ještě stále účelné využívat i holosečné prvky, kdy přirozená obnova často výrazně předčí obnovu umělou (WOLSKI & ROBAKOWSKI 2008; SIMONSEN 2013), nicméně zde velmi záleží na vzdálenosti mateřského porostu. Dojde-li k odlesnění plochy lesa a půda je vystavena permanentnímu oslunění, často dochází k jejímu přehřívání a vysychání (BOLIBOK & ANDRZEJCZYK 2008), po realizaci velkoplošné přípravy půdy či dokonce kompletnímu shrnutí nadložních humusových vrstev

i k úplné degradaci půdy na daném stanovišti (MAROZAS et al. 2018). Šetrnějším způsobem obnovy borových porostů tak na základě výše zmíněných faktů, může být podrobní hospodaření (VACEK & PODRÁZSKÝ 2006). Podrobní hospodaření spočívá v počátečním proředění mateřského porostu (na zakmenění 5; **Obr. 2**), po úspěšném vzejití semen a existenci nové generace lesa se nejčastěji přistupuje k další seči (na zakmenění 3), díky čemuž je nálet uvolněn ze zástinu mateřského porostu (**Obr. 3**). S ohlednutím na ekologické nároky borovice (SLAVÍKOVÁ 1986; LINDER 1997; MUSIL 2003; VACEK et al. 2007; HEIKE 2008; HORSÁK a CHYTRÝ 2010) se v mateřském porostu kontinuálně přistupuje k dalším zásahům, až k případnému dotěžení vrchní etáže. Na přirozených borových stanovištích je třeba respektovat, že obnova v první fázi vývoje je schopna zástin tolerovat po dobu nepřesahující 10-20 let (COBAN et al. 2016; BÍLEK et al. 2018a). PARDOS (2017) či LUNDGVIST et al. (2019) v tomto kontextu uvádí, že pro nálet borovice je optimální mírné oslunění, nikoli plné. V našich podmínkách se tak pravděpodobně jedná o zakmenění 3–4. Každopádně se prakticky v jakémkoli zástinu mateřského porostu zvyšuje štíhlostní kvocient jedinců obnovy. Výška stromů již mýtního věku vzniklých přirozenou obnovou pod porostem navíc běžně nedosahuje výšky stromů vzniklých na holoseči (GAUDIO et al. 2011). Dalším negativním faktorem může být nevratné poškození následného porostu při jednorázovém odtěžení vrchní etáže. BELAND et al. (2000) proto doporučuje započít uvolňování náletu tehdy, dosáhne-li obnova výšky alespoň 0,5 m, dotěžení mateřského porostu je ale dle jejich závěrů vhodné až při 6 m výšky spodní etáže.





**Obr. 2** *Mateřský borový porost uvolněný na zakmenění 4, Doksy 2019. Foto: Jakub Brichta*



**Obr. 3** *Přirozená obnova pod mateřským porostem uvolněným na zakmenění 4, Doksy 2019. Foto: Jakub Brichta*

Stejně jako je očekávána dobrá až zvýšená kvalita borovice při pěstování smíšených porostů (HOLUŠA & HOLUŠA 2000), předpokládá se zvýšení kvality dřeva borovice i při uplatnění podrobných postupů (BELAND et al. 2000). Zvýšení kvality dřevní hmoty v tomto kontextu

reprezentuje zejména pravidelnost tloušťek letokruhů a vyšší hustota letního dřeva (SCHÖNFELDER et al. 2017; SCHÖNFELDER et al. 2018), což poté pozitivně ovlivňuje výrobu designových sortimentů, jakož i mechanické vlastnosti stavebního řeziva. Z důvodu lepší stability porostů vzniklých přirozenou obnovou pod mateřskými jedinci (CHURCHILL et al. 2013; SPATHELF et al. 2015; MERLIN et al. 2015), lze navíc tyto pěstební přístupy hodnotit také jako účinný management rizika, tedy jako opatření, které zvyšuje pravděpodobnost dopěstování porostu či alespoň jeho části do myšlného věku. Z četných výzkumů navíc vyplývá, že přirozená obnova borovice lesní pod porostem může být nákladově efektivnější nežli umělá obnova na holé ploše (SCHERMAN 1991; HYPPÖNEN et al. 2013; ALEKSANDROWICZ-TRZCIŃSKA et al. 2017; DRÖSSLER et al. 2017; BRICHTA et al. 2020). Existence horní stromové etáže tedy zaručuje částečnou ochranu proti nepříznivým abiotickým faktorům, ale také zvyšuje biodiverzitu lesního prostředí, zaručuje lepší hospodaření s vodou (MONTERO et al. 2001; MATÍAS & JUMP 2012) a zlepšuje půdní podmínky v porostu (ALEKSANDROWICZ-TRZCIŃSKA et al. 2017). Mateřské stromy také brání poškození nově vzniklého podrostu mrazem (EEREFUR et al. 2008). Dle simulací AMEZTEGUI et al. (2017) porosty borovice lesní se sníženým zakmeněním lépe odolávají negativním účinkům klimatických extrémů. Z různých výzkumů v rozvolněných borových porostech vyplývá, že stejně jako prosty smrkové (SOHN et al. 2016), i porosty borové se ve formě sníženého zápoje vyznačují větší rezistencí vůči suchým obdobím (GIUGGIOLA et al. 2013). Podrovní hospodaření může být nástrojem zachování borových porostů v takovém stavu, aby byly schopné plnit zároveň jejich ekologické funkce. Zejména se jedná o produkci kyslíku, ale také zadržování vody v krajině, které dnes s nedostatkem srážek obecně nabývá na důležitosti (del CAMPO et al. 2014; IPCC 2023).

Dalším významným aspektem borových porostů pěstovaných podrovními způsoby je fakt, že dojde-li k rozpadu vrchní etáže, ať už vlivem abiotického či biotického činitele, podúroveň v porostu alespoň částečně zůstává, a krajina tak neztrácí lesní charakter. Náhlé odlesnění borového porostu vede často ke ztrátě základních půdních živin (uhlíku, dusíku, draslíku či fosforu), jejichž optimální množství se do lesního porostu navrácí další desítky let (MAROZAS et al. 2018). Nutné je dodat, že ponechaná vrchní etáž mateřských borovic může mít negativní vliv na objemový přírůstek porostu v podúrovni (JAKOBSSON 2005) a je tedy doporučováno dvougenerační jedince nepředržovat v porostu v příliš velkém počtu. Zároveň je na některých stanovištích vhodné ponechat staré jedince jako útočiště pro různé druhy živočichů



(DJUPSTRÖM & WESLIEN 2019), biotop houbových organismů (STENKERBURG et al. 2019) či coby biologické dědictví následně ve formě mrtvého dřeva (FRANKLIN et al. 2007; KJUČUKOV et al. 2014; KOMONEN et al. 2000; JONÁŠOVÁ 2013; SANTANIELLO et al. 2016) nebo alespoň potěžební zbytky a pařezy jako zásobárnu živin (NOVÁK et al. 2017). Pro estetický dojem a krajinný ráz je podrobné hospodaření, respektive pěstování diferencovaných borových porostů vhodné zejména na lokalitách, kde jsou vyžadovány mimoprodukční funkce lesa ve větší míře. Plní-li zde různověké borové porosty tyto další služby dostatečně, případné ztráty na produkci, mohou být dle AHLSTRÖM (2016) v určité míře tolerovány. V kontextu pěstování strukturně diferencovaných porostů borovice lesní se tedy na základě dostupných informací lze domnívat, že se jedná o vhodnou počáteční fázi vytváření strukturně diferencovaných borových porostů.

#### ***3.4.2 Světlostní přírůst jedinců mateřského porostu***

Nejen, že lze v borových porostech uplatnit přirozenou obnovu pomocí výstavků či s využitím částečné clony mateřského porostu, ale ponechání jedinci vrchní etáže mohou navíc na uvolnění reagovat zvýšeným tloušťkovým přírůstem (VALINGER 1992; SOUČEK 2006; SVOBODA et al. 2015; MONTERO et al. 2001; BRICHTA et al. 2019).

Přes obecný předpoklad minimální schopnosti dospělých borovic reagovat na uvolnění zvýšením přírůstu (SIMON & VACEK 2008; TESAŘ 2010) bylo zjištěno, že borovice mýtního věku na některých stanovištích (CHS 19, 23 a 43) na uvolnění reagují výrazným světlostním přírůstem, a to průměrně po dobu 18 let po momentu uvolnění (BRICHTA et al. 2019). Podobných výsledků dosáhla studie AHLSTRÖM (2016), kde je konstatováno zvýšení objemu vybraných jedinců. Nicméně je při výběru cílových stromů třeba respektovat fakt, že změny tloušťkového přírůstu ovlivňuje jak charakter uvolnění, tak i samotné postavení jedinců v porostu (SOUČEK 2010). K očekávanému světlostnímu přírůstu po uvolnění dochází zejména díky snížení konkurence mateřských jedinců, zlepšení dostupnosti vody a živin v půdě, jakož i množství slunečního záření (KELLOMÄKI 1998). Ačkoli je v praxi zažité pěstování borových porostů v hustém zápoji tak, aby nedocházelo k nadměrné sukatosti kmenů, přistupuje se dnes stále častěji k rozvolňování porostů již středního věku. Cílem je umožnit dokonalý rozvoj korun stromů, optimalizovat přírůstové poměry a konečně i zvýšit mechanickou stabilitu takto

vychovávaných porostů (SPATHELF & AMMER 2015; MONTERO et al. 2001; KOJOLA et al. 2012; NOVÁK et al. 2019; 2021). Stromy s vyvinutou korunou jsou vhodné pro uvolnění také během obnovní doby. Totéž jako v případě výstavků či jedinců mateřského porostu uvolněných clonnou sečí (BRICHTA et al. 2019), lze očekávat také u jedinců horní etáže v již strukturně diferencovaných porostech, kde zpravidla nedochází k vysoké korunové konkurenci mateřských jedinců.

Vedle předpokladu zvýšení ekonomické efektivity pěstování rozvolněných porostů formou podrovního hospodaření, je dalším často uváděným pozitivem i zvýšení odolnosti porostu proti abiotickým i biotickým činitelům (SPATHELF et al. 2015; CHURCHILL et al. 2013; MERLIN et al. 2015). Některé zdroje (LINARES et al. 2011; SOHN et al. 2016) navíc hovoří o tom, že při optimálním uvolnění porostu a snížením konkurence, se uvolněný porost stává odolnějším vůči extrémním výkyvům klimatu i dlouhodobým suchům. Tento jev je zřetelný zejména v oblastech vyloženě náchylným k suchu (SÁNCHEZ-MIRANDA et al. 2016). Navzdory výše zmíněným výhodám rozvolněných porostů, máme ale o samotné reakci ponechaných jedinců na uvolnění zápoje stále velmi málo informací (BEBBER et al. 2004), proto lze zatím celou řadu našich myšlenek klasifikovat jako domněnky. Stejně tak skromné a fragmentované jsou zjištění o efektu uvolnění na hustotu dřeva borovic, často i protichůdné (PELTOLA et al. 2007; FILIPESCU et al. 2014, DONIS et al. 2013). SOHN et al. (2016) také upozorňuje na to, že v období sucha po proředění porostu nemusí ke kýženému zvětšení radiálního přírůstu docházet. Stres z nedostatku vláhy tedy následný světlostní přírůst potlačuje (PRIMICIA et al. 2013), což je velmi aktuální zejména v době posledních desetiletí, kdy jsou borové porosty citelně postihovány suchými obdobími (ŠPULÁK & ČERNÝ 2023). Špatné načasování uvolnění porostu může taktéž zapříčinit ztráty jak na přírůstu jednotlivých letokruhů, tak i ve výsledku na celkové zásobě porostu (KOJOLA et al. 2012).

### ***3.4.3 Vliv přípravy půdy na existenci přirozené obnovy***

Vliv lesního hospodáře při iniciaci přirozené obnovy spočívá vedle úpravy porostní hustoty rovněž v možnostech úpravy půdního povrchu (BÍLEK et al. 2018b). Přirozená obnova borovice lesní, ať už v podmínkách holoseče či pod krytem mateřského porostu, pro své vzejití často vyžaduje narušení alespoň vrchního půdního horizontu. Skarifikace půdy je tradiční již z doby,

kdy v lesích probíhala pastva dobytka a hrabání steliva pro chov hospodářských zvířat. Právě v porostech částečně zbavených hrabanky a předně přízemní vegetace, se tak dařilo přirozené obnově, aniž by se jednalo o pěstební záměr (HILLE & OUDEN 2004). Některé studie (PICON-COCHARD et al. 2006), odkazují na ekologickou plasticitu borovice a její schopnost obnovy i ve vysoké buřeni, nicméně borovice se většinou v husté buřeni v dostatečných počtech neprosadí (HYPPÖNEN et al. 2013). Jako světlomilná dřevina je tak borovice ve srovnání se stín snášejícími dřevinami daleko více citlivá na kořenovou kompetici (EREFUR et al. 2008). Aby bylo možné aplikovat její přirozenou obnovu, je často třeba buřň odstranit (VARMOLA et al. 2004; SAURSAUNET & MATRISEN 2018). Vřes obecný (*Caluna vulgaris*) či brusnice borůvka (*Vaccinium myrtilus*) skrze kořenovou konkurenci a zastínění přirozenou obnovu značně komplikují (HYPPÖNEN et al. 2013). Ačkoli je přirozená obnova borovice vnímána jako opatření ekonomické efektivity, její iniciace často vyžaduje narušení půdního povrchu a odstranění výše zmíněné bylinné vegetace. V přírodních podmínkách se tak děje za pomoci přízemních požárů (ENGELMARK et al. 1994; CORACE et al. 2009; JONGEPIEROVÁ et al. 2012), kdy je půdní povrch zbaven nežádoucí vrstvy vegetace a klíčení semenáčků borovic je o to snadnější. Při absenci tohoto přirozeného procesu přistupujeme k přípravě půdy, především pro samotnou existenci přirozené obnovy a její přijatelnou hustotu (AKCZELL 1993; SAURSAUNET & MATRISEN 2018; BRICHTA et al. 2020), ale také pro lepší odrůstání (KARLSSON & ÖRLANDER 2000). Jelikož skarifikace půdy zvyšuje hustotu přirozené obnovy (AKCZELL 1993; SAURSAUNET & MATRISEN 2018) a zhoršuje se tak přehlednost a prostupnost terénu, dochází také k menším škodám zvěří, které s ohledem na větší hustotu obnovy nebývají zásadní (WALLGREN et al. 2013; VACEK et al. 2019). KARLSSON & TAMMINEN (2013) dokonce hovoří o tom, že pozitivní vliv přípravy půdy na borovou obnovu je znatelný i v době, kdy se vzniklý porost nachází ve stadiu tyčoviny či kmenoviny.

Samotné přípravě půdy pod porostem často předchází uvolnění porostu alespoň v takové míře, aby byla možná mobilita lesní, respektive zemědělské mechanizace. Mezi nejběžnější způsoby přípravy půdy patří orba či frézování. Nestací-li jedna etapa skarifikace půdy koncem léta či na podzim (KARLSSON & ÖRLANDER 2000), po samotném naorání se ještě na jaře dalšího roku přistupuje k urovnání povrchu smykáním (MAUER 2002). Nicméně celoplošná příprava půdy se pro vysoké náklady příliš nepoužívá, bývá tak nahrazována zejména pruhovou přípravou diskovými branami (**Obr. 3**). Tato metoda se však nedoporučuje na lokalitách

ohrožených erozí (KRIEGEL 1998). Obecně platí, že čím je samotná skarifikace půdy intenzivnější, tím větší hustotu přirozené obnovy můžeme očekávat (ALEKSANDROWICZ-TRZCIŃSKA et al. 2014).



**Obr. 4** Varianty přípravy půdy pod porostem pro iniciaci přirozené obnovy; kombinovaná fréza KSH 700 (vlevo), lesní fréza Meri Crusher 1,8 ST (vpravo), Doksy 2019. Foto: Jakub Brichta

Rizikem přípravy půdy s ohledem na vzniklou přirozenou obnovu borovice může být především zvýšená teplota půdy bez stínu bylinného krytu (BEDFORD & SUTTON 2000; OLESKOG & SAHLÉN 2000), nicméně vlhkost půdy se v řadě případů i tak jeví jako stabilní (OLESKOG & SAHLÉN 2000). Dalším potenciálním rizikem může být vylouhování živin z nakypřené půdy (PIIRAINEN et al. 2007) či zamrzání kořenových soustav jedinců obnovy (CHANTAL et al. 2003).

#### **3.4.4 Mimoprodukční funkce strukturně diferencovaných borových porostů**

Význam lesa pro lidskou společnost se se zvyšujícími potřebami společnosti mění, samozřejmě také ve světle klimatických změn. Lesy plní celou řadu funkcí, vedle typických produkčních funkcí lesa pak společenské a kulturní funkce, ochranné funkce, ekologické funkce či funkce ochrany klimatu a biodiverzity (POLENO et al. 2009; ŠIŠÁK 2013). DOBBS et al. (2011)

lesní krajinu navíc posuzuje jako nedílnou součást duševního zdraví člověka. Díky různým funkcím lesních ekosystémů, které jsou navíc vymezeny zákonem (MZE 1995), lesní hospodářství označujeme jako polyfunkční (ŠIŠÁK 2013). V dnešní době nabírá na důležitosti zejména funkce ochranná, klimatická, či funkce produkce kyslíku (GAMFELDT et al. 2013; MATTONE & SHEAVES 2017).

Díky lepším podmínkám podrostního hospodaření v porostech stín snášejících dřevin, plní mimoprodukční funkce zdánlivě lépe stín snášející dřeviny. Nicméně i borové porosty, jako v mnoha případech jediná dřevinná společenstva schopná růstu na chudých až extrémních stanovištích, mají potenciál splňovat celou řadu mimoprodukčních funkcí lesa (BÍLEK et al. 2017). Konkrétně na písčitých a extrémních stanovištích, často na stanovištích reliktních borů (CHS 01) (MIKESKA et al. 2008) borové porosty hrají klíčovou roli také v procesu ochrany půdy. Faktem také je, že na některých stanovištích je borovice téměř nezastupitelná dřevina (SLAVÍKOVÁ 1986; LINDER 1997; MUSIL 2003; HEIKE 2008; HORSÁK & CHYTRÝ 2010; VACEK et al. 2007), která svou existencí udržuje samotný charakter lesní krajiny. Jakožto druhá nejzastoupenější dřevina v ČR (MZE 2022) může mít borovice velký vliv na nabídku ekosystémových služeb lesa vůbec, či funkcí sociálních a zdravotně-rekreačních. Velké možnosti podpory mimoprodukčních funkcí lesa je především na lokalitách, kde je borovice autochtonní, tedy jako náhorní či chlumní ekotyp borovice lesní (KAŇÁK 2011). V hospodářsky významných porostech oblastí původního výskytu borovice lesní (KOVÁŘ et al. 2013) by však z ekonomických důvodů měla převládat funkce hospodářská. MIKESKA et al. (2008) nicméně hovoří o tom, že na přirozených borových stanovištích jsou hospodářské a ekologické funkce zpravidla vyrovnané, kdy se jedná o lokality výrazně ohrožené suchem, degradací půdy či zamokřením. Mimoprodukční funkce lesa jsou v borových lesích v porovnání s homogenními porosty ve větší míře plněny skrze strukturně diferencované borové porosty, ať už diferencovaných horizontálně, například v podobě určitého smíšení nebo heterogenní textury porostu (CZEREPKO 2004; PRETZSCH et al. 2015; FELTON et al. 2016; DRÖSSLER et al. 2018), či vertikálně prostřednictvím několika etází (BARZDAJN & ZIENTARSKI 2007; BÍLEK et al. 2017; LUNDGVIST et al. 2019). V reliktních borových porostech (CHS 01), které jsou většinou vázány na velmi mělké nevyvinuté půdy, skalnatá či suťová stanoviště nebo extrémně chudé lokality či rašeliniště, je prvořadným úkolem lesního hospodáře zachování lesa na těchto stanovištích. Často se tak jedná o bezzásahová území, nicméně i management jednotlivého

výběru zde připadá v úvahu, aby byla zajištěna obnova cenných místních populací a byla zachována podoba víceetážového porostu (BÍLEK et al. 2017). Je-li žádoucí dosáhnout skutečně přirozené struktury rozrůzněného borového porostu, je třeba počítat s opravdu dlouhým časovým obdobím. EDWARDS & MASON (2006) tak hovoří o zhruba 300 letech, během kterých by mělo samovolně dojít ke kýžené přirozené struktuře diverzifikovaného borového porostu. Zmíněná studie také pojednává o tom, že dosažení změn ve prospěch dynamického lesního ekosystému v kratším období bude rozhodně vyžadovat hospodářské zásahy v podobě uvolňování mateřského porostu či podsadeb ostatních dřevin. Jedním ze základních aspektů borového porostu, jenž se blíží přirozené struktuře a plní tak zejména ekologické funkce, je bezesporu přítomnost mrtvého dřeva. Jeho význam popisuje mnoho autorů (KOMONEN et al. 2000; FRANKLIN et al. 2007; JONÁŠOVÁ 2013; KJUČUKOV et al. 2014; SANTANIELLO et al. 2016), kteří vesměs tvrdí, že mrtvé dřevo jako biologické dědictví zvyšuje úroveň biodiverzity lesního ekosystému a pozitivně ovlivňuje koloběh živin v půdě. Existence mrtvého dřeva v porostu navíc podporuje také obraz krajinného rázu lesa a pomáhá plnit i další funkce lesa, jako je zadržování vody a fixace uhlíku (RUSSELL et al. 2015; VACEK et al. 2018).

Odhlédneme-li od porostů na extrémních stanovištích (CHS 01), kde borové porosty plní zejména funkci ochrannou, většinu borových porostů nalézáme na SLT: 0K, 0M, 1M, 0Q, 0P a 0O (CHS 13), či na 0T a 0Q (CHS 39). V porostech nacházejících se na stanovištích SLT 0M, je s ohledem na ekologicky orientované pěstování lesa racionální vyvarovat se velkých holosečí, podpořit přimíšenou břízu, zachovat genotyp místní populace a využívat přirozenou obnovu (PRŮŠA 2001). Na SLT 0K a 1M lze v případě nekvalitních porostů postupovat holosečně, v kvalitních porostech násečně, v našem případě zejména podrostopně. Často se zde objevují i přimíšené listnaté dřeviny, které je zde třeba ponechávat pro udržení kvality půdy (PEŘINA & VINTROVÁ 1958). Na stanovištích, kde hrozí zamokření a poškození mrazem (0O, 0P a 0Q), je z důvodu alespoň částečného krytu opět vhodné podrostopní hospodaření (ULBRICOVÁ et al. 2017). Na SLT 0T a 0G, která reprezentující živinově velmi chudá stanoviště, je aktuální otázkou již zmíněné ponechávání těžebních zbytků a většího množství mrtvého dřeva (KOMONEN et al. 2000; FRANKLIN et al. 2007; JONÁŠOVÁ 2013; KJUČUKOV et al. 2014; SANTANIELLO et al. 2016).



Se stále větší informovaností veřejnosti, ale také při vzrůstající aktivní součinnosti různých lesnických i nelesnických organizací, dnes stále častěji dochází k nalézání společných ekologicko-ekonomických cílů, a to nejen na úrovni výzkumu. Konkrétně ve Švédsku v provincii Dalarna na ploše cca 3 400 ha funguje spolupráce vlastníka lesa, výzkumného ústavu a akciové společnosti provádějící lesnické služby, a to již od roku 2012 (DJUPSTRÖM & WESLIEN 2019). V dospělých hospodářských borových porostech se zde za přispění všech zmíněných orgánů snaží prostřednictvím napodobování přirozených procesů vytvářet heterogenní prostředí pro zvyšování biodiverzity lesního ekosystému. Podobný příklad nicméně známe také z prostředí České republiky, na majetku Městských lesů Doksy, s. r. o., jehož borové porosty jsou charakteristické velmi vysokou potřebou vyhovět jak požadavkům rekreačním, ochraně biodiverzity, tak ekonomice lesního hospodářství. V lesních porostech provincie Dalarna (DJUPSTRÖM & WESLIEN 2019; Švédsko) tak s ohledem na boreální charakter lesů polyfunkčnost lesních porostů naplňují napodobováním přirozeného rozpadu lesa. V Doksech či v některých porostech nedaleko Třeboně a v dalších oblastech, je potřeba plnění kompletní škály funkcí lesa naplňována prostřednictvím pěstování strukturně diferencovaných borových porostů (**Obr. 4**). Navíc již známe práce (BARZDAJN & ZIENTARSKI 2007), které dokazují, že pěstování strukturně diferencovaných borových porostů je nejen možné, ale zároveň účelné, jak z hlediska plnění funkcí lesa, tak nákladovosti lesní výroby.



**Obr. 5** Vícegenerační strukturně diferencovaný borový porost, Třeboň 2019. Foto: Jakub Brichta



### 3.5 Smíšené borové porosty

S ohledem na klimatické změny se dnes na většině stanovišť udržování a zakládání smíšených borových porostů jeví jako možnost zvyšování adaptability lesních ekosystémů (PRETZSCH et al. 2015). Ačkoli kulturní nesmíšené borové porosty v ČR převažují, smíšení porostů s břízou zde ve větší míře vznikají již od preboreálu (MIKESKA 2008). Bříza se navíc na přirozených borových stanovištích vyskytuje přirozeně (SUCHOMEL et al. 2014) a mnohdy je jedinou dřevinou, která borovici dokáže konkurovat už od stádia nárostu (ULBRICOVÁ et al. 2017) a tvořit s ní v budoucnu směs alespoň v roli přimíšené dřeviny (MASON & CONNOLLY 2016). V suchých obdobích bříza ve směsi s borovicí zvyšuje svou stabilitu a konkurenceschopnost, na rozdíl od ostatních druhů dřevin v přimíšení v tomto stavu setrvává (BAUMGARTEN et al. 2019). V případě smíšených porostů borovice lesní a břízy bělokoré ve vhodných klimatických podmínkách dokonce dochází ke zvýšení přírůstu obou těchto pionýrských dřevin (KAITANIEMI & LIN-TUNEN 2010).

Smíšené borové porosty díky své rozmanitosti obecně lépe využívají dostupné zdroje na celé řadě stanovišť (chudá písčitá stanoviště, extrémní a půdně obnažené lokality apod.), a tak zmírňují dopady sucha a dalších poškození biotickými a abiotickými činiteli. Z hlediska extrémů klimatu zde tedy často vykazují vyšší vitalitu a stabilitu porostu (CZEREPEKO 2004; PRETZSCH et al. 2015; ŠPULÁK & ČERNÝ 2023). Dle mnohých zdrojů navíc existence přimíšených dřevin zvyšuje produktivitu borových porostů. Empirické studie, modelace a metaanalýzy (MORIN et al. 2011; ZHANG et al. 2012; BIELAK et al. 2014) navíc potvrdily, že průměrná produkce smíšených porostů může předčít průměrnou produkci nesmíšených porostů. Nárůst produkce tak může činit až 50 %, a to zejména ve smíšení s dřevinami vázajícími dusík (FORRESTER et al. 2006), 20–30 % v ostatních směsích (PRETZSCH et al. 2013a).

V podmínkách střední Evropy (NOVÁK et al. 2020; BRABEC et al. 2024), ale také v boreálních lesích Skandinávie, jsou velmi častá smíšení se smrkem (DRÖSSLER et al. 2018; FELTON et al. 2016), kdy borovice je v tomto spojení situována v úrovni a nadúrovni, kdežto smrk tolerující zástin tvoří podúroveň. Tato směs má dle výše zmíněných autorů v daných podmínkách také pozitivní vliv na půdní charakteristiky, včetně vláhových poměrů. Navíc zvyšuje estetickou hodnotu porostu, ale především snižuje riziko ohrožení porostu abiotickými

i biotickými činiteli, a to jak pro borovou, tak i pro smrkovou etáž (BIELAK et al. 214). S ohledem na tuto směs však narážíme také na riziko, že smrk v podúrovni prostřednictvím korunové intercepce a mezikořenové konkurence bude snižovat množství vláhy v půdě, což je v řadě případů pro vrchní borovou etáž zároveň limitem (ŠPULÁK 2019; NOVÁK et al. 2020).

Zdárný vývoj borových porostů často vyžaduje příměs stinných či polostinných listnatých dřevin v podúrovni: habru obecného (*Carpinus betulus* L.), buku lesního (*Fagus sylvatica* L.) či lípy (*Tilia spp.*). Zpravidla tak dochází ke zvyšování stability porostu a vyvětvování vrchní borové etáže (POLENO et al. 2009). Pěstování a obnova borovice s dalšími dřevinami, a to jak v podúrovni, tak v úrovni, bývá prospěšné i samotné kvalitě dřevní suroviny (HOLUŠA & HOLUŠA 2000). Další nespornou výhodou listnatého smíšení je jednoznačně pozitivní vliv na hladinu pH v půdě, kdy optimalizuje pH po kyselém borovém opadu (PEŘINA & VINTROVÁ 1958). Dřeviny vhodné ke smíšení s borovicí se podle stanovišť liší. Na chudých vysychavých stanovištích bývá nejvhodnější příměs dubu, nejčastěji se jedná o tzv. borové doubravy (CHYTRÝ 2010). V nižších polohách je také vhodná směs s habrem (VACEK & PODRÁZSKÝ 2006). Ve středních polohách je vhodné smíšení s bukem, často je ale obtížné založit směs současně, neboť současně vysazené buky nejsou schopné přizpůsobit se růstovému tempu borovice (DRAGOUN et al. 2015). Podaří-li se však udržet směs borovice s bukem do mýtního věku porostu, můžeme očekávat navýšení tloušťkového přírůstu borovice až o 14 % (ZELLER et al. 2017). Na zonálních stanovištích či za procesu sukcese ve fázi přípravného lesa se nejčastěji samovolně vyskytuje smíšení s břízou (SUHOMEL 2014). Nicméně dle DRAGOUNA et al. (2015) se jako nejvýhodnější jeví smíšení s lípou v podúrovni. Konkrétně u této příměsi očekáváme výrazně pozitivní vliv na výškový přírůst borovice, výčetní tloušťku a souhrnně na celkovou zásobu porostu. Také KOŠULÍČ st. (2008) doporučuje zakládat výsadby borovice lesní vždy s příměsí listnatých dřevin, vedle dubu, habru či lípy uvádí jako žádoucí rovněž příměs olše a osiky. PRETSZCH et al. (2020) popisuje výrazně vyšší přírůst borovice ve směsi s dubem. Ve prospěch smíšení borovice lesní s dalšími dřevinami hovoří také nedávná aplikační metodika (NOVÁK et al. 2021), která v pro smíšení s borovicí na přirozených borových stanovištích doporučuje dokonce hned několik dřevin. Dobrou zpevňující funkci v tomto kontextu může dle NOVÁK et al. (2021) plnit spolu s borovicí douglaska tisolistá (*Pseudotsuga menziesii* (Mirb.) Franco), dub zimní (*Quercus petraea* (Matt.) Liebl.), habr obecný, jedle bělokorá, modřín opadavý (*Larix decidua* Mill.) či buk lesní. Metodika však zároveň doporučuje také smíšení se smrkem ztepilým.

V důsledku klimatických změn a posouvání areálu borovice lesní do vyšších poloh (VACCHIANO a MOTTA 2015; HUNZIKER et al. 2022) se dnes v Evropě čím dál častěji skloňuje také přestavba borových monokultur ve prospěch smíšených porostů. Dle studie SOUČEK (2006) je nejčastějším postupem umělé přestavby borových porostů podsadba listnatými dřevinami. Dostatečný průnik slunečního záření a množství srážek může zajistit růst spodní listnaté etáže i bez výrazných přírůstových ztrát. Na stanovištích, kde se nachází dobré zásoby vody a živin, a borovice zde není v původní dřevinné skladbě, je nakonec změna druhové skladby žádoucí, a obecně s ní nebývá závažnější problém. Masivní přestavby borových monokultur probíhají již řadu let například v Polsku, kde bývají uskutečňovány prostřednictvím podsadeb buku a jedle (**Obr. 6**), podsíjemi jedle, či skupinovitými holosečnými prvky v šachovnicovém uspořádání s následnou umělou obnovou listnatých dřevin. Důležitým procesem těchto přestaveb je vyřezávání případných listnatých náletových dřevin, které často vytváří hustý podrost a komplikují tak ujímavost podsadeb (KOZEL 2010). Dalším reprezentativním příkladem změny druhového složení je přeměna borových porostů clonným způsobem s kotlíky v severovýchodním Německu. Do dospívajících porostů jsou zde vkládány kruhové kotlíky s výsadbou dubu, v okolních borových porostech je pak uplatňována přirozená obnova pomocí dalších clonných sečí (SOUČEK 2006). Vhodnost smíšení či přestavby cestou kotlíků světlomilných listnatých dřevin doporučují také další studie (MASON & CONNOLLY 2016; WAITZ & SHEFFER 2021). Zajímavou možností vkládání listnatých dřevin do borových porostů je také využití dubu červeného, který se pro tuto směs jeví jako velmi vhodný. Na rozdíl od dubu zimního či letního, neztrácí vitalitu ani pod porostem borovice, a naopak se prostřednictvím zejména zvěře a ptactva šíří po porostu, kde vytváří stabilní podrost (WOZIWODA et al. 2018). V ČR již na některých místech probíhá přestavba borových monokultur na smíšené porosty, nicméně se jedná o proces trvající minimálně desítky let, samozřejmě v závislosti na podmínkách prostředí; konkrétně v NP Podyjí je odhadována přestavba borových porostů skupinovitým výběrem na dobu minimálně 40 let (VRŠKA 2012).



**Obr. 6** Porost borovice lesní s podsadbou jedle bělokoré (vpravo), zavedené pomocí kotlíkové seče, Janów Lubelski (Polsko) 2021. Foto: Jakub Brichta

### 3.6 Vliv klimatických extrémů na zdravotní stav borových porostů

Klimatické modely 21. století ukazují, že průměrná teplota se během krátké časové periody zvýší o 3-4 °C, a zároveň srážky se radikálně sníží (IPPC 2013, 2023). CHRISTENSEN et al. (2007) hovoří o tom, že do roku 2100 dojde ke zvýšení průměrné teploty dokonce až o 5 °C. V podmínkách ČR taktéž předpokládáme výrazný nárůst průměrných teplot. Dle MŽP (2015) se v období 2010-2039 teplota vzduchu zvýší o 1 °C, v období 2040-2069 se předpokládá výraznější oteplení, kdy se na jaře a v létě oteplení může pohybovat v rozmezí od 2,3 °C po 3,2 °C, v období 2070-2099 dosáhne oteplení v létě průměrně 4 °C. Trend zvyšování průměrných teplot a snižování dostupnosti srážek a hladiny spodních vod, se nepříznivě projevuje na stavu lesních porostů (ŠRÁMEK & HELLEBRANDOVÁ et al. 2016), dochází tak k výraznému usychání porostů různých dřevin, což pozorujeme v měřítku takřka celého světa (ALLEN et al. 2010).

V podmínkách střední Evropy jsou ohroženy především porosty smrku, které tak ztrácí obranyschopnost proti škodám podkorním hmyzem, a to zejména na lokalitách mimo jeho ekologické optimum (HOLUŠA & LIŠKA 2002; SLODIČÁK 2014; JENIŠ 2014; NOVÁK & DUŠEK 2014). Nedostatek vláhy se ale velmi nepříznivě projevuje také na stavu borových porostů

(BURAS et al. 2018), kdy sucho často bývá primárním původcem jejich plošného odumírání, a to nejen v podmínkách ČR (LČR 2019; ŠPULÁK & ČERNÝ 2023), ale běžně již také v boreálních lesích Finska (GAO et al. 2017). Výrazné zhoršení vitality nejen borových porostů je nejvíce patrné od roku 2015, který byl charakteristický několika periodami extrémně vysokých letních teplot, zároveň byl v tomto období patrný výrazný srážkový deficit. Nedostatek srážek v roce 2015 zapříčinil významný pokles hladiny podzemní vody. Zmíněné zhoršení klimatických podmínek platilo pro celou střední Evropu, dokonce se jednalo o rok, kdy suma letních srážek byla podstatně nižší než hodnoty srážek předchozích 114 let (ORTH et al. 2016). V podmínkách České republiky se zdravotní stav borových porostů prokazatelně postupně zhoršuje už od roku 2013 (ŠPULÁK & ČERNÝ 2023), velmi prudké zhoršení zdravotního borovice zde pozorujeme od roku 2018, který byl charakteristický srážkovým deficitem pro celou střední Evropu (BOERGENS et al. 2020). Nicméně je nutné rovněž konstatovat, že již na přelomu století byly zjištěny proschlé borové porosty dokonce v oblastech Alp (OBERHUBER 2001), zde lze opět sledovat neustálou kontinuitu v prosychání borových porostů, o čemž dále hovoří BIGLER et al. (2006). Dle těchto autorů bylo usychání borovice lesní sledováno už před rokem 2001, a to to jak v Rakousku, Švýcarsku, tak v Itálii (BIGLER et al. 2006). Na špatnou adaptabilitu borových porostů upozorňuje dokonce už MASON & ALÍA (2000) ve tvrzení, že i přes výrazný posun v informovanosti o genetické rozmanitosti borovice lesní, nebudou borové monokultury schopny reagovat na měnící se podmínky prostředí, a to na většině plochy jejího výskytu. Tedy už před více než 19 lety různé studie shodně uváděly, že sucho negativně ovlivňuje vitalitu borových porostů, a dojde-li k několika suchým rokům za sebou, pak i k jejich celkové mortalitě. S ohledem na informace o nízké adaptabilitě porostů borovice lesní vůči změnám klimatu, se zdají být velmi ohroženy zejména porosty stejnověké (SAVVA & VAGANOV 2002). Stejnověkým porostům tedy hrozí, že budou v budoucnu negativně ovlivňovány suchem stále více (BOTTERO & VACCHIANO 2015; VACEK et al. 2016). Vhodné je rovněž uvažovat o vlivu klimatických extrémů na borovice různého charakteru. Ačkoli MARQUES et al. 2022 tvrdí, že sucho prokazatelně snižuje přírůst borovic bez ohledu na jejich vitalitu, tak vitální jedinci po uplynutí suché periody vykazují vyšší přírůsty a lepší schopnost regenerace než stromy oslabené (CAMARERO et al. 2018). VEJPUŠTKOVÁ et al. (2020) pak tvrdí, že klimatické extrémy nejvíce ohrožují porosty středního až vyššího věku. CUKOR et al. (2022) ve své studii navíc zmiňuje, že na extrémy klimatu hůře reagují také stromy poškozené

loupáním zvěří. Výsledky studie BURAS et al. (2018) upozorňují na různou lokaci porostů poškozených suchem. Dle závěrů BURAS et al. (2018) se nejvíce poškozené porosty nachází na okrajích lesa, což je navíc umocněno vytěžením těchto porostů, kdy následně dochází ke kontinuálnímu narušování porostního okraje. Na základě výše zmíněného zjištění tak lze nicméně rovněž konstatovat, že existence porostního okraje může výrazně zmírnit klima uvnitř lesa, i za předpokladu, že je porostní okraj z větší části proschlý (BURAS et al. 2018).

Ve světle změny klimatických podmínek je adaptabilita celého hospodaření s borovicí lesní v podmínkách ČR o to složitější, že pro borovici lesní prakticky nelze taxativně odvodit vhodné klimatické podmínky, zde tedy není na místě hospodaření upravovat v důsledku posunu lesních vegetačních stupňů (MŽP 2015; MŽP 2021). To je dáno především její širokou ekologickou amplitudou, a sice délkou vegetační doby 90-200 dnů, či ročním úhrnem srážek 200-1 800 mm (MUSIL 2003). Zmíněné podmínky zaujímají prakticky celé území ČR. Uplatnění borovice je zde tedy skutečně dáno její konkurenceschopností a vazbou zejména na podloží, nikoli klimaticky (ČERMÁK & MIKITA 2014). Další překážkou ve snaze zvyšování adaptability borového hospodářství může být značná genetická diverzita borovice lesní (KOŠULIČ 2007; KAŇÁK et al. 2009; ČÁP et al. 2016). Dle ČÁP et al. (2016) v ČR navíc ještě neexistuje kompletní seznam jejích ekotypů. HUNZIKER et al. (2022) však konstatuje, že borovice postupně ustupuje z nižších nadmořských výšek, i navzdory své vysoké genetické variabilitě.

Nutné je však zmínit, že ačkoli suchá období porosty borovice lesní obecně poškozují, na kvalitu jejího osiva prokazatelně nemají negativní vliv (BEZDĚČKOVÁ & MATĚJKA 2018). Jinak je to však v případě množství osiva, které se v borových porostech samozřejmě snižuje s počtem odumřelých mateřských jedinců (VILÀ-CABRERA et al. 2014). Velmi teplá a suchá léta jsou obecně doprovázena zvýšeným opadem jehličí (OZOLINČIUS et al. 2009; POLJANŠEK et al. 2015), což opět narušuje fyziologickou vitalitu jedince. Defoliace borovice bývá ovlivněna zejména nedostatkem srážek předchozího roku (REBETEZ & DOBBERTIN 2004). Předčasný opad jehlic způsobený stresem ze sucha probíhá rovněž v první až druhé následující vegetační sezoně (NIINEMETS & LUKJANOVA 2003). Defoliace se samozřejmě projevuje také snížením tloušťkového přírůstu borovic (VACEK et al. 2017). Stres způsobený nedostatkem vláhy nicméně často způsobuje výrazné snížení obranyschopnosti borových porostů proti rozvoji jmelí bílého (*Viscum album*), jehož rozšíření v koruně stromu vede nejen k dalšímu snížení dostupnosti vody, ale také minerálních živin (RIGLING et al. 2010; ZWEIFEL et al. 2012; MUTLU



et al. 2016). Jmelí tak čím dál častěji doprovází suchem stresované borové porosty, a následkem jeho parazitismu a vylučování jedovatých metabolických látek do pletiv hostitele, dochází k odumírání částí koruny či nakonec i celého stromu (ROLOFF et al. 2012; TRIEBENBACHER et al. 2019). Stres způsobený nedostatkem vláhy dále napomáhá ke snížení obranyschopnosti proti podkornímu i listožravému hmyzu a přispívá také k rozvoji fytopatogenů (HÓDAR & ZAMORA 2004; DOBBERTIN et al. 2007; WERMELINGER et al. 2008). Zvláště je potřeba uvažovat riziko následného napadení oslabených borovic podkorním hmyzem, který se na území ČR velmi rozšířil po srážkově extrémně deficitním roce 2018 (LUBOJACKÝ et al. 2022). Sucho navíc často způsobuje zvyšování rizika výskytu lesních požárů (ALLEN et al. 2010; MŽP 2015; MŽP 2021), na přirozených borových stanovištích chudých na vodní zdroje obzvláště.

Jedním z obranných mechanismů borovice lesní k aktuálním extrémům klimatu je bezesporu silná vosková vrstva na jehlicích a zapuštěné průduchy na jejich vnitřní straně. Obranný mechanismus borovice se při vláhovém deficitu projevuje tak, že dochází k uzavření průduchů, tedy k přerušení evapotranspirace (SANCHO-KNAPIK et al. 2017). Nutné je však dodat, že se jedná o krátkodobé opatření, neboť uzavření průduchů zároveň omezuje fotosyntetickou aktivitu stromu (RIEK & RENGGER 1994). Vodu, kterou borovice přijímá ze vzduchu, následně transportuje do větví, v některých případech dokáže dále distribuovat do kořenové soustavy stromu. Známa je studie o transportu vody z větví do kořenů u semenáčků borovice (ROLOFF 2004). Práce LOPEZ et al. (2021) nicméně prokázala, že borovice jsou stresovány kratšími suchými periodami méně než smrk ztepilý, to je pravděpodobně způsobeno vyšší hustotou jemných kořenů v horních 15 cm půdního profilu (FINÉR et al., 2007), ale také rychlejším růstem kořenové biomasy (BØRJA et al., 2008).

## 4. METODOLOGIE

Metodické postupy této disertační práce byly poměrně široké, předně s ohledem na různá témata odborných publikací uvedených v kapitole 5. Výsledky. V této kapitole uvádím základní a souhrnné charakteristiky lokalit, sběru, zpracování a analýzy dat.

### 4.1 Popis lokalit

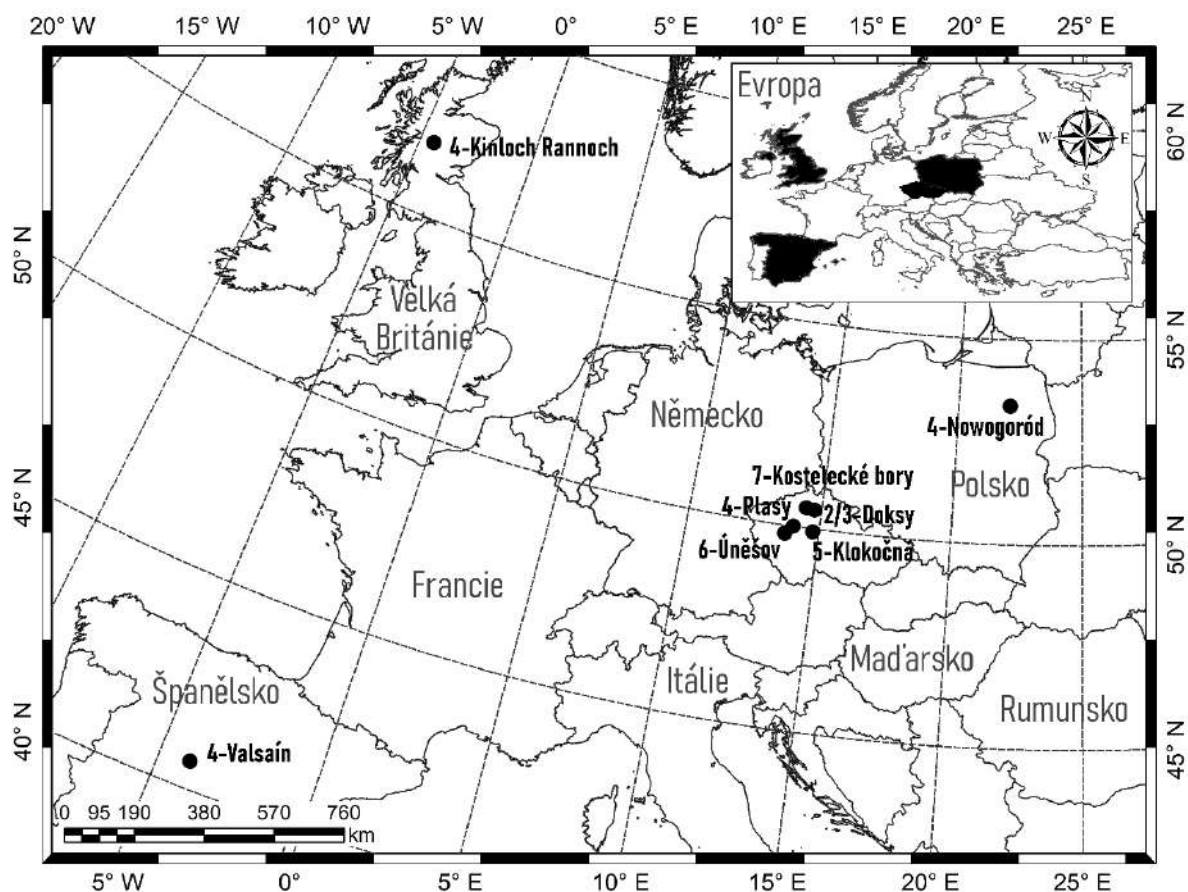
Výzkumné aktivity předložené disertační práce probíhaly na několika lokalitách, a to jak v prostředí České republiky, tak dalších států Evropy (**Obr. 7**). V případě 1. a 7. publikace se jednalo o porosty minimálně ovlivněné člověkem, se zvýšeným stupněm ochrany, data publikace 2. a 5. publikace byla pořízena v běžných hospodářských mýtních porostech, pro 3. publikaci byla data získána z výchovných homogenních porostů, studie 6. publikace byla řešena ve smíšených a nesmíšených přírodě blízkých porostech. **Tab. 1** zobrazuje souhrnný přehled lokalit jednotlivých publikací, včetně stručného popisu přírodních podmínek.

**Tab. 1** Charakteristika výzkumných lokalit

| Publikace                | Země | Lokalita        | GPS                             | Nadmořská výška | Průměrná roční teplota | Roční úhrn srážek | Půdní podmínky                     |
|--------------------------|------|-----------------|---------------------------------|-----------------|------------------------|-------------------|------------------------------------|
| 1.VACEK et al. (2019)    | ČR   | Kostelecké bory | 50.5692283 N, 14.4545308 E      | 433 m n. m.     | 7,33 °C                | 650 mm            | Podzol arenický, kambizem arenická |
| 2.BRICHTA et al. (2020)  | ČR   | Doksy           | N 50°33.77548', E 14°43.49143'  | 300 m n. m.     | 7,30 °C                | 635 mm            | Podzol arenický                    |
| 3.CUKOR et al. (2022)    | ČR   | Úněšov          | 49.8154944N, 13.2322244E        | 459 m n. m.     | 8,4 °C                 | 488 mm            | Kambizem modální                   |
| 4.BRICHTA et al. (2023)  | –    | –               | –                               | –               | –                      | –                 | –                                  |
| 5.ŠLEGLOVÁ et al. (2023) | ČR   | Doksy           | N 50°33.77548', E 14°43.49143'  | 300 m n. m.     | 7,30 °C                | 635 mm            | Podzol arenický                    |
| 6.BRABEC et al. (2023)   | ČR   | Klokočná        | 49°58'29"N, 14°43'05"E          | 455 m n. m.     | 7,5 °C                 | 600 mm            | Kambizem, Luvizem, Pseudoglej      |
| 7.BRICHTA et al. (2024)  | ČR   | Plasy           | 49°54'35.653" N 13°11'59.617" E | 590 m n. m.     | 7,95 °C                | 492 mm            | Podzol glejový                     |
| 7. BRICHTA et al. (2024) | SP   | Valsaín         | 40°49'2.102" N 3°59'8.730" W    | 1 680 m n. m.   | 6,55 °C                | 1 326 mm          | Kambizem, Luvizem                  |
| 7. BRICHTA et al. (2024) | PL   | Nowogoród       | 53°19'12.130" N 21°40'19.159" E | 130 m n. m.     | 7,34 °C                | 553 mm            | Podzol arenický                    |
| 7. BRICHTA et al. (2024) | VB   | Kinloch Rannoch | 56°40'29.170" N 04°20'51.520" W | 250 m n. m.     | 5,67 °C                | 1 552 mm          | Podzol glejový                     |

\* Poznámka 1: 4. publikace je literární rešerší, proto chybí ve výčtu lokalit.

\* Poznámka 2: Data o přírodních podmínkách daných lokalit byla zjištěna z nejbližších klimatických stanic a ústavů, za využití půdních map a informací z dalších odborných publikací. Konkrétní zdroje jsou k nalezení v jednotlivých člácích, v kapitole 5. Výsledky.



**Obr. 7** Mapa Evropy s body zájmových lokalit jednotlivých studií

## 4.2 Sběr dat

### 4.2.1 Význam a potenciál borovice lesní (*Pinus sylvestris* L.) ve 21. století (4. publikace)

Zejména v rámci realizaci studie BRICHTA et al. (2023) proběhl sběr dat formou syntézy literárních zdrojů, předně dostupných v databázi Scopus a WOS. Vyhledávání aktuálních informací o taxonu bylo zpravidla provedeno také prostřednictvím webového portálu Google Scholar, kde byla používána následující klíčová slova: *pinus sylvestris*; *scots pine*; *climate change*; *drought*; *structural diversity*; *forests*; *close to nature*; *silviculture*; *ecology*; *threats*; *wood production*; *European forests*; *shelterwood*

Knižní publikace či starší odborné publikace, nedostupné v elektronické podobě, byly zapůjčeny v knihovnách Fakulty lesnické a dřevařské ČZU v Praze, stejně jako ve Studijním informačním centru ČZU.

#### 4.2.2 Inventarizace jedinců přirozené obnovy a semenného materiálu (1.; 2.; 5. publikace)

Přirozená obnova byla inventarizována na ploše s designem různých variant hustoty mateřského porostu (BRICHTA et al. (2020); zakmenění 0,8; 0,6; 0,4 a holoseč) a zároveň různých variant přípravy půdy (shrnovač klestu, lesní fréza, kombinovaná lesní fréza, kontrolní varianta). V každé z kombinací zakmenění mateřského porostu a přípravy půdy, byly vytyčeny dva transekty (**Obr. 8**) o rozloze  $2 \times 60$  m ( $n = 64$ ), které byly dále rozděleny na čtverce o  $2 \times 2$  m (viz kapitola 5.2). Pro každý jednotlivý čtverec byly inventarizováni všichni jedinci obnovy (u jedinců vyšších 10 cm byla zaznamenána celková výška a šířka koruny s přesností na 1 cm). Všechna měření byla provedena na podzim 2018, tedy 3 roky po clonné seči a skarifikaci půdy. V rámci inventarizace dat práce ŠLEGLOVÁ et al. (2023) bylo celkem 32 jedinců přirozené obnovy z výše zmíněných ploch měřeno také v laboratorních podmínkách (nadzemní i kořenová část rostliny), za pomoci technologie magnetického digitizéru Fastrak Polhemus pro účely 3D modelování architektury rostlin. V roce 2016 bylo na plochu každé varianty hustoty mateřského porostu umístěno také 7 semenospadů (velikost  $1 \times 1$  m) ( $n = 28$ ), jejichž obsah byl vždy inventarizován koncem vegetační doby (měřeno od roku 2016 do roku 2018). Semenospady byly umístěny do středu jednotlivých ploch tak, aby bylo předejito vlivu okrajového efektu.

Inventarizace přirozené obnovy v již diferencovaných porostech (VACEK et al. 2019) probíhala na celkem 6 výzkumných plochách o rozloze 0,25 ha na předem vytyčených zájmových transektech ( $10 \times 50$  m), založených již před zahájením aktivit disertační práce. Inventarizace přirozené obnovy zde proběhla v letech 2006 a 2016. Pomocí technologie Field-Map (IFER-Monitoring and Mapping Solutions Ltd.) byla stanovena poloha daného jedince. Výška, výška nasazení koruny a její šířka koruny, byly měřeny prostřednictvím tyčového výškového měřidla (s přesností 1 cm).



**Obr. 8** Inventarizace jedinců přirozené obnovy na vytyčených transektech, Doksy 2021. Foto: Jakub Brichta

#### 4.2.3 Zjištění vodního potenciálu půdy a teploty půdy (2. publikace)

Měření vodního potenciálu bylo prováděno pomocí absorpčních bloků GB–2 (Delmhorst Instrument Company) připojených k dataloggerům Micro-Log SP3 (EMS Brno). K dataloggeru bylo připojeno také teplotní čidlo (čidla třídy A Pt1000, EMS Brno). Sádrové senzorové bloky byly umístěny 7–9 cm pod povrch půdy; pro jednu variantu hustoty mateřského porostu byly instalovány vždy 4 senzory ( $n = 16$ ). Zařízení na měření vodního potenciálu půdy a její teploty byla umístěna doprostřed ploch.

#### 4.2.4 Měření struktury porostu (1.; 6.; 7. publikace)

V případě výzkumu BRICHTA et al. (2024) byla v letech 2015–2016 k zachycení struktury porostu použita technologie Field-Map (IFER-Monitoring and Mapping Solutions Ltd., Jílové u Prahy, Česká republika; **Obr. 9 a 10**), konkrétně ke stanovení struktury stromového patra a produkčních parametrů výzkumných ploch. Na celkem 16 výzkumných plochách o rozloze 50 x 50 m (0,25 ha) byly na území České republiky, Španělska, Polska a Velké Británie zaznamenány pozice všech jedinců stromového patra s výčetní tloušťkou (DBH)  $\geq 8$  cm. Během zaznamenávání pozic pomocí technologie Field-Map byla měřena také projekce korun

stromových jedinců (za pomoci 4 bodů, umístěných při obvodu koruny). Metodologie VACEK et al. (2019) byla z hlediska parametrů celkem 6 výzkumných ploch podobná (0,25 ha), avšak s tím rozdílem, že všechny zájmové plochy byly změřeny v roce 2006 a v roce 2016 se zde měření opakovalo. Coby stromoví jedinci byly inventarizovány borovice  $\geq 4$  cm. V případě šetření BRABEC et al. (2023). byla struktura porostu měřena na základě obdobných pravidel, nicméně byly zaznamenávány jedinci s tloušťkou stromu  $\geq 7$  cm, a to na ploše 25 x 50 m (0,125 ha). Ve všech případech byly inventarizováni také jedinci hraniční, jejichž DBH byla z větší části na území dané výzkumné plochy.

Inventarizace mrtvého dřeva (VACEK et al. 2019) proběhla na všech 6 plochách studie (0,25 ha), a to v intencích pětibodové stupnice, upravené dle SPETICH et al. (2001) (1 – nenarušený kmen, 5 – konečná fáze rozkladu). U mrtvého dřeva byl dále stanoven jeho objem a podíl na celkové zásobě porostu.





**Obr. 9** Kompletní zařízení Field-Map (vlevo); **Obr. 10** obrazovka tabletu s již zaznamenanými záměry jedinců borovice lesní (vpravo), Plasy 2020. Foto: Jakub Brichta

#### 4.2.5 Základní dendrologická měření stromů a jejich částí (1.; 3.; 6.; 7. publikace)

Metodologie šetření VACEK et al. (2019), CUKOR et al. (2022), BRABEC et al. (2023) a BRICHTA et al. (2024) obsahovala také měření jedinců stromového patra (všech přítomných dřevin), měřeno tak bylo: tloušťka stromu, výška stromu a nasazení jeho koruny. Tloušťka stromu byla téměř ve všech případech měřena pomocí manuální lesnické průměrky Mantax Blue (Haglöf, Långsele, Švédsko) s přesností 1 mm, a to pomocí průměru minimálně 2 na sebe kolmých měření (v případě inventarizace VACEK et al. (2019) se jednalo o manuální lesnickou průměrku Kinex). Výšky stromů, stejně jako nasazení koruny byly měřeny prostřednictvím laserového výškoměru Vertex (Haglöf, Švédsko) s přesností 0,1 m.

#### 4.2.6 Inventarizace poškození jednotlivých mateřských stromů a jedinců přirozené obnovy (1.; 3. publikace)

Inventarizace stromových jedinců CUKOR et al. (2022) byla rovněž doplněna o měření skutečného poškození stromů loupáním lesní zvěří, resp. následnou hnilobou. U každého zájmového stromu byl zaznamenán obvod místa poškození, vertikální délka poškození a vzdálenost středu poškození od země. Poškození kmene (čerstvé i starší) bylo měřeno standardním krejčovským metrem, a to v nejširším místě poranění stromu, s přesností na 1 mm. V případě mnohočetných poranění (na kmeni umístěných nad sebou) byl zaznamenán součet obvodů těchto poškození, v jejich nejširších místech. Měřené stromy byly rozděleny do 3 kategorií dle poškození zvěří: zdravé stromy (poškození  $\leq 1/8$  obvodu kmene), stromy s menším poškozením (poškození  $> 1/8$  a  $\leq 1/3$  obvodu kmene) a rozsáhlé poškození (poškození  $> 1/3$  obvodu kmene) (KOSMALA et al. 2008; CUKOR et al. 2019; VACEK et al. 2020). Sběr dat v tomto případě proběhl v r. 2020 také formou odebrání pokácených vzorníků z celkem 40 borovic (DBH v rozmezí 10,1–24,6 cm) s různým stupněm poškození. Vzorníky byly odebírány po řezech (délka řezu činila 20 cm) od místa nejširšího poškození obvodu, a to jak směrem k vrcholu, tak k patě kmene. Každý vzorník (**Obr. 11**) s přítomností hniloby byl zároveň zaznamenán na fotografii fotoaparátem Canon (Canon, 'Ota, Japonsko). Rozsah hniloby na vzornících byl následně měřen pomocí programu ImageJ (Schindelin et al., 2015). Fotografie oblastí poškozených hnilobou byly změřeny v programu pro zpracování ImageJ (SCHINDELIN et al., 2015). Pomocí příčných řezů vzorníků byl stanoven také rok prvního poškození stromu, a to dle prvního poškozeného letokruhu (započítána byla také korekce 4 letokruhů dorostu do průměrné výšky bodu poškození – 0,9 m).





**Obr. 11** Vzorník pro stanovení rozsahu hniloby, Úněšov 2021. Foto: Jakub Brichta

Metodologie inventarizace poškození okusem zvěří (VACEK et al. 2019) byla stanovena jako prosté zaznamenávání všech jedinců evidentně poškozených okusem zvěří, a to s ohledem na všechny přítomné dřeviny. Okus byl detekován coby ostré přerušení terminálního pupenu dané rostliny. Inventarizace okusu lesní zvěří byla v tomto případě provedena v roce 2006 a následně v roce 2016.

#### **4.2.7 Odebírání dendrochronologických vzorků (1.; 6.; 7. publikace)**

Dendrochronologické vzorky byly odebírány pro všechny studie disertační práce shodně, pomocí Presslerova přírůstového nebozezu, a to ve výšce 1,3 m od země, směrem do středu stromu, vzorky byly následně lepeny do speciálně vytvořených dřevěných krytů s drážkami. Pro účely práce BRICHTA et al. (2024) byly vzorky odebrány z celkem 163 kodominantních a dominantních jedinců borovice lesní na různých výzkumných plochách všech 4 zaujatých zemí (Česká republika, Španělsko, Polsko, Velká Británie). Data práce VACEK et al. (2019) tvořilo celkem 150 dendrochronologických vzorků, odebraných z dominantních (případně

kodominantních) stromů, kdy pro každou ze 6 ploch byl vytvořen soubor 25 vzorků. V případě výzkumu BRABEC et al. (2023) bylo odebráno celkem 60 vývrtů z kodominantních a dominantních stromů: 30 vývrtů z borovice lesní a 30 vývrtů ze smrku ztepilého. Veškeré odebrané vzorky pocházely z jedinců horního stromového patra, s registrační hodnotou tloušťky > 30 cm. S ohledem na odlišnou metodologii CUKOR et al. (2022) byl odběr dendrochronologických vzorků v tomto případě stanoven na celkem 60 vývrtů borovice lesní, z toho 30 vzorků pocházelo ze zdravých stromů v porostu, dalších 30 vzorků ze stromů značně poškozených. Kodominantní a dominantní stromy pro vzorkování byly v porostech vybírány náhodně (funkce RANDBETWEEN, MS Excel). V případech všech zmíněných publikací byly kodominantní a dominantní stromy stanoveny dle Kraftovy klasifikace (KRAFT 1884).

Podobně pro všechny 3 zmíněné výzkumy proběhlo následné vyhodnocení vzorků v laboratorních podmínkách, konkrétně byla měřena šířka všech letokruhů daného vzorku (přesnost 0,01 mm) pomocí binokulární lupy Olympus na měřicím stole LinTab. Data byla následně zapisována prostřednictvím softwaru TSAP-Win (verze 4.64, RINNTECH, Heidelberg, Německo).

## **4.3 Zpracování a analýza dat**

### **4.3.1 Využité statistické nástroje a metody (1.; 2.; 5.; 6.; 7. publikace.)**

Data předložené disertační práce byla statisticky testována pomocí celé řady různých metod a testů, stejně jako při použití několika statistických softwarů. Využívány byly následující softwary: R (R CORE TEAM 2019); CANOCO 5 (ŠMILAUER & LEPŠ 2014); PAST (verze 4.5, 2008) (KNIBBE 2007); STATISTICA 13 (verze 13.4.0, 2018). Statistické testování proběhlo prostřednictvím využití parametrických (analýza rozptylu – ANOVA, Tukeyho HSD) i neparametrických testů (Kruskal-Wallisova test, Shapiro-Wilkův test), včetně využití regresní a korelační analýzy. Pro stanovení výsledků byla také použita vícerozměrná PCA analýza. Přičemž platí, že pro všechny využité statistické testy byla zvolena hladina významnosti  $\alpha=5\%$ . Detailní rozbor použitých statistických metod je uveden v konkrétních publikacích, v kapitole 5. Výsledky.

#### 4.3.2 Vyhodnocení dendrochronologických a klimatologických dat (1.; 6.; 7. publikace)

Dendrochronologická analýza byla shodně pro práce VACEK et al. (2019), BRABEC et al. (2023) a BRICHTA et al. (2024) prováděna shodně v programu R (verze 4.3.1) (R CORE TEAM 2019). Jednotlivé metodologie zmíněných publikací byly shodné také v dalších krocích dendrochronologické a klimatologické analýzy. Před samotnou letokruhovou analýzou byla každá série letokruhů předem detrendována (zbavena věkového trendu) dle instrukcí balíčku 'dplr' (BUNN 2018). Následně byl k analýze dendrochronologických křivek v kombinaci s měsíčními klimatickými daty využit program DendroClim 2002. Detrendovaná data o šířce letokruhu borovice lesní byla použita k výpočtu EPS (vyjádřený populační signál). EPS je hodnotou vyjadřující spolehlivost chronologie. Limitem pro použití dat k porovnání vůči klimatickým údajům byla signifikantní hranice EPS, tak aby  $EPS > 0.85$  (BUNN et al. 2018). Dále byly stanoveny ukazatele odstupe signálu od šumu dané chronologie (SNR). Ukazatel SNR představuje sílu signálu dané chronologie (populace). Následně byly stanoveny také mezisériové korelace (R-bar) a autokorelace prvního řádu (Ar1) (WIGLEY et al. 1984; FRITTS 2001). Všechny zmíněné ukazatele (EPS, SNR, R-bar, Ar1) byly vypočítány dle pokynů balíčku „dplr“ (BUNN et al. 2018). Zásadním prvkem dendrochronologické analýzy bylo odhalení záporných let růstu stromu (letokruh, který nedosahuje 40 % průměrného přírůstku ze čtyř předchozích let) (SCHWEINGRUBER 1996; DESPLANQUE et al. 1999). Výskyt takového záporného roku byl statisticky prokázán v případě, že k tak výraznému snížení přírůstu stromu došlo alespoň u 20 % stromů daného porostu/zájmové plochy. K vyjádření vztahu mezi klimatickými charakteristikami (průměrné měsíční/roční teploty a úhrn srážek v jednotlivých měsících/letech) a radiálním růstem byl použit software DendroClim (verze 1.0, 2002) (BIONDI, WAIKUL 2004). Vícerozměrná analýza hlavních komponent (PCA) byla provedena v software CANOCO 5 (ŠMILAUER & LEPŠ 2014), a to za účelem analýzy vztahu mezi produkcí dřeva, strukturou a diverzitou porostů, ale zároveň také radiálním růstem stromů (index šířky letokruhu) a klimatickými faktory (teplota a srážky) ve vztahu ke změně klimatu.

Data letokruhových sérií BRICHTA et al. (2024) byla rozdělena na 2 období (období 1: 1951–1985, období 2: 1986–2016), aby bylo možné vyhodnotit reakci borovice lesní na měnící se klimatické podmínky. Toto časové období bylo definováno jako průsečík dostupnosti dat z důvodu dostupnosti srovnatelných předpovědí srážek a teplot. V případě šetření BRABEC et al. (2023) byly porovnávány letokruhové série borovice lesní a smrku ztepilého, a to jak v rámci

rozdílu mezi jednotlivými druhy, tak s ohledem na vliv smíšení porostu. Dendrochronologická analýza CUKOR et al. (2023) hodnotila rozdíl růstu letokruhů mezi zdravými a silně poškozenými jedinci borovice lesní.

#### **4.3.3 Hodnocení struktury a produkce porostu (1.; 6.; 7. publikace)**

Parametry základní struktury, diverzity a produkční charakteristiky stromového patra daných porostů byly hodnoceny pomocí růstového simulátoru SIBYLA Triquetra 10 (FABRIKA & ĎURSKÝ 2005), pro výpočet charakteristik horizontálního rozložení jedinců na zájmové ploše byl pro 1. publikaci využit také program PointPro 2.1 (ZAHRADNÍK & PUS, ČZU). Součástí hodnocení parametrů struktury bylo využití několika indexů. Pro vyhodnocení prostorového rozmístění stromů byl vypočítán agregační index (CLARK & EVANS 1954). Strukturní diverzita byla hodnocena Arten-profil indexem (PRETZSCH 2006), dále byl stanoven index tloušťkové (TMd) a výškové diferenciacce (TMh) (FÜLDNER 1995), korunová diferenciacce, vertikální diverzita a celková diverzita porostu (JAEHNE & DOHRENBUSCH 1997). Zásoba porostů borovice lesní (resp. smrku ztepilého) byla vypočtena podle tabulek PETRÁŠ (1991). Biomasa stromů byla vypočtena z jejich nadzemní (stonek, větve a jehlice) a podzemní biomasy (kořeny a pahýly). Nadzemní biomasa borovice byla odvozena z modelu SEIFERT (2006). Biomasa kořenů borovice byla vypočtena pomocí modelu z DREXHAGE & COLIN (2006). Obsah uhlíku (C) v borovicích byl vypočítán na základě metodologie studie BUBLINEC (1994), pomocí obsahu jednotlivých prvků v 10 mg kg<sup>-1</sup> sušiny. Byl také stanoven index relativní hustoty porostu (SDI) (REINEKE 1933) a projekce korunového zápoje (CROOKSTON & STAGE 1933). Všechny indexy použité v předložené disertační práci jsou zobrazeny také níže v **Tab. 2**.



**Tab. 2** Přehled indexů popisujících diverzitu porostů a jejich společná interpretace

| Kritérium              | Index                  | Zkratka     | Citace                      | Hodnocení                                                                                           |
|------------------------|------------------------|-------------|-----------------------------|-----------------------------------------------------------------------------------------------------|
| Horizontální struktura | Agregační index        | $R$ (C&Ei)  | CLARK & EVANS, (1954)       | Střední hodnota $R = 1$ ; agregované $R < 1$ ; pravidelné $R > 1$                                   |
| Vertikální struktura   | Arten-profil index     | $A$ (Pri)   | PRETZSCH (2006)             | rozsah 0-1; vyrovnaná vertikální struktura $A < 0.3$ ; výběrná struktura $A > 0.9$                  |
|                        | Vertikální diverzita   | $S$ (J&Di)  | JAEHNE & DOHRENBUSCH (1997) | nízká $S < 0.3$ , střední $S = 0.3-0.5$ , vysoká $S = 0.5-0.7$ , velmi vysoká diverzita $S > 0.7$   |
| Strukturní diferenciac | Tloušťková diferenciac | $TM_d$ (Fi) | FÜLDNER (1995)              | rozsah 0-1; nízká $TM < 0.3$ ; velmi vysoká diferenciac $TM > 0.7$                                  |
|                        | Výšková diferenciac    | $TM_h$ (Fi) |                             |                                                                                                     |
|                        | Korunová diferenciac   | $K$ (J&Di)  | JAEHNE & DOHRENBUSCH (1997) | nízká $K < 1.0$ , střední $K = 1.0-1.5$ , vysoká $K = 1.5-2.0$ , velmi vysoká diferenciac $K > 2.0$ |
| Celková diverzita      | Diverzita porostu      | $B$ (J&Di)  | JAEHNE & DOHRENBUSCH (1997) | homogenní struktura $B < 4$ , heterogenní struktura $B = 6-8$ , velmi heterogenní struktura $B > 9$ |

## 5. VÝSLEDKY

Výsledky jsou zde popsány ve formě několika tematických bloků, sdružujících celkem 7 odborných publikací. Vedle originálního znění článku je vždy v úvodu dané kapitoly uveden jeho stručný souhrn v českém jazyce.

### **5.1 Ekologický a ekonomický význam porostů borovice lesní, možnosti jejich adaptace na měnící se podmínky prostředí**

#### **5.1.1 4. publikace: *Význam a potenciál borovice lesní (Pinus sylvestris L.) ve 21. století***

**Originální název:** Importance and potential of Scots pine (L.) in 21 century

**Časopis:** Central European Forestry Journal (časopis zařazen do databáze SCOPUS a WOS, aktuálně IF – 1.4, 2. Q)

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#### **Souhrn:**

Cílem předložené studie byl detailní popis borovice lesní, a to s ohledem na její morfologii, ekologii a geografické rozšíření. Dalším cílem práce bylo popsat způsoby hospodaření s daným taxonem, rovněž ve světle adaptace na klimatické změny.

Publikace vznikla jako syntéza více než 200 různých studií z let 1952–2022, dostupných v databázích SCOPUS a WOS, či v tištěné knižní podobě. Rešeršní práce byla dále rozdělena do několika tematických bloků, v nichž byly následně popsány jednotlivé atributy borovice lesní.

Předložená studie poskytla souhrnný náhled na borovici lesní z hlediska biologických projevů a potřeb, ale také s ohledem na způsoby jejího pěstování a možnosti adaptace na klimatickou změnu. Rešeršní studie dále upozornila na fakt, že jednou z nejvíce postižených

dřevin klimatickými výkyvy je dnes v podmínkách střední Evropy právě borovice lesní, a to i navzdory tomu, že byla dlouhou dobu považována za téměř rezistentní vůči působení sucha. Borovice lesní se však rovněž vyznačuje nejen významnou genetickou variabilitou svých populací, ale také širokou ekologickou plasticitou. Široká valence biotopu této dřeviny odůvodňuje její ekonomický význam. Ve světle klimatických změn se však postupy pěstování borovice lesní také mění z tradičního holosečného hospodaření na přírodě bližší varianty obnovy těchto porostů. S ohledem na změnu klimatu se také pomalu mění areál rozšíření této dřeviny. Do budoucna je však klíčové zaměřit se na detailní a komplexní studium proveniencí borovice lesní v kontextu lesnictví v podmínkách klimatické změny. S ohledem na rostoucí potřeby společnosti je však nezbytné zabývat se i neprodukčními funkcemi borových porostů, které jsou díky charakteru tohoto taxonu na některých stanovištích takřka nezastupitelné.

## Importance and potential of Scots pine (*Pinus sylvestris* L.) in 21<sup>st</sup> century

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### Abstract

We are currently witnessing significant global changes in climate conditions. We cannot change the natural conditions, but with regard to sustainable landscape management, we can increase our knowledge of tree species and adapt forest management to them. Surprisingly, one of the most affected tree species in Central Europe today is Scots pine (*Pinus sylvestris* L.). The following literature review summarizes over 200 studies from 1952–2022 regarding Scots pine across its entire range while addressing various topics in the ecology and management of this taxon. It is a tree species with a large natural range, nearly covering the entire Eurasian area. In the Czech Republic, it is the second most important tree species in terms of industrial wood production. Scots pine is characterized not only by a significant genetic variability of its populations but also by its wide ecological plasticity. Typically, it grows on sandy soils, poor habitats, and stony scree—but also in peat bogs. The wide habitat valence justifies the economic significance of this species, both in terms of its high production potential (mean annual increment of up to 10.8 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>) but also its wide range of use. However, in the light of climate variations, the practices of Scots pine silviculture are also gradually transforming from the traditional reforestation by clear-cutting to a more natural system—shelterwood felling. In view of climate change, its range of distribution is changing, as with other species, but Scots pine remains a very resistant tree species, depending on the habitat.

**Key words:** silviculture; ecology; threats; wood production; European forests

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### 1. Introduction

Scots pine (*Pinus sylvestris* L.) is one of the most ecologically and economically important tree species in Europe (Krakau et al. 2013; O'Reilly-Wapstra et al. 2014; Sevik & Topacoglu 2015; Wójkiewicz et al. 2016). It is a taxon with a wide climatic and edaphic range (Kelly & Connolly 2000; Úradníček et al. 2001; Durrant et al. 2016; Vacek et al. 2016). Due to the fact that it does not tolerate considerable shading—among other things—it tends to be displaced from rich habitats by competing tree species (Průša 2001; Mikeska et al. 2008). However, extensive forest stands of Scots pine are typically found on dry and poor sandy soils, in areas with sandstone subsoils, and on extreme sites with limited soil depth, as well as on peatland (Kučera 1999; Vacek et al. 2017, 2021a; Șofitea et al. 2020).

In Europe, Scots pine occurs at elevations ranging from lowlands to mountains, and in different ecotypes

(Bílek et al. 2016; Hebda et al. 2017; Łabiszak et al. 2017; Vacek et al. 2022). Different ecotypes of Scots pine are based on populations that have survived from the Late Glacial period in the form of isolated refugia in Central Europe (Jankovská & Pokorný 2008; Mikeska et al. 2008; Tóth et al. 2017). Presumably, some of the refugia of autochthonous Scots pine may have provided the basis for the developmental lineages of the different ecotypes occurring in Central Europe. The oldest pine forests in the Czech Republic grow on rock outcrops, in rock formations, on serpentinite, and mineral-poor and dry sands. Regarding development, pine forests on peat bogs are younger (Pliva 1971; Mikeska et al. 2008; Poleno et al. 2009). The natural habitat for Scots pine ranged from the oligotrophic to herb-rich pine forests (Øyen et al. 2006; Mikeska et al. 2008; Vacek et al. 2022).

Historically, the oldest acrofossil evidence and sedimentary records showed the presence of Scots pine

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between 70,000 BP in Carpathian Basin to 20,000 BP in Hungarian plain (Magyari 2011; Tóth et al. 2017). However, current autochthonous pine and pine-oak forests were formed by the evolution of vegetation mostly during the 10,000 years of the Postglacial era. Scots pine and silver birch (*Betula pendula* Roth.) were the most abundant tree taxa in the Early Postglacial. The present occurrence of Scots pine can, therefore, be considered as a remnant of its original range and a relic of the Early Postglacial phases, especially on such ecotopes that were not suitable for other tree species due to edaphic reasons (Staszkiwicz 1968; Jankovská & Pokorný 2008). Although these azonal communities have gradually evolved since the Preboreal, they have only been preserved in extreme habitats with limited competition from other tree species. The first stands of pine and birch appeared in Central Europe in the older Holocene—in the Preboreal (Husová 1999; Mikeska et al. 2008). In the Boreal period, light pine forests with an admixture of common hazel (*Corylus avellana* L.) appeared in the mentioned area. In the Atlantic period of climatic optimum, mixed deciduous forests predominated by oak (*Quercus* spp.) developed, but at the same time, in colder and more humid areas, Norway spruce (*Picea abies* [L.] Karst.) also spread rapidly. Approximately 6200 to 4000 years ago, European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) began to spread, especially in the mid-elevations (Bolte et al. 2007; Mikeska et al. 2008). All of these tree species then gradually forced pine into habitats where they could not compete with it in terms of autoecology. In the Epi-atlantic, a natural zonation of climax vegetation was established, and pine thus retreated to habitats of an extreme and azonal nature (poor sands, rocks, peat bogs). In extreme habitats that were unapproachable to human intervention, communities similar to the current ones eventually formed (Husová 1999; Poleno et al. 2007; Mikeska et al. 2008).

However, what is the role of Scots pine in the 21<sup>st</sup> century, when climate change is altering the range of forest tree species and their growth optimum (Falk & Hempelmann 2013; Dyderski et al. 2018; Klopčič et al. 2022)? This literature review, based on over 200 studies, aims to assess the dynamics, opportunities, and risks of Scots pine from the perspective of climate change in European forests with a focus on the Czech Republic. Specifically, the review focuses on (i) morphological description of the species, (ii) taxonomic classification, (iii) natural range and distribution, (iv) habitat and ecological preferences, (v) silviculture and production, (vi) importance and uses, and (vii) threats and diseases, all within the context of climate change.

## 2. Morphological description of the species

Scots pine is characterized by a highly variable habitus, growing to an average height of 26 m but reaching up to 40 m in optimum conditions, while in extreme habitats, we find dwarf pines or shrubby pines (Mikeska et al. 2008; Praciak et al. 2013). Scots pine can live up to 300 years (exceptionally, up to 750 years) (Pokorný 1963; Koblížek 2006; Musil & Hamerník 2007; Wallenius et al. 2010). Many different ecotypes of Scots pine can be distinguished, including different characteristics of tree size or crown shape (Svoboda 1953; Businský 1999).

The root system of the pine is massive, consisting, in most cases, of a taproot with richly branched lateral roots (Poleno et al. 2009). Pine roots are very plastic with respect to habitat conditions, but they also react to, for example, the tilting of the tree (Čermák et al. 2008). It is the significant plasticity and resistance of the pine root system that makes the pine a valuable stabilizing tree in some habitats (Kacálek et al. 2017). In the northern and



Fig. 1. Habitus of the tree, branch, needle, cone, and seed of Scots pine (*Pinus sylvestris* L.).



northeastern parts of the European range, the Scots pine crown is slender with fine branching, whereas arched to umbrella-shaped crowns and thick branches are typical for pines in Central and Southern Europe. The trunk of the tree is most often straight, but on extreme sites, it is often crooked and twisted (Pokorný 1963; Koblížek 2006; Musil & Hamerník 2007; Praciak et al. 2013). At the base of the trunk, the pine is covered with a thick, cracked, grey-brown bark. In the upper parts of the tree, the bark turns orange or rusty red, and it peels off in scaly patches (Úradníček et al. 2001; Musil & Hamerník 2007). Scots pine has greenish-brown and glabrous annuals, and older twigs tend to be grey-brown (Fig. 1). The needles of Scots pine are stiff and pointed, with a slight longitudinal twist, 1–8 cm long, up to 2 mm wide, dark green or bluish grey-green in color, and generally growing in pairs on brachyblasts, with a life span of 2–3 years. The buds at the ends of the annuals are elongated-ovate, pointed, without resin, or weakly resinous, and covered with rusty-colored, membranous scales (Pokorný 1963; Úradníček et al. 2001; Koblížek 2006; Praciak et al. 2013; Krakau et al. 2013).

Scots pine is a monoecious tree species; male and female strobili differ in Scots pine. While male strobili are ovoid, 4–8 mm long, usually yellow (rarely red), female strobili are 5–6 mm long, usually pink. The male strobili grow at the base of the elongating shoot instead of needles, most often in the lower part of the crown, while the female strobili grow at the end of the last year's branches in the upper part of the crown (Úradníček et al. 2001; Musil & Hamerník 2007). The cones are usually single or in groups of 2–3, pedunculate or nearly sessile, ovoid-conical, rounded at the base, often asymmetrical, nonglossy, grey-brown,  $2.5\text{--}7 \times 2\text{--}3.5$  cm. Seed scale shields are rhombic, more developed on the illuminated side, and flat to pyramidal. The cone umbo is small, flat, or short-tipped, light brown, shiny, and without black edging. Seeds are ovoid, 3–4 mm long, whitish, brown or grey to black, with 3–4 times longer brownish to reddish brown wings, and pincer-like at the base (Koblížek 2006; Musil & Hamerník 2007; Praciak et al. 2013).

Pines flower in spring and early summer (April–June) for the first time, at around the age of 15 years. In a closed stand, they do not flower until the age of 30–40 (Úradníček et al. 2001; Musil & Hamerník 2007). The flower primordia of male and female strobili are formed in the summer of the previous year (Johnson & More 2006). More than 12 months after pollination, the germinating pollen resumes its growth and fertilizes the egg. Shortly after, in June (year 2), the entire formation rapidly enlarges and reaches the final cone size in the summer. In early October, the cones ripen. In favorable weather, a small number of seeds emerge during October–December, but the main period of cone opening is in the spring of year 3. The empty cones fall off during the summer of the 3<sup>rd</sup> year after pollination. A seed year in pine occurs on average every 3<sup>rd</sup> to 6<sup>th</sup> year (Pokorný 1963; Úradníček et

al. 2001; Koblížek 2006; Musil & Hamerník 2007; Poleno et al. 2009; Praciak et al. 2013). The number of pure seeds in 1 kg is 74–245 thousand. The average weight of 1,000 seeds is 6.3 g. Well-stored seeds can remain viable for up to 15 years (Musil & Hamerník 2007; Poleno et al. 2009).

### 3. Taxonomic classification

According to Řepka & Koblížek (2007), Scots pine (*Pinus sylvestris* L.) is classified into the following taxonomic categories: Domain: *Eukarya*; Kingdom: *Plantae*; Subkingdom: *Viridiplantinae*; Developmental lineage: *Streptophytae*; Developmental branch: *Cormophytae*; Developmental stage: *Gymnospermae*; Division: *Pino-phyta*; Family: *Pinaceae*; Genus: *Pinus*; Species: *Pinus sylvestris*, however, splits into numerous lower taxa. Given the vast Eurasian range of Scots pine, an intraspecific taxonomic system is very difficult to set (Kindel 1995). Nevertheless, Scots pine can be divided into the following four varieties: *Pinus sylvestris* var. *syvestris*; *Pinus sylvestris* var. *lapponica* Hartm., 1849; *Pinus sylvestris* var. *mongolica* Litvinov, 1905, and *Pinus sylvestris* var. *hamata* Steven, 1838.

The variation within the taxon *Pinus sylvestris* is indeed extremely large. Over 140 subspecies, varieties, and forms have been studied. In terms of distribution, approximately 22 geographical varieties are categorized. Svoboda (1953) divides the species into three basic climatypes: northern, steppe, and mountain pine. Łabiszak et al. (2017) demonstrated the distinct character of following groups: mountain, lowland and coastal populations. Businský (1999) divides Scots pine into varieties according to geography and morphological features: *P. sylvestris* var. *syvestris* (including the former var. *sibirica*), *lapponica*, *hamata*, and *mongolica*. In addition to the subdivisions mentioned above, a number of forms have also been detailed in terms of their economic utility—according to the quality of the timber and habitus of the pine (in the Czech Republic, “Třeboň pine” or “Týniště pine”). Other forms are based on the variability of needles, bark, and cones (according to the shape of the shield, f. *plana*, f. *gibba*, f. *reflexa*, and according to size, f. *macrocarpa*, f. *microcarpa*). In nature, Scots pine forms spontaneous hybrids with *Pinus mugo*, *Pinus uncinata* and *Pinus uncinata* subsp. *uliginosa* (Businský 1999; Musil & Hamerník 2007; Poleno et al. 2009; Sobierajska et al. 2020).

### 4. Natural range and distribution

Scots pine has the largest range of all described pines. The distribution range of Scots pine mainly includes the temperate and cooler belts of much of Europe and Asia (this



area is otherwise known as Eurasia), and in Europe from northern Portugal and Scotland to the Far East between 37°–70.5° N latitude. The center of its range is Siberia. In Europe, Scots pine is rarely found in the Mediterranean. The northernmost occurrence in Europe is in Lapland (Fig. 2; Úradníček et al. 2001; Musil & Hamerník 2007; Durrant et al. 2016).

*Pinus sylvestris* var. *sylvestris* (Syn. *P. sylvestris* subsp. *sibirica* [Ledebour] Businsky) is typical in Europe (north to ca. 62° N), its range extending to the Far East (to ca. 142° E). *Pinus sylvestris* var. *lapponica* (Hartman) occurs from northern Scandinavia to NW Siberia, approximately north of 62° N latitude. *Pinus sylvestris* var. *hamata* (Steven) (Syn. *Pinus armena* K. Koch; *P. kochiana* Klotzsch ex K. Koch) is found in the Caucasus region and Transcaucasia south to S Armenia, W Azerbaijan, and Turkey. *Pinus sylvestris* var. *mongolica* (Litvinov) (Syn. *Pinus sylvestris* subsp. *kulundensis* Sukaczew) occurs in Northern Mongolia, NE China, and SE Siberia (Businský 2008).

The Scots pine does not occur naturally on the steppes of southern Ukraine, southern Russia, or in the oceanic lowlands of the British Isles and Denmark. Outside its core Eurasian range, however, Scots pine has also secondarily spread in North America, where it is mainly cultivated on plantations (Poleno 1990; Úradníček et al. 2001; Musil & Hamerník 2007; Schildler et al. 2010).

In Central Europe, deciduous forests are the dominant communities (Leuschner & Ellenberg 2017), while pine forests are restricted to poor habitats (Ahti & Oksanen 1990). In the Czech Republic, Germany, and Poland, native Scots pine currently grows only in islands in extreme relict habitats (Heinken 2007; Chytrý 2013). In Poland, Scots pine is the main economic tree species, covering 58% of the forest area (DGLP 2021). In the Czech Republic, Scots pine occupies 16.1% of the forest area (MZe 2021), with its lowest frequency in the Polabí sandy terraces of poor loamy sands, on the serpentinite rocks of the Slavkov Forest and the Bohemian-Moravian Highlands, and on the boulder slopes and scree of the

Šumava Mountains (the highest occurrence of Scots pine in the Czech Republic is on the scree near Plešné Lake at an altitude of 1,070 m). Scots pine is also found on sands and peaty soils, the edges of peat bogs in the Třeboň region, on sandstone cliffs and rock formations in Northern and Northeastern Bohemia, and on rocky and steep slopes of river valleys. It also grows on the outcrops of the Dražanská vrchovina (Dražany Uplands), on the scree of the Hrubý Jeseník Mountains, and on limestone rocks of Southern Moravia. Typically, however, Scots pine is also cultivated in many places outside of its natural range, which is only 3.4% out of the current total of 16.1% in the forests of the Czech Republic (Musil & Hamerník 2007; Mikeska et al. 2008; Poleno et al. 2009; MZe 2021).

The frequency of pine forests in the Czech Republic is shown in Fig. 3. In natural forest areas (NFA), the highest abundance of pines can be seen in the North Bohemian Sandstone Plateau and the Bohemian Paradise – NFA 18 (36.6%), in the South Bohemian Basin – NFA 15 (19.7%), the West Bohemian Upland – NFA 6 (17.14%), and the Lusatian Sandstone Upland – NFA 19 (11.78%). In other natural forest areas of the Czech Republic, the representation of pine is significantly lower.

Pine forests have a unique position in the development and zonation of vegetation. Regarding the coexistence of Scots pine with other tree species, its colonization of most of the landscape in the Postglacial times was a critical moment. Later, Scots pine spread to soils and habitats where other tree species could not adapt (Horsák & Chytrý 2010). Naturally preserved, Scots pine retained its dominant position only on sandstone bedrock and sandy sediments in general, primarily on Cretaceous sandstones and sands, serpentinite, and, in extreme conditions, also on limestone, peats, and on rocky outcrops of various acid rocks (relict). In particular, fires were more frequent on dry sands, an essential natural factor in the colonization of the landscape by pine. The majority of the sites mentioned above are located approximately in the climate range of forest vegetation zones 3–4, i.e.,



Fig. 2. Scots pine distribution in Eurasia; ■ native range; ■ introduced and naturalised (synanthropic) area (Caudullo et al. 2017).

300–700 m above sea level. Contrarily, some inversion sites with spruce, or higher, precipitation-deficient areas on sediments can be assessed as climatically “higher” (Mikeska et al. 2008; Vacek et al. 2022).

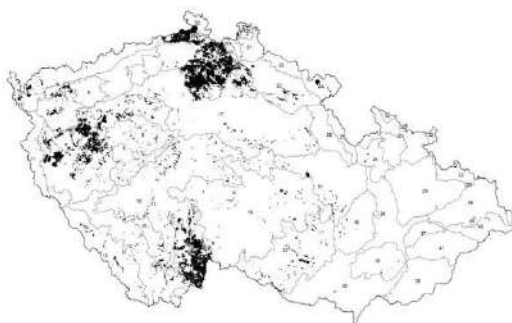


Fig. 3. Representation of natural pine forests (forest altitudinal zone 0 – pine forest) in the Czech Republic (GIS-ÚHÚL Brandyš n. L., modified according to Mikeska et al. 2008).

## 5. Habitat and ecological preferences

Scots pine is a typical pioneer tree species (Linder et al. 1997; Durrant et al. 2016). It is a distinctly light-demanding tree species that barely tolerates shading but can adapt to a wide range of conditions in terms of soil and climate requirements (Pliva 1971; Mikeska et al. 2008; Poleno et al. 2009). The soils of pine forests on which pine appears are predominantly sandy to gravelly, permeable, arid, and acidic types of arenaceous podzol or arenaceous cambisol. On extreme geological substrates, it is lithic leptosol, podzolic ranker, and arenaceous regosol. On sites influenced by water, it is mainly stagnic cambisol, stagnic podzol, and gleyic podzol. On transitional peatlands with groundwater, fibric histosol, occasionally gleyic histosol and gleyic podzol occur. Only in sporadically occurring basophilous pine forests do we find haplic rendzic leptosol, cambic r. l., detrital r. l., or modal leptosol (Vacek et al. 2022).

Scots pine adapts to a wide climatic range, with a vegetation period of 90–200 days, an annual precipitation of 200–1,780 mm, and a common mean annual temperature of 5–9 °C. It tolerates frost and the occasional lack of precipitation, as well as poor soil of extreme – rocky, sandy, and peaty – habitats, where it is unrivaled in monocultures (Richardson 1998; Mikeska et al. 2008). Its deep root system and thick bark make Scots pine resistant to fires and able to regenerate on the mineral soil of burn sites. Its ecological optimum is far from the physiological one. Scots pine does not occur naturally in nutrient-rich habitats but is often cultivated there locally (Úradníček et al. 2001; Musil & Hamerník 2007; Koblížek 2006; Poleno et al. 2009).

Three groups of relict pine forests can be characterized in Central Europe:

- Continental Eastern European to South Siberian pine forests growing in contact with sub-xerophilous oak forests on gravelly terraces of larger rivers (class *Pulsatillo-Pinetea sylvestris*, alliance *Pulsatillo-Pinion*), their marginal distribution in the Alps is linked to the rain shadow of the inner Alpine valleys.
- Basophilous (flowery) pines on marl, limestone, and dolomite rocks and on serpentinites (class *Erico-Pinetea*, alliance *Erico-Pinion*), whose distribution extends from the Balkans through the limestone foothills of the Alps to Central Europe.
- Oligotrophic pine forests belonging to the boreal coniferous forests (class *Vaccinio-Piceetea*), within which they form a group including primary relict pine forests of siliceous rocks, sandy soils, and peat bog pine forests (alliance *Dicrano-Pinion*). While the first two groups are only marginally found in the Czech Republic, oligotrophic pine forests are relatively common in the Czech Republic (Kučera 1999; Mikeska et al. 2008).

Within the European Forest Types (EFT) (Marchetti 2007), all pine forests are designated by the units: 1.2 Pine and pine-birch boreal forest; 2.2 Sub-boreal Scots pine forest; 2.4 Sub-boreal black pine forest; 2.5 Mixed pine-birch forest (Scots pine); 2.6 Mixed pine-oak forest (pine-oak forest – Scots pine and common oak); 3.1 Subalpine larch-Swiss pine-dwarf pine forest (European larch, Swiss pine, and dwarf pine); 3.3 Alpine pine forest (Scots pine and black pine); 10.1 Thermophilous Mediterranean pine forest; 10.2 Black pine forest of the Mediterranean and Anatolia region; 10.3 Canary Island pine forest; 10.4 Scots pine forest of the Mediterranean and Anatolia region; 10.5 Mountain Mediterranean pine forest; 11.1 Coniferous and mixed peat forest; 11.3 Birch peat forest.

In Europe, in the poorest habitats, Scots pine forms monocultures. In slightly richer habitats or boggy and upland areas, it grows together with oaks (*Quercus petraea*, *Quercus robur*), European beech (*Fagus sylvatica*), silver birch (*Betula pendula*), Norway spruce (*Picea abies*), European larch (*Larix decidua*), silver fir (*Abies alba*), and other pines (primarily *Pinus nigra*, *Pinus uncinata*) (Mason & Alia 2000; Kelly & Connolly 2000; Úradníček et al. 2001; Musil & Hamerník 2007).

In the Czech Republic, Scots pine is found mainly in alliance associations *Erico-Pinion*, *Dicrano-Pinion*, and *Vaccinion*, in rock alliance associations *Alysso-Festucion pallentis*, *Asplenion serpentini*, *Seslerio-Festucion glaucae* (Chytrý et al. 2001). The accompanying tree species of lowland and wooded-hill variants of Scots pine are mainly *Quercus petraea*, *Tilia cordata*, *Carpinus betulus*, *Acer campestre*, and *Betula pendula*. Within the upland variant, Scots pine grows with *Picea abies*, *Abies alba*, *Fagus sylvatica*, *Larix decidua*, and *Betula pendula* (Mikeska et al. 2008; Poleno et al. 2009).

In terms of habitat, three basic variants of Scots pine can be identified:

- Lowland – pioneer: grows primarily on sandy soils, in monocultures with a minimal or no admixture of other tree species, regenerates on mineral soil in clearings and open areas. It grows quickly when young, bears fruit early and does not tolerate competition from other species;
- Wooded-hill – pioneer: grows mainly on sandy soils, rocky ecotopes, and peat soils, mostly in monocultures with little admixture of other tree species, regenerates on mineral soil in clear-cuts and open areas;
- Montane – climax: grows mostly in mixtures (with spruce, fir, and beech) at higher altitudes (700–1,000 m) but also descends to lower altitudes. It regenerates under the canopy and does not tolerate open habitats (clear-cuts). It sometimes dominates its competitors in height and has a large wood production (Mikeska et al. 2008; Poleno et al. 2009).

Under conditions of global climate change, Scots pine is increasing its range at higher altitudes and in northern locations, and, conversely, declining due to dieback in the southern part of its European range (Benito Garzón et al. 2008; Reich & Oleksyn 2008; Matias & Jump 2012).

## 6. Silviculture and production

In silviculture and production, forest structure is a crucial element, quantified primarily by stand density, canopy, vertical canopy structure, stand basal area, horizontal tree distribution, heterogeneity in the spatial arrangement of trees, the volume of deadwood, or categorization of individuals into tree classes (Pommeroy 2002; Puettmann et al. 2008; Silver et al. 2013). Stand structure noticeably influences most variables in the forest ecosystem, but in the context of forest regeneration and the silviculture of different tree species, it also influences the existence and establishment of natural regeneration, especially for shade-tolerant tree species (Jaworski 2000; Poleno et al. 2009). The aforementioned forest structure issue is crucial for Scots pine silviculture, which requires a high intensity of light for its successful growth in juvenile stages (Vacek et al. 2016); Oleskog & Sahlén (2000) reported about 30% of free space light. Numerous studies, e.g., Urbietta et al. (2011), Carnicer et al. (2014), and Martín-Alcón et al. (2015) show that as light availability decreases, the quantity and quality of natural regeneration decreases in pine stands with higher canopy density. In contrast, Pardos (2017), Schönfelder et al. (2017, 2018), and Lundqvist et al. (2019) report that lower light intensity compared to clear-cuts can lead to higher quality in natural regeneration in Scots pine. Brichta et al. (2020) also mention in their study that partial cover of the parent stand in turn may have a positive effect on the abundance of natural regeneration. Of course, light con-

ditions of natural regeneration can also be impaired by competition from herbaceous vegetation (Lucas-Borja et al. 2011; Mirschel et al. 2011; Prévosto et al. 2012; Hyppönen et al. 2013). If we proceed with the clear-cut, the use of seed trees is recommended, not only as part of supporting natural regeneration, but also to increase the radial growth of the remaining mature individuals (Brichta et al. 2019).

However, one of the most important factors for the success of natural regeneration of Scots pine is the weather conditions, i.e., temperature and precipitation in close relation to light during seed germination and initial seedling growth (Oleskog & Sahlén 2000b; Puhlick et al. 2012). Pine seeds are able to germinate at 6 °C, however, the optimum temperature is up to 20–25 °C with a seed moisture content of approximately 35% (Oleskog & Sahlén 2000). Another factor limiting seed germination can be a thick layer of surface humus, which prevents roots from penetrating the mineral soil layer (Hille & den Ouden 2004; Oleskog & Sahlén 2000a). Scots pine germinates optimally only on mineral soil, and therefore soil scarification is usually used in pine regeneration (Örlander et al. 1996; Remeš et al. 2015; Aleksandrowicz-Trzcńska et al. 2017; Saurasunet et al. 2018; Ilintsev et al. 2021). The germination of Scots pine seeds can also be supported artificially - by cold stratification (Houšková et al. 2021) or low-intensive coherent seed irradiation (Novikov et al. 2021). Some sources describe wood ash fertilization for improving the soil environment (Remeš et al. 2016; Petrovský et al. 2018). On dry sites, soil preparation also improves the water supply in the root zone because transpiring herbaceous vegetation is removed by these interventions (Fleming et al. 1994). Moreover, bare mineral soil has less variability in water availability than a humus layer (Oleskog & Sahlén 2000a). Soil preparation increases soil temperature (Nilsson & Örlander 1999; Bedford & Sutton 2000), accelerates humus decomposition, and increases mineral availability (Lunmark-Thelin & Johansson 1997; Nilsson, Örlander 1999; Nilsson et al. 2006), thus increasing the probability and rate of seedling growth (Karlsson & Örlander 2000; Mattsson & Bergsten 2003; Nordborg & Nilsson 2003) and reducing soil bulk density (MacKenzie et al. 2005).

Scots pine produces seeds annually, but moderate to heavy seed years typically occur every 3–6 years (Poleno et al. 2009; Przybylski et al. 2021). Pine seeds are dispersed primarily by wind, with effective seed dispersal occurring up to a maximum distance of 30–100 m from the parent tree (Farmer 1997; Adams 1992; Mikeska et al. 2008). However, sufficient soil moisture is required for seed germination and seedling establishment (MacKenzie et al. 2005). Seedling numbers in Scots pine stands have been reported to range from 0.5–2.3 pcs m<sup>-2</sup> (Nilsson et al. 2002; Karlsson & Nilsson 2005; Erefur et al. 2008; Marcos et al. 2007; Marozas et al. 2007; Beghin et al. 2010; Mirschel et al. 2011; Jäärats et al. 2012) with a maximum of 10 pcs m<sup>-2</sup> (Mirschel et al. 2011). Under-



story recovery typically starts at 10% relative radiation (Ulbrichová et al. 2018).

In the first years of seedling development, due to unfavorable abiotic and biotic factors, seedlings undergo considerable self-thinning. (Aleksandrowicz-Trzcińska et al. 2018). The ecotone effect also influences seedling growth, with a higher density of seedlings tending to occur at the edge of the stand compared to the interior (Vacek et al. 2017b). A risk for newly established pine stands can be, for example, grubbing by the pine weevil (*Hylobius abietis* L.) (Kovalchuk et al. 2015; Lundborg et al. 2016) or the formation of proleptic shoots, which, however, are removed in sparse cultures and growths by cutting or simple selection regeneration individuals (Slodičák & Novák 2007). Although the natural regeneration of Scots pine is generally dominated by small-scale clear-cuts and border cutting areas, shelterwood methods of natural regeneration are increasingly used in the context of global climate change (Bílek et al. 2016; Brichta et al. 2020). Shelterwood natural regeneration methods are now common, for example, in Scandinavia (Hyppönen et al. 2013; Lundqvist et al. 2019), Germany (Spathelf et al. 2015; Drössler et al. 2017), Poland (Bielak et al. 2014; Aleksandrowicz-Trzcińska et al. 2017, 2018), and also in some areas in the Czech Republic (Bílek et al. 2017, 2018; Brichta et al. 2020). This way of natural regeneration is more favorable with respect to the nature of microhabitats under advancing global climate change (Montero et al. 2001; Matías & Jump 2012; Aleksandrowicz-Trzcińska et al. 2014, 2017, 2018; Vítámvás et al. 2019; Brichta et al. 2020).

Thus, within the diverse conditions of pine management, natural regeneration can be achieved by a clear-cutting system with different sizes and orientations of cutting. These also include border cutting, patch cutting, large- and small-area shelterwood cutting, transitioning to group or individual selections (Poleno et al. 2009). Within ecologically oriented management, two basic silvicultural approaches can be implemented. The first is to aim for the areal initiation of natural regeneration under the parent stand; the second is small-area group regeneration with a transition to selection principles. In both cases, the start of regeneration must be preceded by the determination of a suitable time frame for the silvicultural development of the stand. Determining the minimum stand age for the start of regeneration depends on the specific conditions of the stand, taking into account its age, quality, expected production, the presence of spontaneous regeneration, habitat conditions, and the nature of the vegetation. The parent stand must not incur production losses by premature harvesting, especially of the best quality trees (Poleno et al. 2009; Bílek et al. 2016, 2018; Vacek et al. 2022).

The first cleaning and thinning from above are carried out by negative selection, i.e., by removing dominant, malformed, or damaged individuals at the crown and dominant level. Thinning from below is not desirable,

but self-thinning is a natural process in pine stands. On the other hand, higher numbers of individuals  $\text{ha}^{-1}$  are recommended in the age of up to about 10 years of growth in order to achieve a better morphological quality of the trees (Houšková & Maurer 2014). Even before reaching a height of 5 m, however, it is necessary to thin out the stand in order to increase its stability against the action of wet snow (Novák et al. 2013). The height to diameter ratio is then most affected by thinning in young pine stands, as the stand's age increases, the growth response to thinning also decreases (Dušek et al. 2011). But it is also possible to maximize production or reduce silviculture costs by thinning the stand (Sloup & Lehnerová 2016). In most habitats, the healthy development of pine stands requires an understory of shade or semi-shade tree species. These are usually self-seeding trees, which are intentionally left in the stand during the process of pine stand tending. Later, at about 50 years of age, a combined thinning is carried out to encourage the development of as many quality individuals as possible depending on the production capacity of the site (about 150–300 target trees). In addition to trees suppressing the crowns of the target trees, we remove damaged, diseased, and severely malformed trees through stand-improving tending operations. We encourage the presence of soil-improving and admixed tree species to increase the species diversity of pine stands (Poleno et al. 2009; Vacek et al. 2022). Considering the mostly very poor pine habitats, it is recommended to leave the residual biomass after thinning in the stand (Novák et al. 2017), and this despite the consideration of soil pH deterioration (Peřina & Vintrová 1958).

Pine stands are generally restored by border cutting and small- and large-area clear-cutting, but shelterwood cutting is becoming a common practice too. However, the yield from pine stands during regeneration cannot be precisely totaled. Considering the significant genetic variability of Scots pine (Kosínska et al. 2007; Busínský 2008) but also its wide ecological amplitude and habitat range (Pliva 1971; Mikeska et al. 2008; Poleno et al. 2009), the production indices of Scots pine stands vary widely (Table 1). Depending on the parameters mentioned above, as well as on the type and intensity of management, we can conclude that Scots pine stand stock volumes in Europe are indeed quite variable. While the studies by Starr et al. (2005) or Makkonen & Helmisaari (1999) describe roughly 140-year-old pine stands with a stand volume up to  $100 \text{ m}^3 \text{ ha}^{-1}$  from the lowlands of Finland, the work by Gallo et al. (2020) reports stand volume up to  $441 \text{ m}^3 \text{ ha}^{-1}$  in montane pine stands in Spain. Substantially high stocks are in the lowland areas in Poland, where the stock of Scots pine stands over 130 years reaches up to  $740 \text{ m}^3 \text{ ha}^{-1}$  (Bielak et al. 2014). Particularly in Poland, Scots pine is a common tree species and is even considered the primary economic tree species (DGLP 2021). The highest mean annual increment (MAI) in the Czech Republic is reported by Vacek et al. (2021a) –  $10.87 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ . The high production

**Table 1.** Overview of available publications related to Scots pine (*Pinus sylvestris* L.) production parameters.

| Study                      | Country        | Altitude<br>[m a.s.l.] | Age<br>[year] | DBH<br>[cm] | Height<br>[m] | Basal area<br>[m <sup>2</sup> ha <sup>-1</sup> ] | Volume<br>[m <sup>3</sup> ha <sup>-1</sup> ] | MAI<br>[m <sup>3</sup> ha <sup>-1</sup> yr <sup>-1</sup> ] | Density<br>[trees ha <sup>-1</sup> ] |
|----------------------------|----------------|------------------------|---------------|-------------|---------------|--------------------------------------------------|----------------------------------------------|------------------------------------------------------------|--------------------------------------|
| Vacek et al. (2016)        | Czech Republic | 245–267                | 70–130        | 26–31       | 21–24         | 33–40                                            | 320–434                                      | 3.08–5.50                                                  | 508–660                              |
| Bilek et al. (2016)        | Czech Republic | 270–600                | 129–191       | 25–42       | 14–25         | 25–47                                            | 177–456                                      | 0.93–2.39                                                  | 476–1,072                            |
| Bilek et al. (2016)        | Poland         | 470                    | 191           | 42          | 19            | 19                                               | 159                                          | 0.83                                                       | 200                                  |
| Vacek et al. (2017)        | Czech Republic | 575–630                | 123–130       | 24–36       | 15–23         | 12–33                                            | 91–267                                       | 0.70–2.05                                                  | 172–512                              |
| Gallo et al. (2020)        | Czech Republic | 600–590                | 142–145       | 25–27       | 16–19         | 27–28                                            | 240–245                                      | 1.69                                                       | 488–552                              |
| Gallo et al. (2020)        | Spain          | 1710                   | 140           | 21–46       | 9–20          | 33–46                                            | 231–441                                      | 1.65–3.15                                                  | 276–996                              |
| Vacek et al. (2021a)       | Czech Republic | 250–495                | 40–46         | 15–22       | 17–23         | 38–47                                            | 318–500                                      | 7.07–10.87                                                 | 1,355–2,822                          |
| Vacek et al. (2021c)       | Czech Republic | 430                    | 48            | 19          | 17.5          | 45                                               | 364                                          | 7.92                                                       | 1,700                                |
| Starr et al. (2005)        | Finland        | 35–280                 | 35–200        | 12–38       | 10–25         | 11–29                                            | 48–315                                       | 1.37–1.58                                                  | 374–2,660                            |
| Montero et al. (2001)      | Spain          | 1700                   | 41–66         | 17–31       | 15–21         | 49                                               | 364–478                                      | 7.24–8.89                                                  | 635–2,104                            |
| Makonen & Helmsaari (1999) | Finland        | 144                    | 37            | 8           | 8             | 15                                               | 70                                           | 1.89                                                       | 2,660                                |
| Van Oijen et al. (2013)    | Austria        | 495                    | 60            | 27          | 18            | —                                                | —                                            | —                                                          | 790                                  |
| Van Oijen et al. (2013)    | Belgium        | 50                     | 66            | 28          | 20            | —                                                | —                                            | —                                                          | 380                                  |
| Van Oijen et al. (2013)    | Estonia        | 40                     | 73            | 26          | 26            | 32                                               | 374                                          | 5.12                                                       | —                                    |
| Vanninen & Mäkelä (2000)   | Finland        | 150                    | 16–71         | 4–23        | 4–22          | 19–23                                            | —                                            | —                                                          | 595–18,727                           |
| Pretzsch et al. (2015)     | Europe         | 20–1,290               | 69            | 28          | 22            | 41                                               | 413                                          | 11.3                                                       | 970                                  |
| Bidak et al. (2014)        | Poland         | 79–151                 | 124–132       | 39–47       | 30–36         | —                                                | 319–740                                      | 2.57–5.60                                                  | 177–324                              |
| del Río et al. (2008)      | Spain          | 1,200–1,750            | 41–50         | 14–20       | 7–13          | 35–49                                            | 159–321                                      | 3.89–6.42                                                  | 1,415–5,495                          |
| Beker et al. (2021)        | Poland         | 100                    | 25–95         | 13–31       | 15–28         | 27–40                                            | 256–396                                      | 4.17–10.24                                                 | 402–2,590                            |

Notes: DBH – diameter at breast height, MAI – mean annual increment

potential is also illustrated by the work of Vacek et al. (2021c), where Scots pine achieved the highest increment and stand volume of all 12 coniferous tree species studied on reclamation dumps following coal mining. On the other hand, Lovynska et al. (2019) describes that, for example, in the conditions of the Northern Steppe of Ukraine, Scots pine shows a lower volume production than the acacia tree (*Robinia pseudoacacia* L.).

## 7. Importance and use

Scots pine is one of the most important economic tree species not only in Central Europe but also in Eurasia (Praciak et al. 2013; Sevik & Topacoglu 2015; Lundqvist et al. 2019). Due to its dynamic ecological plasticity and ability to occupy hostile habitats, pine plays a crucial role in both forestry and, subsequently, in the timber industry. Pinewood has an orange-brown heartwood and a broader yellow sapwood. The annual rings are very distinctive, hence, there is a considerable difference in density and hardness between spring and summer wood (Pokorný 1963). The density of the wood substance reaches values between 0.412 and 0.541 g cm<sup>-3</sup> (Table 2). It should be added, however, that wood density values for pine have a wide variance; this is due not only to the transition between spring and summer woods but also to the extreme genetic variability of the species. The differences in wood density of Scots pine individuals may also be due to its silviculture and different degrees of stand canopy. While individuals with a well-lit crown exhibit lower wood density, trees sheltered by the parent stand possess higher wood density (Schönfelder et al. 2017). Compared

to the wood density of spruce, which is approximately 0.410 g cm<sup>-3</sup> (Repola 2006; Saranpää 2003), the wood density of pine can be up to 0.100 g cm<sup>-3</sup> higher.

The distinctly differentiated summer rings on pine wood are also complemented by its natural luster; in the case of pine, it is due to its high resin content, which makes the wood very durable, especially in water and humid environments, which is why it is mainly used for water structures, pumps, mine timber, sleepers, masts, poles, and fencing; the wood might require impregnation for increased durability (Milner 1992; Reynolds & Bates 2009; Farjon 2010; McLean 2019). Pine timber is also used to manufacture of timber structures, particularly composite timber, in timber construction, lumber, furniture, and paneling (Davies et al. 2002; Kuklík 2005; Hairstans 2018), as it has similar durability to larch timber (British Standards Institute 1994). Lower-quality wood is used for fiber and fuel (McLean 2019).

The distillation of the wood was used to prepare tar and, subsequently, black pitch, lamp oil, and essential oils. Burning the heavily resinous wood of stumps and roots yielded soot, which was utilized to make domestic ink and printing ink. By scarring the trunks or peeling the bark, the resin was extracted (Neumann 2015). In many countries, including the Czech Republic, the traditional methods of slitting and debarking live Scots pine trees and capturing the resin that oozes out (so-called pitch-ing) are no longer allowed. Resin was widely used for sealing and impregnating ships but also as a medicine or natural glue. It is also a source of natural turpentine, which, together with its distillation residue (colophony), is the starting material for several other products such as varnishes, paint thinning solvents, insecticides, rubbers, printing inks, etc. (Schreiner et al. 2018; Praciak et al.

**Table 2.** Overview of the available publications related to Scots pine (*Pinus sylvestris* L.) wood density.

| Study                         | Schönfelder et al.<br>(2017) | Wagenführ<br>(2002) | Novák<br>(1970) | Lexa et al.<br>(1952) | Repola<br>(2006) | Saranpää<br>(2003) | Auty et al.<br>(2014) | Fundova et al.<br>(2018) |
|-------------------------------|------------------------------|---------------------|-----------------|-----------------------|------------------|--------------------|-----------------------|--------------------------|
| Density [g cm <sup>-3</sup> ] | 0.488–0.541                  | 0.510               | 0.470           | 0.510                 | 0.412            | 0.460              | 0.423                 | 0.430                    |

2013; Gardner 2013; McLean 2019). Black pine wood impregnated with resin was also used to make torches in the Balkans (Musil & Hamerník 2007).

Pine essential oil contains a variety of terpenes. These substances contained in essential oils and other products are known for their pleasant aroma, which helps to calm the nervous system, relieve stress, release anxiety and tension, and refresh the mind. They are also a component of perfumes, aromatic soaps, massage oils, air fresheners, and similar products (Podlech 2002; Schreiner et al. 2018). Pine bark contains antioxidants, flavonoids, tannins, and a variety of vitamins and has been consumed by, for example, Native Americans for centuries. It was used as a remedy against scurvy by Russian Cossacks in Siberia and the Far East (Aleksandrov 1969). Traditionally, the inner bark of Scots pine was used by the Sámi as a source of food and packaging material in Lapland until the late 19<sup>th</sup> century (Zackrisson et al. 2000). Commercially, the shredded bark of Scots pine is considered a valuable by-product in horticulture (Moore 2011). The bark is also used to make insulation products for buildings (Pásztor & Ronyecz 2013).

In the past, the maceration of fresh needles was used to prepare a tissue called *sosnovka* or “forest wool”, which was used to make carpets, blankets, or as a stuffing material. The essential oil contained in pine has medicinal uses. Extracted from the resin, needles, and buds, it has antiseptic properties. It is used to relieve respiratory and lung diseases, and rheumatic disorders, as a sedative, and also in aromatherapy (Ciesla 1998).

In extreme habitats, Scots pine acts as an anti-erosion and reclamation tree species (Vacek et al. 2021a, c). However, besides the soil-protective function, pine also performs other ecological functions; several fungal species form mycorrhizal, parasitic, and saproparasitic associations with pine trees. About 120 fungal species have been observed in ecto- and endotrophic symbiosis with pine roots. For consumption, boletes, Bay boletes, brittlegills, and blewits are collected (Klán 1989; Carlile & Watkinson eds. 1994; Gryndler et al. 2004; Antl 2014). The collection of bilberries and cranberries, as well as other forest fruits are also abundant in pine forests (Šišák 2006).

## 8. Threats and diseases

Currently, the most discussed threat to Scots pine stands is undoubtedly drought and the associated decline in groundwater levels due to climate change (Vacek et al. 2016; Gao et al. 2017; Buras et al. 2018). It is climatic stress periods that negatively affect the photosynthetic activity of Scots pine (Flexas & Medrano 2002; Reddy et al. 2004). Increasing air temperatures, along with low water availability, are responsible for a range of other diseases, as well as reduced tree defense capac-

ity against insect pests (Allet et al. 2015; Haberstroh et al. 2022). Although Scots pine is considered a resistant tree species to precipitation deficiency, pine stands across Europe have still been enormously damaged by recurrent drought in recent years (Merlin et al. 2015; Vacek et al. 2017; Buras et al. 2018), when, in particular, precipitation is the main factor affecting pine growth processes (Vacek et al. 2019). It can be argued that Scots pine is now one of the most threatened tree species in Europe (Gao et al. 2017; Buras et al. 2018; Etzold et al. 2019). As a rule, stands with a homogeneous structure or stands with an unsuitable pine ecotype are the most affected (Bottero & Vacchiano 2015; van Halder et al. 2019). Paradoxically, the cause of pine dieback may be its taproot system (Lokvenec et al. 1985), which does not adapt to absorb available precipitation from surface soil layers as the water table recedes. Not only is the amount of available water gradually becoming depleted, but its nutrients (S, P) are currently lacking in pine stands as well (Prietz et al. 2020). The solution to the decline appears to be the silviculture of structurally differentiated pine stands (del Río Gaztelurrutia et al. 2017; Brichta et al. 2020), as well as mixed pine stands (Czerepko 2004; Pretzsch et al. 2013; Zeller et al. 2017; Vacek et al. 2019). In some places, pine is already spontaneously shifting its range into communities of deciduous trees (Haberstroh et al. 2022). However, it is still a relatively resistant tree species to the effects of climate change, considering the habitat. For example, Vacek et al. (2021c) reported that Scots pine was the most resistant of the 12 tree species studied concerning the effects of climate extremes in the Czech Republic.

Common insect pests of pine trees include the nun moth, pine tree lappet, common pine shoot beetle, bark beetles (genus *Dendroctonus*), or tortrix. Trees can also be attacked by plant parasites and semi-parasites such as mistletoe and related species (Mutlu et al. 2016). Trees weakened by pests or by various abiotic stresses (e.g., drought) are susceptible to damage by fungal pathogens, the spread of which may be enhanced in monospecific commercial plantations. For example, *Sphaeropsis sapinea* and *Cenangium ferruginosum* cause withering and dieback of pine trees, while *Mycosphaerella pini*, *Lophodermium seditiosum*, and related species cause needle cast. Various species of rust and cenangium are also damaging. *Cronartium asclepiadeum* infests primarily Scots pine. Pine twisting rust (*Melampsora pinitorqua*) is a dioecious rust that causes typical twisting of shoots, especially in Scots pine (Fjellborg 2009). *Naemacyclus* needle cast, which causes browning and needle dieback, is caused by the fungus *Cyclaneusma minus*. Among the wood-destroying fungi are fire sponge, *Onnia triquetra*, crisped sparassis, honey fungus, or velvet-top fungus (Businský & Velebil 2011; Pešková & Čížková 2015). The sawfly species *Diprion pini* and *Neodiprion sertifer* can cause severe defoliation, making the tree susceptible to attack by other pests (Virtanen et al. 1996; Langström



et al. 2001). Scots pine is also attacked by *Ips acuminatus*, *Pityogenes chalcographus*, *Tomicus piniperda*, *Tomicus minor*, *Phaenops cyanea*, and *Ips typographus*, which can also be a vector of various fungal pathogens, such as *Armillaria ostoyae* (Kirschner et al. 2001; Jankowiak & Hilszczański 2011; Giordano et al. 2013; de Rigo et al. 2016). The most important pest of pine seedlings cannot be neglected, namely the pine weevil (*Hylobius abietis* L.) (Modlinger 2015; Kovalchuk et al. 2015; Lundborg et al. 2016). New seedlings and individuals of natural regeneration can also be attacked by *Armillaria mellea* (Nárovcová 2010). For these reasons, fungal pathogens and not only bark insects in pine stands need to be given increased attention, and remediation measures should be implemented quickly in case of their occurrence (Zahradník & Zahraníková 2014).

Dieback of pine seedlings and saplings is also caused by biotic factors, especially fungi of the genera *Fusarium* and *Alternaria* (Petersson & Örlander 2003; Hódar & Zamora 2004; Dobbettin et al. 2007; Wermelinger et al. 2008; Nowakowska & Oszak 2008; Rigling et al. 2010; Zweifel et al. 2012; Mutlu et al. 2016), and abiotic factors, primarily drought (Oleksyn et al. 1994; Prus-Głowacki & Godził 1995; Baquedano & Castillo 2006; Sudachkova et al. 2009). The seeds of pine trees can be eaten by birds (crossbills, woodpeckers), rodents (squirrels, voles, various mice), and, as a dietary supplement, by some carnivores (martens, minks, sable). Young pine needles are consumed by game, birds (capercaillies), and caterpillars of many insect species, which can cause considerable damage (Musil & Hamerník 2007). Cloven-hoofed game also inflicts damage on Scots pine by browsing and bark-stripping, yet it is a very resistant tree species compared to spruce or fir (Čukor et al. 2022).

## 9. Conclusion

Scots pine is a tree species resistant to many environmental factors; it is a fast-growing Eurasian pine that is one of the most economically significant coniferous tree species in the Czech Republic and Europe. In suitable habitats, it has a high production potential and can provide high-quality, easily workable timber for various construction purposes and furniture. This is of considerable importance in terms of carbon sequestration and adaptation to ongoing climate change. Scots pine, due to its pioneering strategy, is also an outstanding reclamation tree. Until recently, it was also considered to be a drought-tolerant species because of its deep taproot, although this is now proving to be a disadvantage due to the fact that the water table is dropping. Nevertheless, it is still a relatively resistant species to climatic extremes compared to other tree species. In the future, however, it is crucial to focus on a detailed and comprehensive study of European Scots pine provenances in the context of silviculture under climate change. Yet, in light of the

increasing needs of society, a study of the non-productive functions of pine stands is also essential.

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## **5.2 Vliv strukturujících pěstebních zásahů na úspěšnost přirozené obnovy borovice lesní**

### **5.2.1 2. publikace: *Je podrostitní hospodaření s borovicí lesní v podmínkách přirozených borových stanovišť za měnících se podmínek prostředí vhodnou alternativou k tradičnímu holosečnému hospodaření?***

**Originální název:** Does shelterwood regeneration on natural Scots pine sites under changing environmental conditions represent a viable alternative to traditional clear-cut management?

**Časopis:** Central European Forestry Journal (časopis zařazen do databáze SCOPUS a WOS, aktuálně IF – 1.4, Q2)

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#### **Souhrn:**

Cílem předložené studie bylo zhodnotit efekt holosečného a podrostitního hospodářství (zakmenění 0,4, 0,6 a 0,8) a přípravy půdy (fréza, kombinovaná fréza - řádkovač, shrnovač klesu) na přirozenou obnovu borovice lesní (*Pinus sylvestris* L.) v podmínkách přirozených borových stanovišť (severní Čechy).

Pro potřeby iniciace přirozené obnovy bylo na experimentální ploše MARIANA I provedeno několik různě silných zásahů v mateřském porostu, a to ve formě clonných sečí a zároveň holoseče jako varianty kontrolní představující obvyklý způsob obnovy borových porostů. Tři roky po zmíněných zásazích byly zaznamenány počty, výšky a šířky korun jedinců přirozené obnovy na transektech, které reprezentovaly všechny kombinace variant hustoty mateřského porostu a přípravy půdy. Byly zároveň instalovány semenospady pro stanovení počtu spadlých semen, od roku 2016 do roku 2018. Prostřednictvím vláhových čidel byl také měřen vodní potenciál půdy (Delmhorst Instrument Company) a pomocí teplotních čidel teplota půdy (čidlo Pt1000 A-class, EMS Brno).

Výsledky studie stanovily vyšší počty jedinců přirozené obnovy na plochách s přípravou půdy (fréza, kombinovaná lesní fréza, shrnovač klesu), ve srovnání s kontrolní variantou bez přípravy půdy. Nejvyšší hustota jedinců přirozené obnovy byla souhrnně pozorována na plochách s přípravou půdy



kombinovanou frézou. Inventarizace jedinců přirozené obnovy v různých variantách hustoty mateřského porostu potvrdila, že nejvyšší počty jedinců přirozené obnovy se vyskytují na ploše se zakmeněním mateřského porostu na úrovni 0,4 (kombinovaná fréza  $32\,402 \pm 34\,208$  ks/ha; fréza  $26\,832 \pm 24\,088$  ks/ha; shrnovač klesu  $24\,496 \pm 22\,913$  ks/ha). Absolutně nejvyšší počty přirozené obnovy byly zaznamenány při kombinaci zakmenění mateřského porostu 0,4 a přípravy půdy kombinovanou frézou:  $32\,402$  ks/ha. Na jednotlivých plochách byly měřeny také dimenze jedinců obnovy, kde nejvyšších hodnot v případě výšky rostliny a šířky korun, bylo průměrně dosaženo na holoseči. Další měření (množství semen v semenospadech, teplota a vlhkostní potenciál půdy) potvrdily, že s rostoucí hustotou mateřského porostu narůstá množství spadlých semen, zároveň jsou na variantách se zakmeněním 0,4; 0,6 a 0,8 také příznivější vláhové a teplotní poměry v půdě. Dospěli jsme k závěru, že obnova porostů borovice lesní v podmínkách přirozených borových stanovišť může být dobrou alternativou k tradičnímu holosečnému hospodaření. S ohledem na vysoké počty jedinců přirozené obnovy a příznivé vláhové a teplotní poměry v půdě, můžeme doporučit prvotní snížení zakmenění mateřského porostu na úroveň 0,4.

## Does shelterwood regeneration on natural Scots pine sites under changing environmental conditions represent a viable alternative to traditional clear-cut management?

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### Abstract

In the context of climate change, the crucial question is how silvicultural treatments should be modified, in order to reach favourable conditions for initiating natural regeneration of forest stands. The aim of the study was to evaluate the influence of clear-cutting, basal area reduction (0.4, 0.6 and 0.8) and soil preparation (milling cutter, forestry mulcher, brush rake and control variant without soil preparation) on the regeneration of Scots pine (*Pinus sylvestris* L.) in the conditions of natural pine sites (Northern Bohemia). Seedling numbers, heights and crown widths were recorded on transects representing all combinations of stand densities treatments and soil preparations variants three years after the silvicultural operations. Seed traps were installed to determine the numbers of seeds from 2016 to 2018. Soil water potential (Delmhorst Instrument Company) and soil temperature (sensor Pt1000 A–class sensors, EMS Brno) were measured. All variants of soil preparation had higher numbers of seedlings compared to control variant. When comparing stand densities, total numbers of seedlings were the highest in stand density 0.4 (cutter  $32,402 \pm 34,208$  S.D. ind.ha<sup>-1</sup>; mulcher  $26,832 \pm 24,088$  S.D. ind.ha<sup>-1</sup>; rake  $24,496 \pm 22,913$  S.D. ind.ha<sup>-1</sup>). This stand density was also beneficial with respect to seed numbers, seedling characteristics and soil moisture and temperature characteristics. We conclude that shelterwood regeneration on natural Scots pine sites is promising silvicultural approach and may become an important tool in mitigating negative effects of climate change in the future.

**Key words:** stand density, soil preparation, fructification, natural regeneration, soil moisture, soil temperature

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### 1. Introduction

Scots pine (*Pinus sylvestris* L.) is the main tree species in half of Europe's forests (Sharma et al. 2017; Lundqvist et al. 2019). Its natural occurrence is associated with dry and/or poor sites with limited competition of climax tree species (Linder 1997; Musil & Hamerník 2007; Vacek et al. 2010, 2019). Although pine is mainly considered resistant to limited water availability, pine stands all across Europe have been massively damaged by repeated drought events in recent years (Merlin et al. 2015; Vacek et al. 2016, 2017; Gao et al. 2017; Buras et al. 2018). Drought is probably the primary factor of damage that triggers the infestation with bark beetles and fungal diseases (Hódar & Zamora 2004; Dobbervin et al. 2007; Wermelinger et al. 2008) or mistletoe (*Viscum album* L.) (Rigling et al. 2010; Zweifel et al. 2012; Mutlu et al. 2016). Mature stands with homogenous structure and often of unsuitable ecotype are mostly affected (Bottero & Vacchiano 2015, van Halder et al. 2019).

Basic tool for increasing the adaptability of forest stands to changing environmental conditions is their spatial structuring (Schütz 2002; del Río Gaztelurrutia et al. 2017; Ameztegui et al. 2017) and species mixing (Czerepko 2004; Pretzsch et al. 2013; Zeller et al. 2017; Vacek et al. 2019b). It is expected that such stands have greater resistance to biotic and abiotic disturbances, thus these silvicultural approaches can also become an effective tool to mitigate climate change due to the increased carbon storage (Ercanli 2018).

However, on natural pine sites the option of species mixing is very limited and the main approach remains spatial structuring (Montero et al. 2001; Gaudio et al. 2011a; Kojola et al. 2012; Spathelf & Ammer 2015). Besides different thinning regimes in young stands that mostly create structural heterogeneity within one cohort of trees, in mature stands shelterwood regeneration creates temporal stand structures that rest on two partially overlapping tree generations. In addition to the common

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clear-cuts with or without retained seed-trees, different forms of shelterwood management in different parts of Scots pine natural range are in the scope of silvicultural research (Montero et al. 2001; Gaudio et al. 2011a; Kojola et al. 2012; Spathelf & Ammer 2015; Bilek et al. 2016; Tullus et al. 2018; Lundqvist et al. 2019). These alternative methods include uniform large-scale shelterwood as well as small-scale management approaches that result into multi-layered Scots pine stands.

Shelterwood regeneration is a common management practice in Scandinavian countries (Hyppönen et al. 2013; Lundqvist et al. 2019), Germany (Spathelf et al. 2015; Drössler et al. 2017), Poland (Bielak et al. 2014; Aleksandrowicz-Trzcińska et al. 2017), and also in some parts of the Czech Republic (Bilek et al. 2017; 2018). It is often stated that shelterwood regeneration is more favourable with respect to microsite characteristics (Montero et al. 2001; Matias & Jump 2012; Aleksandrowicz-Trzcińska et al. 2017; Vitámvás et al. 2019) and compared to clear-cut area, lower light intensity can lead to higher quality of pine regeneration (Pardos 2017; Schönfelder et al. 2017, 2018; Lundqvist et al. 2019). In the context of climate change, the crucial question is how temperature and moisture characteristics of the microsite can be improved with silvicultural approaches and which treatment is leading to the success of natural regeneration.

Although sporadic studies referring to ecological plasticity of pine suggest very strong competitiveness of pine regeneration (Picon-Cochard et al. 2006), it is distinctly more sensitive to root competition compared to shade tolerant species (Erefur et al. 2008) and pine seedlings usually do not succeed in dense herbal cover of blueberry (*Vaccinium myrtillus* L.) or heather (*Calluna vulgaris* [L.] Hull.) (Hyppönen et al. 2013). Thus, on natural pine sites it is not only necessary to decrease the stand density, but also to disturb the soil surface in order to promote natural regeneration (Varmola et al. 2004; Saursaunet & Matrisen 2018).

In natural conditions the competition of ground vegetation is often temporarily suppressed by fires (Eengelm et al. 1994; Corace 2009). In the absence of these natural processes that would stimulate pulses of natural regeneration, in managed stands soil preparation using different techniques is necessary (Ackzell 1993; Barbeito et al. 2011; Aleksandrowicz-Trzcińska et al. 2014; Saursaunet & Matrisen 2018). They should lead to higher density of natural regeneration and higher vitality of individual seedlings (Karlsson & Örlander 2000). However, also some risks must be considered. High soil temperature without shading of herb cover (Bedford & Sutton 2000; Oleskog & Sahlen 2000), loss of nutrients from exposed soil (Piirainen et al. 2007) or freezing of root systems of regeneration individuals (Chantal et al. 2003) are among the most important. Ploughing and soil

milling are the most common techniques of forest soil preparation. However, as these techniques are expensive, it is also common to use disc harrow or brush rakes instead (Posmetyev et al. 2016).

The aim of the study was to evaluate the influence of clear-cutting, basal area reduction and soil preparation on the regeneration of Scots pine in the conditions of natural pine sites three years after the silvicultural operations. To assess the feasibility of shelterwood regeneration in given conditions we hypothesized that:

- 1) Number of seeds after seed fall increases with stand density and is the lowest in clear-cut.
- 2) Seedling numbers are influenced by parent stand density and soil preparation positively.
- 3) Seedling parameters (height and crown width) are influenced by parent stand density negatively, while the effect of soil preparation is positive.
- 4) Higher soil moisture and lower temperature are associated with higher stand density, the least favourable treatment with respect to moisture and temperature is the clear-cut.

## 2. Material and methods

### 2.1. Study site and experimental design

The area of interest is located near to the municipality Doksy. It is characterized by a large area of natural Scots pine sites. Forest stands in study are managed by Military Forests and Farms of the Czech Republic, state enterprise. The entire study locality (N 50°33.77548', E 14°43.49143') is in a flat terrain, at 300 m a.s.l. Parent rock is sandstone, with dominant soil type Arenic Podzol (Soil map 2020). Mean annual air temperature is 7.3 °C and average maximum temperature is 31.5 °C. Mean annual precipitation is 635 mm (Tolasz 2007).

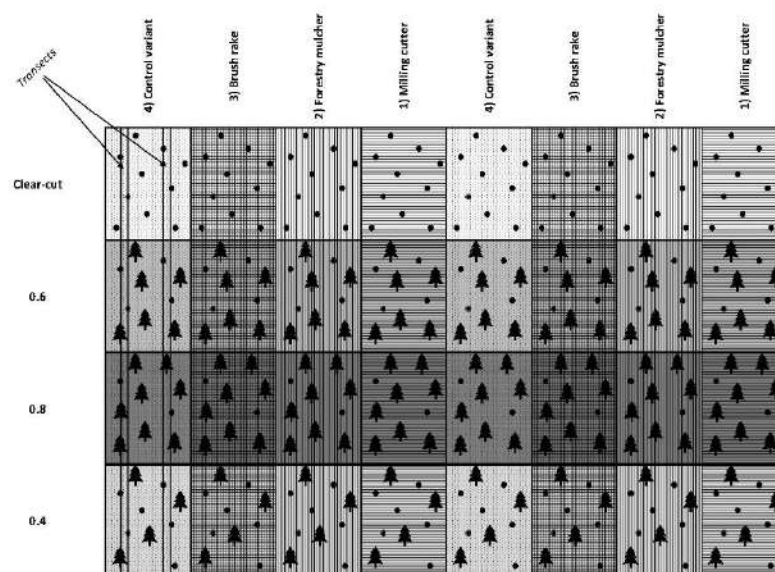
The experimental plots were established for monitoring of natural regeneration success of Scots pine in different stand densities and soil preparation techniques. For this purpose, the parent stand was divided into 4 sections of different harvest intensities (treatments) with resulting four stand densities: clear-cut, 0.4, 0.6 and 0.8 (Table 1). Harvests were conducted in February 2016. Methodology of parent stand inventory is given in Abdollahnejad et al. (2019).

Each of the 4 treatments had a rectangle design of approx. 60 × 250 m. In each of these treatments of stand density, four variants (31.25 m × 60 m) of soil preparation techniques were performed in two repetitions. Variants of soil preparations were following: 1) Milling cutter KSH 700 with treatment in stripes of approx. 1 m distance (Milling cutter); 2) Forestry mulcher Meri Crusher 1.8 ST with full-area character of preparation (Forestry mulcher); 3) Brush rake SH 01 (Brush rake); 4) Control variant without soil preparation (Control) (Fig. 1).

**Table 1.** Summary stand characteristics for individual treatments of basal area reduction derived from field inventory.

| Stand density after harvest | Stand density before harvest | Mean G±S.D.<br>[m <sup>2</sup> ha <sup>-1</sup> ] | Mean V±S.D.<br>[m <sup>3</sup> ha <sup>-1</sup> ] | Mean N±S.D.<br>[ind.ha <sup>-1</sup> ] | Harvest intensity [%] |
|-----------------------------|------------------------------|---------------------------------------------------|---------------------------------------------------|----------------------------------------|-----------------------|
| Clear-cut                   | 0.8                          | 0.0 ± 0.0                                         | 0.0 ± 0.0                                         | 0 ± 0                                  | 100                   |
| 0.4                         | 0.8                          | 10.8 ± 4.0                                        | 123.5 ± 58.5                                      | 121 ± 34                               | 55                    |
| 0.6                         | 0.8                          | 17.8 ± 4.2                                        | 195.2 ± 34.1                                      | 234 ± 59                               | 30                    |
| 0.8                         | 0.9                          | 24.4 ± 3.3                                        | 258.3 ± 47.3                                      | 323 ± 45                               | 20                    |

Note: Stand density – calculated as share of measured stand volume per hectare (before and after the harvest) and the theoretical full stand volume per hectare derived from yield tables; G – basal area (m<sup>2</sup> ha<sup>-1</sup>) after harvest; G – basal area standard deviation (m<sup>2</sup> ha<sup>-1</sup>); V – wood volume (m<sup>3</sup> ha<sup>-1</sup>) after harvest; V – wood volume after harvest standard deviation (m<sup>3</sup> ha<sup>-1</sup>); N (ind.ha<sup>-1</sup>) – number of trees per 1 ha after harvest; Harvest intensity (%) – calculated as percentage of harvest on the measured stand volume before harvest; S.D. – standard deviation. Wood volumes were calculated according to Petráš & Pajůk (1991).

**Fig. 1.** Design of the experimental plot: different treatments of stand density (clear-cut; 0.4; 0.6; 0.8) and different variants of soil preparation: 1) Milling cutter; 2) Forestry mulcher; 3) Brush rake; 4) Control).

## 2.2. Data collection

For each treatments of stand density and variant of soil preparation technique, two transects covering  $2 \times 60 \text{ m}^2$  each were established ( $n = 64$ ) (Fig. 1). The transect was divided into squares of  $2 \times 2 \text{ m}^2$ , for each square plot all seedlings according to species were registered. For seedlings higher than 10 cm, total height and crown width were recorded (accuracy 1 cm). All measurements were done in autumn 2018 three years after the harvest operation and soil preparation treatment.

After the harvest in 2016 in each treatment of stand density 7 seed traps (size  $1 \times 1 \text{ m}^2$ ) were placed ( $n = 28$ ). Traps were installed permanently from 2016 to 2018, each trap was placed at a boundary of two variants of soil preparations always in the middle section of each stand density treatment. Seeds were counted always in November after the end of the vegetation period.

Water potential measurement was carried out using absorption GB-2 gypsum sensor blocks (Delmhorst Instrument Company) connected to data loggers Micro-Log SP3 (EMS Brno). Temperature sensor (Pt1000 A-class sensors, EMS Brno) was connected to the data-

logger. The gypsum sensor blocks were placed 7–9 cm under the soil surface; for one stand density always 4 sensors were installed in the central part of the treatment to avoid the effect of stand edges ( $n = 16$ ). The soil temperature (depth 7–9 cm) was measured together with the soil water potential in the same position. Interval of measurements was 1 hour.

## 2.3. Data analysis

The differences in seed numbers between selected stand densities in 2016–2018, as well as the differences in regeneration density, seedling height and crown width between selected soil preparation techniques and stand densities were analysed by Kruskal-Wallis test, as normality of data (tested by Shapiro-Wilk normality test) was violated in all cases. Subsequent multiple comparisons were conducted according to Siegel and Castellan (1988). The soil water potential and soil temperature were plotted separately for each stand density treatments, in case of soil temperature, one-week moving average curves are also shown.



All computations were performed using R (R Core Team 2019), plots were made by “ggplot2” (Wickham, 2016) and “ggpubr” (Kassambara, 2020) packages. All statistical tests were conducted at significance level  $\alpha = 0.05$ .

### 3. Results

#### 3.1. Seed numbers

The highest mean seed numbers per 1 m<sup>2</sup> were registered for stand density 0.8 ( $58 \pm 16$  S.D. in 2016, respectively  $37 \pm 11$  S.D. in 2017, respectively  $41 \pm 7$  S.D. in 2018). Conversely, during the whole observation period the lowest mean seed numbers per 1 m<sup>2</sup> were consistently registered on clear-cut area (stand density 0.0) ( $4 \pm 3$  S.D. in 2016, respectively  $4 \pm 1$  S.D. in 2017, respectively:  $2 \pm 2$  S.D. in 2018). Stand densities 0.4 and 0.6 were intermediate in seed numbers, nevertheless statistically significant differences were registered mostly for stand density 0.0 (Fig. 2).

#### 3.2. Regeneration density

Regeneration density for different stand densities and soil preparation techniques 3 years after the harvest is displayed in Fig. 3C. Generally, all variants of soil preparation had higher numbers of seedlings compared to control variant. Total numbers of seedlings were the highest in stand density 0.4. The highest mean total number of seedlings was registered for following combinations of stand density treatment and soil preparation variant: 0.4

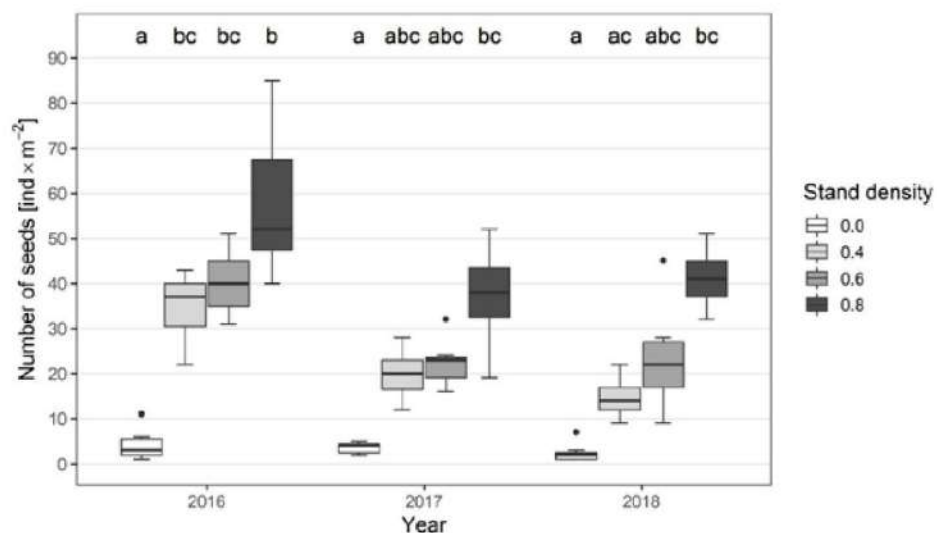
– cutter ( $32,402 \pm 34,208$  S.D. ind. ha<sup>-1</sup>); 0.4 – mulcher ( $26,832 \pm 24,088$  S.D. ind. ha<sup>-1</sup>) and 0.4 – rake ( $24,496 \pm 22,913$  S.D. ind. ha<sup>-1</sup>). Conversely, the lowest mean total number of seedlings was registered for the variant 0.5 – control ( $5,972 \pm 12,897$  S.D. ind. ha<sup>-1</sup>) and 0.7 – control ( $5,960 \pm 9,047$  S.D. ind. ha<sup>-1</sup>).

Number of seedlings lower than 10 cm (Fig. 3A) had the highest density in combinations 0.4 – cutter ( $19,824 \pm 29,340$  S.D. ind. ha<sup>-1</sup>) followed by 0.8 – cutter ( $15,090 \pm 18,847$  S.D. ind. ha<sup>-1</sup>) and 0.4 – rake ( $13,876 \pm 17,230$  S.D. ind. ha<sup>-1</sup>). The worst with respect to seedlings numbers were the control variants in combination with stand density treatment 0.6 ( $4,037 \pm 10,097$  S.D.) and 0.8 ( $3,990 \pm 7,240$  S.D. ind. ha<sup>-1</sup>).

Number of seedlings higher than 10 cm (Fig. 3B) was the highest in combination clear-cut – cutter ( $14,979 \pm 16,654$  S.D. ind. ha<sup>-1</sup>) and 0.4 – cutter ( $12,578 \pm 14,894$  S.D. ind. ha<sup>-1</sup>). The control variant showed the lowest values in all cases of stand density treatments (0.0:  $4,980 \pm 4,656$  S.D. ind. ha<sup>-1</sup>; 0.3:  $3,780 \pm 5,036$  S.D. ind. ha<sup>-1</sup>; 0.6:  $1,898 \pm 3,758$  S.D. ind. ha<sup>-1</sup>; 0.8:  $1,970 \pm 3,682$  S.D. ind. ha<sup>-1</sup>).

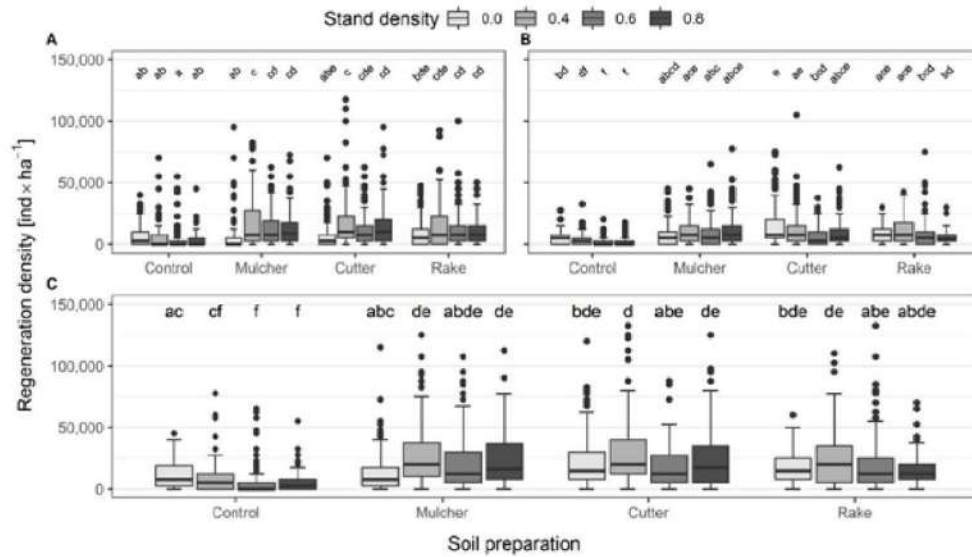
#### 3.3. Seedlings characteristics

Superior mean heights of seedlings were observed in stand density treatments clear-cut (stand density 0.0) (20.0 – 21.9 cm) and 0.4 (18.0 – 21.3 cm). In all soil preparation variants, there were significantly lower seedlings in stand densities 0.6 (13.7 – 18.3 cm) and 0.8 (13.5 – 15.7 cm) (Fig. 4). The stand density treatment 0.0 was also superior with respect to crown widths of individual seedlings (19.6 – 21.3 cm) (Fig. 5).

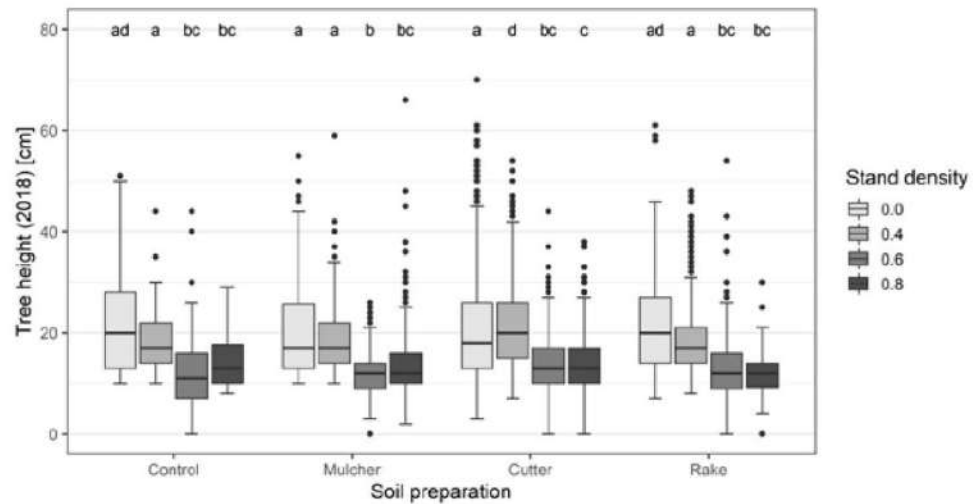


**Fig. 2.** Number of seeds per 1 m<sup>2</sup> in different stand densities. Different letters indicate significant differences among groups ( $p < 0.05$ ); values represent medians of number of seeds, upper and lower quartile.

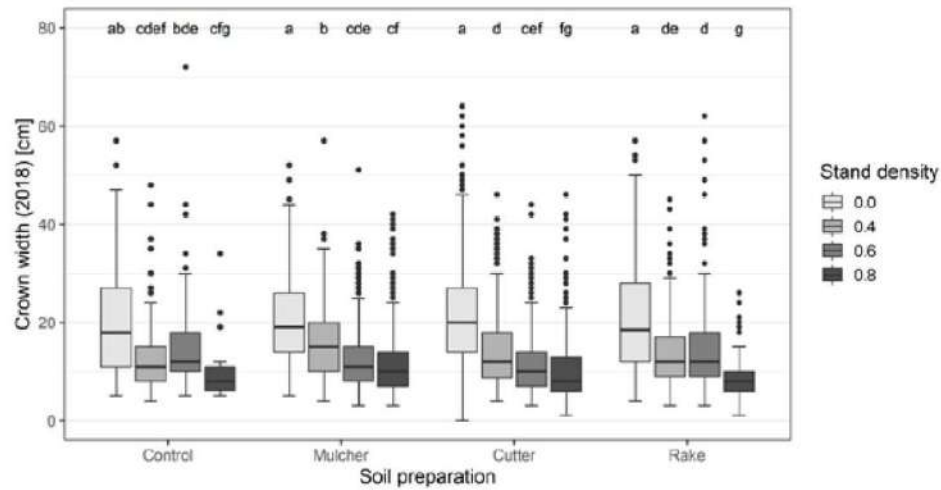




**Fig. 3.** Numbers of seedlings per 1 ha for different stand densities and soil preparation techniques: Number of seedlings lower than 10 cm (A); Number of seedlings higher than 10 cm (B); and total number of seedlings (C). Different letters indicate significant differences between groups ( $p < 0.05$ ); values represent median, upper and lower quartile.



**Fig. 4.** Height of seedlings in different variants of soil preparation and stand density (individuals higher than 10 cm; year 2018). Different letters indicate significant differences between groups ( $p < 0.05$ ); values represent median, upper and lower quartile.



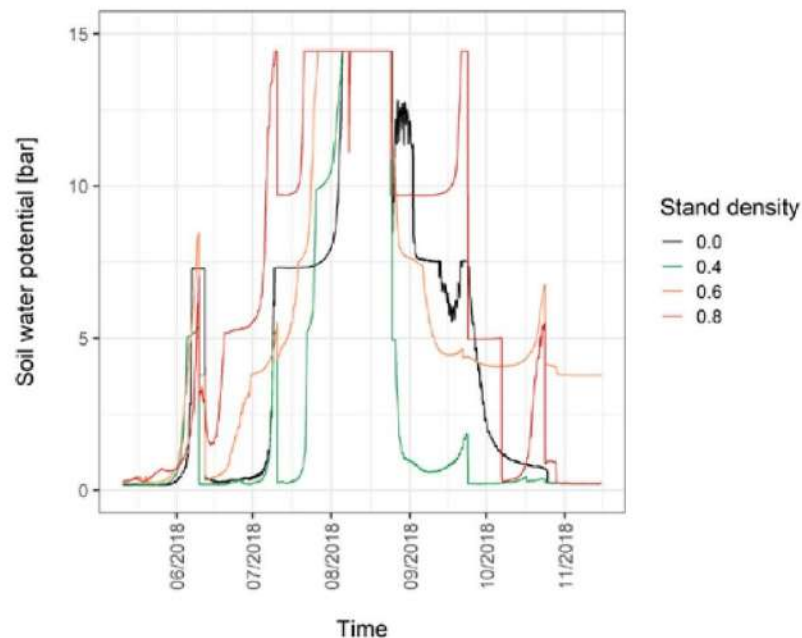
**Fig. 5.** Crown width of seedlings in different variants of soil preparation and stand density (individuals higher than 10 cm; year 2018); different letters indicate significant differences between groups ( $p < 0.05$ ); values represent median, upper and lower quartile.

### 3.4. Soil water potential and soil temperature

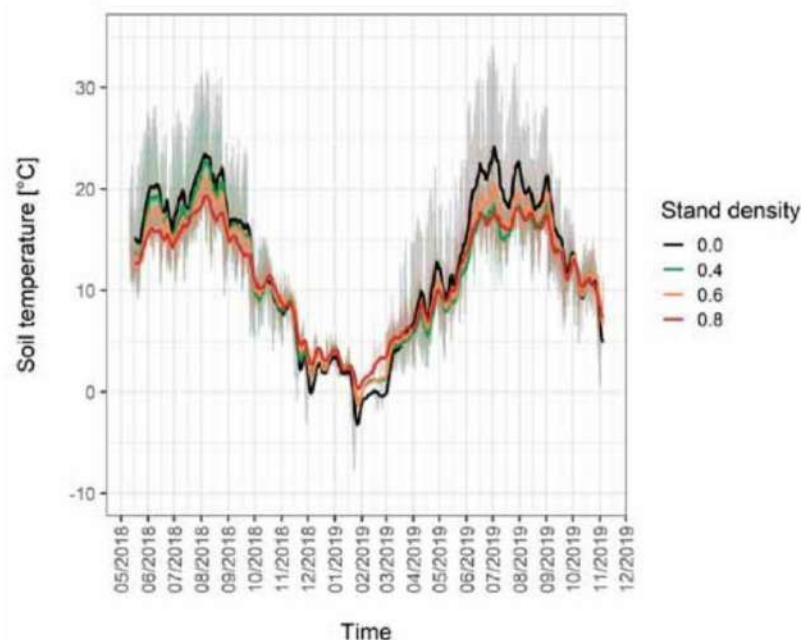
Early increase of soil water potential was observed in stand densities 0.8 and 0.6, whereas on clear-cut (density 0.0) and in stand density 0.4 the soil water potential increased with a delay and the drought period was less

pronounced (Fig. 6). For example, the period with values of soil water potential above 5 bar lasted in stand density 0.8 from late June to the end of October, whereas in stand density 0.4 it lasted from early August to September.

Figure 7 shows temperatures 7–9 cm under the soil surface from June 2018 to November 2019. The high-



**Fig. 6.** Soil water potential in vegetation period 2018 for different stand densities.



**Fig. 7.** Soil temperature in individual months in 2018/2019 for different stand density plots. The original values (in background) are for better readability represented by one-week moving average curves.

est temperatures in summer as well as the lowest temperatures in winter were measured on clear-cut (stand density 0.0). To the contrary, the lowest amplitude of soil temperatures was observed in the case of highest stand density 0.8. These values of stand densities 0.4 and 0.6 were between the two mentioned treatments. Generally, the absolute differences in mean temperatures between clear-cut and stand density 0.8 were the highest in July and August, intermediate in February, March and low in the remaining months.

## 4. Discussion

### 4.1. Seed numbers

In accordance with our first hypotheses, the highest seed numbers were in all years (2016 – 2018) recorded in the highest stand density, whereas on the clear-cut area the seed fall was the lowest. Differences between the particular stand densities from 0.4 to 0.8 were apparent, yet not statistically significant. Since most seeds are generally in close proximity to seed trees (Kuuluvainen & Pukkala 1989), the high density of these mature individuals guarantees high seed density over the entire area. It is important to note that seed traps were placed always in the middle section of each stand density, and particularly in the case of clear-cut, higher seed numbers can be expected with decreasing distance to adjacent mature stands.

As released trees increase the diameter increment (Zdors & Donis 2017; Brichta et al. 2019) and crown volume (Spathelf & Ammer 2015), they probably also increase masting ability (Mukassabi et al. 2012). As these processes are gradual and depend on the responsiveness of individual trees, with increasing time since seed harvest smaller differences in seed numbers between lower and higher stand densities can be expected. Similar results were reported by Parker et al. (2013), who stated that total seed production expressed on a per hectare and unit pine basal area basis did not differ by harvest treatment. The same authors conclude that the seed cut of the uniform shelterwood system applied to the second growth of white pine stands is unlikely to adversely affect white pine (*Pinus strobus* L.) seed production, seed quality, or potential for natural regeneration during mast seeding events.

### 4.2. Regeneration density

We partly reject the second hypotheses, as the most favourable conditions for seedling establishment and resulting seedling numbers 3 three years after the seed cut were reached in stand density 0.4. Parent stand density itself cannot be simply regarded as a factor with only positive effect on regeneration density. Mature trees represent competition for resources among themselves but they also have adverse effect on regeneration individu-

als in the understory (Wiedemann 1925; Valkonen et al. 2002; Sánchez-Salguero et al. 2015). This negative effect may not be apparent immediately after the seed fall, but will increase with the growth of juvenile trees (Belend et al. 2000). Similar conclusions have been found for example by Pitt et al. (2011) in white pine stands. To the contrary, lower regeneration density on the clear-cut results probably from lower initial seed numbers as described in the first part.

Beland et al. (2000) used a similar experiment design with soil preparation by disc cutter and division of the stand into several treatments of stand density (200 stems  $\text{ha}^{-1}$ ; 160 stems  $\text{ha}^{-1}$ ; clear-cut area of approx. 2.5 ha). While in our study the highest seedling numbers (32,402  $\text{ha}^{-1}$ ) were recorded in the stand density 0.4 (approx. 121 stems  $1 \text{ ha}^{-1}$ ), in their study for low stand density (160 stems  $\text{ha}^{-1}$ ) 53,000 seedlings  $\text{ha}^{-1}$  were reported. Even higher numbers of regeneration were then found in the stand with the highest density (200 stems  $\text{ha}^{-1}$ ; 90,000 seedlings  $\text{ha}^{-1}$ ). Their study also found a very low number of seedlings on clear-cut area (3,700 seedlings  $\text{ha}^{-1}$ ) with cutter soil preparation, specifically this value for total number of seedlings is significantly lower than our clear-cut area values on all soil preparation variants (cutter: 21,960; mulcher: 13,550; brush rake: 17,110; control: 11,500 seedlings  $\text{ha}^{-1}$ ). However, our results may be affected by higher temperatures and distinct moisture deficit in 2018 (ČHMÚ 2019) resulting probably in higher seedling mortality during the vegetation period. Although pine is mainly considered resistant to limited water availability, in recent years pine stands all across Europe have been massively damaged by repeated drought events (Merlin et al. 2015; Vacek et al. 2016, 2017; Gao et al. 2017; Buras et al. 2018). Therefore, we assume that even in the local natural pine habitats, the seedlings were damaged by drought. Relatively lower stand densities are reported also from Turkey (Kara & Topaçoğlu 2018), where 5 years after reducing the parent stand density to 50%, average seedling numbers amounted to 7,000  $\text{ha}^{-1}$ . Aleksandrowicz-Trzeńska et al. (2014) reported 9,190 seedlings  $\text{ha}^{-1}$  on plots after the scarification by forest plough on clear-cut of 2.5 ha.

In accordance with the second hypotheses, a positive effect of soil preparation on the seedlings numbers in all treatments of stand densities was confirmed. Similar findings were reported by many authors (Örlander et al. 1990; Karlsson & Örlander 2000; Hille & Ouden 2004; Barbeito et al. 2011). Besides immediate regeneration success, mainly deeper soil preparation also significantly lowers the C/N ratio, increases the amount of P, Mg and S (Örlander et al. 1996) and suppresses the competition of ground vegetation (Hille & Ouden 2004; Nilsson et al. 2006; Gaudio et al. 2011b; Hyppönen et al. 2013). Deeper soil preparation is also recommended by Posmetyev et al. (2016), who adds that not only does it achieve good results in terms of natural regeneration density, but is also economically effective. Despite this, there are large

differences in preferences and value of soil preparation according to a particular habitat (Ackzell 1993; Ammer et al. 2011; Aleksandrowicz-Trzeńska et al. 2014; Saur-saunet & Matrisen 2018).

#### 4.3. Seedling characteristics

Based on our results, we confirm the hypotheses that seedling height and crown width are influenced by parent stand density negatively, nevertheless the effect of soil preparation on these regeneration parameters was not apparent.

Superior mean heights of seedlings in clear-cut and stand density 0.4 are mainly related to higher resources availability, as was confirmed also in numerous controlled experiments. Vitámvás et al. (2019) reported for 1-year-old seedlings that root length, shoot dry mass and root dry mass were the highest in full light conditions, however the differences in shoot length were not so pronounced. Riikonen et al. (2016) documented high ability of pine seedlings to respond to release cut by primarily increasing the crown width. In older literature, there are many proofs about the superior growth of young plants growing in larger distances to seed trees (eg. Wiedemann 1925).

We were not able to confirm positive effect of soil preparation on seedling growth, nevertheless Nilsson et al. (2006) and Gaudio et al. (2011b) showed superior height growth of regeneration individuals after soil scarification. The reason is better soil chemical and mechanical properties and lower competition of herbaceous vegetation (Karlsson & Örlander 2000; Varmola et al. 2004; Saur-saunet & Matrisen 2018). To the contrary, Pierik & De Wit (2014) related high competition of herbaceous vegetation to superior height growth, but at the expense of crown width and chlorophyll content in assimilation organs.

#### 4.4. Soil water potential and soil temperature

Based on our results, we reject the hypotheses that more favourable soil moisture and temperature characteristics are associated with higher stand density, and that the least favourable treatment with respect to moisture and temperature is the clear-cut. Although the lowest amplitude of soil temperatures was observed in the case of highest stand density 0.8, and the highest temperatures in summer as well as the lowest temperatures in winter were observed on the clear-cut, higher stand densities (0.6 and 0.8) were related to lower soil moisture and possibly higher risk of drought stress for seedlings. Similar results presented several authors (Limousin et al. 2008; del Campo et al. 2014; Gebhardt et al. 2014) who stated that the release cut had a positive effect on the amount of water in the transplantation streams of mature trees, but also the soil water potential itself. The reason for the



increase in the amount of water in the stand is mainly the lower rate of mature trees crown interception (Limousin et al. 2008), but also their lesser competition and evapotranspiration (Kellomäki et al. 1997; Giuggiolia et al. 2013). Del Campo et al. (2014) also stated that a strong stand density reduction increased the amount of water in the soil by up to 20–40%.

## 5. Conclusion

Based on our research, we conclude that the best outcome of natural regeneration was achieved after seed cut decreasing the stand density to 0.4. This was manifested by sufficient seed numbers, highest regeneration density, superior seedling characteristics and positive effect on soil moisture and temperature characteristics. The effect of soil preparation of any type was crucial for the regeneration success, but the best results were documented for treatment with milling cutter (3-fold increase in total mean numbers of seedlings compared to control variant versus 2.6-fold increase for forestry mulcher and 2.4-fold increase for brush rake). We conclude that shelterwood regeneration with initial stand density reduction to 0.4 on natural Scots pine sites represents justified alternative to clear-cutting and may in the future become an important tool in mitigating negative effects of climate change.

## Acknowledgment

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### 5.2.2 5. publikace: *Měření architektury koruny přirozené obnovy pomocí 3D digitizéru Fastrak Polhemus*

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**Časopis:** Sensors (časopis zařazen do databáze SCOPUS a WOS, aktuálně IF – 3.7, Q2)

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#### **Souhrn:**

Cílem předloženého článku bylo přesnější stanovení dimenzí jedinců přirozené obnovy borovice lesní a získání dalších informací o architektuře jejich korun, z prostředí různě hustého mateřského porostu. Výzkum si kladl za cíl také ověřit možnosti měření architektury korun jedinců přirozené obnovy pomocí speciálních technologií snímání biomasy.

Metodologie tohoto výzkumu navazuje na design pokusu BRICHTA et al. (2020) z prostředí lokality MARÁNA I., odkud byli odebrány celé rostliny borovice pro následné laboratorní zpracování prostřednictvím měření jedinců digitizérem Fastrak Polhemus. V laboratorních podmínkách byly měřeny dimenze rostliny, včetně rozlišování různých řádů větví koruny borovic.

Bylo zjištěno, že hustota mateřského porostu v procesu přirozené obnovy ovlivňuje počet větví jedinců obnovy v různých řádech, stejně jako jejich výšku. Detailní měření ukázalo, že nejvíce řádů větví se nachází na jedincích z holoseče (hustota mateřského porostu = 0,0), nejnížší větvení bylo na ploše s nejvyšší hustotou mateřského porostu (zakmenění 0,8). Z výsledků vyplynulo, že intenzita větvení (měřená jako počet větví třetího řádu) závisí na celkovém počtu větví různých řádů, ale také na hustotě mateřského porostu, pod kterým jedinci přirozené obnovy rostou. Důležitým výsledkem této studie byla negativní korelace mezi větvením stromu a výškou stromu. Výsledky naznačují, že čím se rostlina více větví, tím je nakonec nižší. Níže popsaná studie potvrdila schopnost digitizéru Fastrak Polhemus realizovat přesné 3D měření architekturu koruny jedinců přirozené obnovy. Nutné je však dodat také fakt, že podobná data lze získat pomocí senzorů Lidar, nicméně s velkým rozdílem v přesnosti, ve prospěch použitého digitizéru Fastrak Polhemus.



## Article

# Measuring the Canopy Architecture of Young Vegetation Using the Fastrak Polhemus 3D Digitizer

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**Abstract:** In the context of climate change conditions, addressing the shifting composition of forest stands and changes in traditional forest management practices are necessary. For this purpose, understanding the biomass allocation directly influenced by crown architecture is crucial. In this paper, we want to demonstrate the possibility of 3D mensuration of canopy architecture with the digitizer sensor Fastrak Polhemus and demonstrate its capability for assessing important structural information for forest purposes. Scots pine trees were chosen for this purpose, as it is the most widespread tree species in Europe, which, paradoxically, is very negatively affected by climate change. In our study, we examined young trees since the architecture of young trees influences their growth potential. In order to get the most accurate measurement of tree architecture, we evaluated the use of the Fastrak Polhemus magnetic digitizer to create a 3D model of individual trees and perform a subsequent statistical analysis of the data obtained. It was found that the stand density affects the number of branches in different orders and the heights of the trees in the process of natural regeneration. Regarding the branches, in our case, the highest number of branch orders was found in the clear-cut areas (density = 0.0), whereas the lowest branching was on-site with mature stands (density = 0.8). The results showed that the intensity of branching (assessed as the number of third-order branches) depends on the total number of branches of the tree of different branch orders but also on stand density where the tree is growing. An important finding in this study was the negative correlation between the tree branching and the tree height. The growth in height is lower when the branching expansion is higher. Similar data could be obtained with Lidar sensors. However, the occlusion due to the complexity of the tree crown would impede the information from being complete when using the magnetic digitizer. These results provide vital information for the creation of structural-functional models, which can be used to predict and estimate future tree growth and carbon fixation.

**Keywords:** 3D model; Fastrak Polhemus; tree architecture; shading; *Pinus sylvestris*



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## 1. Introduction

Scots pine (*Pinus sylvestris* L.) is not only one of the primary commercial tree species in the Czech Republic but is also the most widespread tree species in almost half of the European forests [1–4]. Despite a current tendency to replace conifers with broadleaves in the Czech Republic [5], the proportion of pine is still significant, especially in places where pine stands cannot be replaced yet. In areas with a substantial proportion of pine, the Czech Republic is trying to adapt management to its ecological requirements considering climate change but also to the needs of industry [6,7]. The pine currently suffers from a significant lack of moisture; its deep tap root [8] is paradoxically unable to respond to decreasing groundwater levels. Foresters in Central Europe have already tried many ways of growing Scots pine, some of which have proven successful in terms of climate change, while others have not. At the same time, the cultivation of pine within the shelterwood system is current. In order to better understand the growth response of young Scots pine trees to different



degrees of shading, a unique method of measuring with a magnetic digitizer was used in our study. Knowledge of canopy architecture is increasingly required in a variety of areas, from stand establishment to harvesting [9]. Thus, to achieve the best possible quality in a mature forest stand during harvesting, we need to understand how environmental influences affect the juvenile tree. But how can we get the most accurate architecture? One way of obtaining 3D tree models is by manual measurements—this method is, however, time-consuming both for the measurements and for the evaluation of the architecture. In addition, it is always possible to view only the 2D model but not the 3D model. The most commonly used methods for forest stand surveys are photogrammetry, Lidar, or laser scanning [10].

Photogrammetry is the science of measurement from photographs, which was originally developed for mapping and survey purposes and quickly found its application in other fields, including forestry. One of the earliest documented uses of photogrammetry in forestry was in Germany in 1920 when aerial photography was used to create detailed maps of forested areas. In the following decades, photogrammetry continued to be used in forestry for a variety of purposes, including timber inventory, forest condition assessment, and forest fire mapping. It has also been used to determine the canopy architecture of individual trees [11]. Measuring 3D models using photogrammetry is time-saving, but it is not possible to represent all parts of the canopy in the models, as shown in Figure 1. Another disadvantage of photogrammetry is that the detection of the components/pixels of the tree of interest against the background of more distant trees in photography requires sophisticated programming and can have significant mistakes.



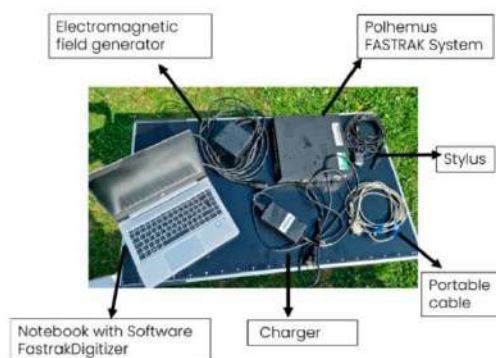
**Figure 1.** Photogrammetric 3D model of a Scots pine tree in a regeneration stand.

Another method that can be used to detect 3D architecture is using Lidar. The first use of Lidar (Light Detection and Ranging) in forestry dates back to the early 1990s. Lidar must be flown either by plane or drone. From the Lidar, point clouds are created that provide a direct 3D view of the surface. A specialized method is needed to extract the canopy architecture from the 3D point cloud to synthesize their qualification into useful measures of tree features. The dataset combined with algorithms representing the forest canopy resulted in a fine-scale architectural model called L-Architect (Lidar data to tree architecture) [11]. L-Architect was proposed as a practical way to synthesize and quantify the spatial distribution of tree components from Lidar point clouds. L-Architect uses geometrically registered Lidar scans of individual trees to reconstruct the geometric and topological structure of the tree. In our case, as we want to achieve high accuracy, this method is not suitable for our purposes (Figure 2), due to the fact that not all parts of the crown are visible.



**Figure 2.** Lidar 3D model showing a stand of Scots pine tree.

The above-mentioned methods are more used to determine the condition of the whole forest but not to determine the trees' architecture. This is because these methods have a large error in displaying 3D models of tree species, as they are not able to display all parts of the canopy [12]. A method for measuring three-dimensional tree architecture that works at the branch level and simultaneously describes plant topology (branching), plant geometry, and branch morphology combines a 3D digitizer [13] (Figure 3) coupled with DiPlAmi software (version1.0) to control the digitizer and collect data [14]. The 3D digitizing method started to be used in 1973 when an articulated arm measuring rotation angles was used for the first 3D digitizing [15]. However, smaller plants rather than mature trees were examined using 3D digitizing equipment. Digitization of smaller plants has been addressed in several different studies, with the general conclusion being that 3D models have the potential to demonstrate differences in structure and development between individuals and under different environmental conditions [16–18].



**Figure 3.** Three-dimensional magnetic digitizer Fastrak Polhemus.

The digitizer Fastrak Polhemus, due to its electromagnetic tracking (EMT), is used in various fields, not only in forestry. One of the most well-known fields is medicine, where this technology enables precise navigation deep within the human body by providing real-time data on the position and orientation of the tracked instruments used by the clinician. In every field, magnetic navigation errors occur due to distortion in the operating environment. Deformers are metal objects that can be static or move relative to the tracking

system transmitter. It is not possible to completely avoid the action of a metallic part in the magnetic field, but it is possible to limit it with the use of multiple coils at once. In fields such as medicine, this option of dealing with metal parts is possible [19]. In our case, where the coils are replaced by a stylus, using multiple styluses at once is not an option. So, we must always be careful of the metal parts. Using a magnetic digitizer, we image all parts of the crowns, even those overlapping in Figure 4. This method is the most accurate but the most time-consuming. This method makes it possible to measure the 3D point coordinates of selected points in space. This method is most often used for small trees. When we measure trees taller than 4 m, we have to divide the tree into several parts and use reference points to reassemble which will be discussed in the methodology section.



**Figure 4.** Three-dimensional model of a Scots pine tree in regeneration stand made with the digitizer Fastrak Polhemus.

This method has already been used, for example, for the architectural description of a 20-year-old, 7 m tall walnut tree, and the visual comparison between the photograph of the tree and the image synthesized from the digitization was satisfactory [20]. Mutke et al. [14] investigated the correlation of topological and geometric variables in individual trees. The correlation was confirmed only with the parameters of the parent shoot that had formed in the previous year. However, smaller plants rather than mature trees were investigated using 3D digitizing equipment. Digitization of smaller plants has been addressed by several studies, with the general conclusion that 3D models can demonstrate differences in structure and development between individuals and under different environmental conditions [16–18]. Water and nutrient content is among other factors that influence the growth and architecture of woody plants. Most published work on this topic has confirmed the hypothesis that transpiration is influenced by both tree morphology and environmental factors [21–23]. Transpiration is higher with the increase in tree height and diameter [24]. Most models of plant growth and architectural development are generally based on open modular structures and their endogenous dynamics: germination, growth, senescence, typology, and geometry [25–27]. Functional-structural tree models can approach crown development through shoot-level processes using a framework of various interacting sub-modules that consider both branch position in the crown and light environment as relative factors for shoot morphology [28–30]. Crown density is an important parameter related to canopy architecture [31]. Our study describes the measurement of architecture using a 3D digitizer in order to evaluate the morphology of individuals under different light conditions according to the actual measured data and to assess the effect of protective timber management on the crown morphology of natural regenerating Scots trees.

Crown architecture and its formation over time affect most management objectives in Scots pine, such as stem formation, the presence of knots, stem cleanliness, the lack of presence of defects, scars, or dead branches, the presence of branch scars, etc. Crown architecture, the number of branches, the number of orders, and other morphological



parameters have not yet been studied, mainly due to the lack of technologies capable of providing reliable data [32]. Historically, many studies have been conducted to study the architecture of trees (specifically pine). The main focus of these studies was tree biomechanics [32–34], branch mechanics [32], root mechanics [28], tree pruning [29], and more recently, studies on growth and dynamics at the architectural level [10]. Our study relates to the latter in that it provides an example of how to support the technical limitations of growth studies by deploying a 3D magnetic digitizer as an alternative to Lidar scanning. We seek to demonstrate the findings on growth dynamics (branching intensities) and how current technology can easily achieve this.

Based on the facts listed above, the hypotheses of this study were as follows: (1) stand density affects the canopy branching of regeneration trees, (2) stand density affects the height of regeneration trees, and (3) canopy branching is related to the height of regeneration trees, and we can provide data to support this hypothesis using 3D magnetic digitizer technology.

## 2. Materials and Methods

### 2.1. Study Area

The subject of the study was a stand of Scots pine near the town of Doksy, on the property of Vojenské lesy a statky, s. p., Mimoň division (50°33.77548' N, 14°43.49143' E) (Figure 5). Almost 100% of the forest stand consists of naturally grown Scots pine. The terrain is flat at 300 m above sea level. The study areas are located in natural pine habitats, and the subsoil is sandstone with the dominant soil type arenaceous podzol [34]. The average annual air temperature is 7.3 °C, and the average maximum temperature is 31.5 °C. The average annual precipitation is 635 mm [35]. Growing seasons last approximately 162 days [36]. The study territory typically has warm, dry summers and cool, dry winters with a narrow annual temperature range (Cfb) according to the Köppen climate classification [37]. The study sites naturally host Scots pine *Pinetum oligotrophic* with a sparse cover of *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. in the herbaceous layer [38]. Natural regeneration is meant here as an alternative for seeding or planting. Thus, it means trees are from natural sources even though the soil is managed.

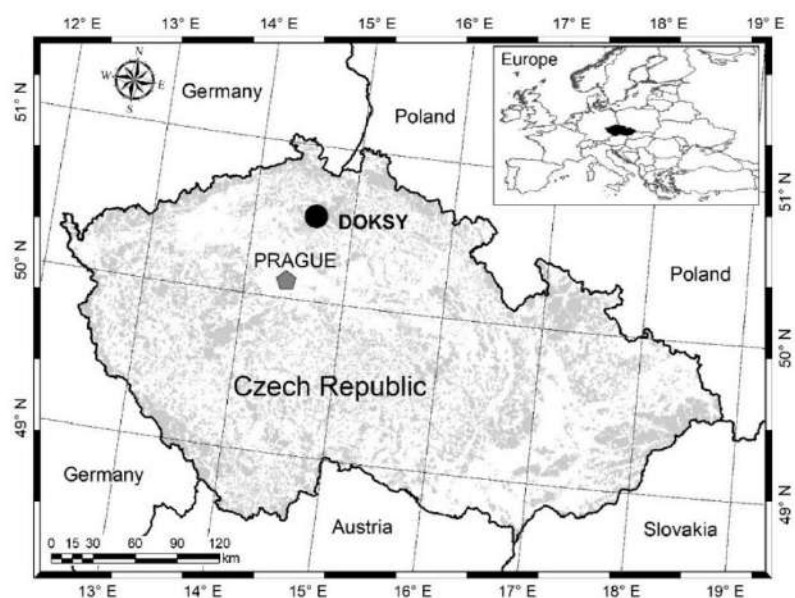
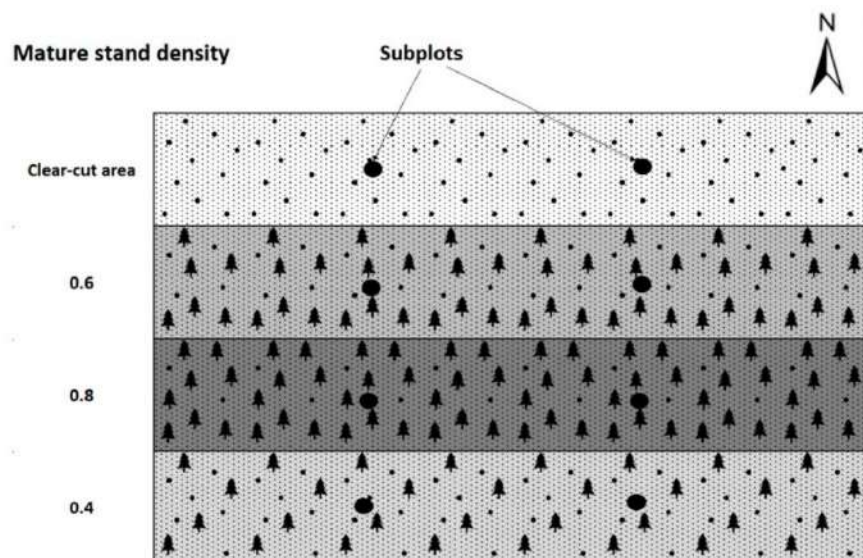


Figure 5. Location of the study area. The black dot represents the interest area in Doksy.

## 2.2. Data Collection

In 2016, an experimental research plot was established to monitor the success of the natural regeneration of Scots pine with different densities of trees per stand and different soil preparation [35]. Part of the design of the Brichta et al. [35] experiment was also utilized in this paper. Plots of interest for data collection were delineated for parts of the stand without soil preparation. Eight trees of natural regeneration were taken from each plot with different mature stand clear-cut areas—no cover shelter, stand density 0.4–40% of the original cover, stand density 0.6–60% of the original cover, and stand density 0.8–80% of the original cover (Figure 6). The trees present in the natural regeneration were selected using random stratified sampling for the laboratory study from two subplots precisely in the middle of the width of the plots with different mature stand densities. This configuration was chosen to minimize the influence from one side or the other by a different variant of stand density or by a cardinal direction effect. Thus, 32 natural regeneration trees, including their entire root systems, were sampled from a total of eight subplots in four plots with different stand densities (Figure 6). The age of all sampled trees was 5 years old.



**Figure 6.** Experimental design, including the location of the subplots for natural regeneration sampling (black circles).

The collected samples were analyzed with the magnetic digitizer Fastrak Polhemus (Company: NEUROSPEC AG City and country: Stans, Switzerland Version of software: 1.0) [13] (Figure 3) to produce accurate 3D models of these trees. One might consider magnetic digitizer to be the most accurate method to obtain the entire tree architecture, especially in cases where some of its parts overlap each other. The digitizer uses a stylus (Figure 7) to measure the position of the points (with an accuracy of 0.07 cm) and the given branching angles (for X, Y, and Z coordinates with an accuracy of 0.15°). The center of the Cartesian coordinate system lies in the center of the magnetic field, where the coordinates X, Y, and Z are equal to zero. During the measurement, the tree must be in the magnetic field generated by the generator (Figure 8) to obtain an accurate and complete crown architecture. The first point is the point at the base of the trunk, and the next point is the point where the branches start (we get a segment or part of the trunk) and continue to the top of the tree. Next, the first-order branch is measured the same way as the trunk, and then the entire branch with the other orders is measured (Figure 9). In this study, the measurement of first-, second-, and third-order branches was the main goal (Figure 10).

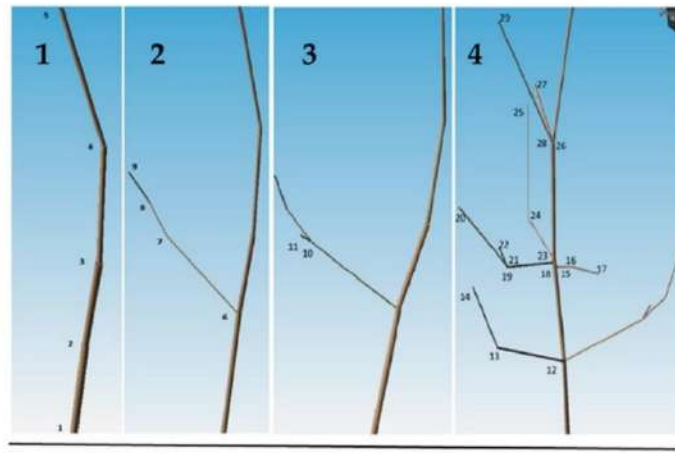




**Figure 7.** Stylus is a pen used to record the coordinates of an object in a given space.



**Figure 8.** Generator of electromagnetic field.



**Figure 9.** Graphical representation of the continuity of the process of 3D modeling of the aboveground plant part of Scots pine individuals. Figure (1–4) shows the sequential 3D modelling of Scots pine with the time sequence shown by the arrow below the figure. Numbers 1–29 are the places where a point is measured.

The stylus (Figure 7) works on the principle of magnetic induction. If this tip is placed in a magnetic field, after its activation, a voltage is induced according to Faraday's law, as shown in Equation (1). The touch position is then calculated using this signal [39]:

$$\varepsilon = -d\Phi B/dt \quad (1)$$

where  $\varepsilon$  is the electromotive force (emf), and  $\Phi B$  is the magnetic flux.

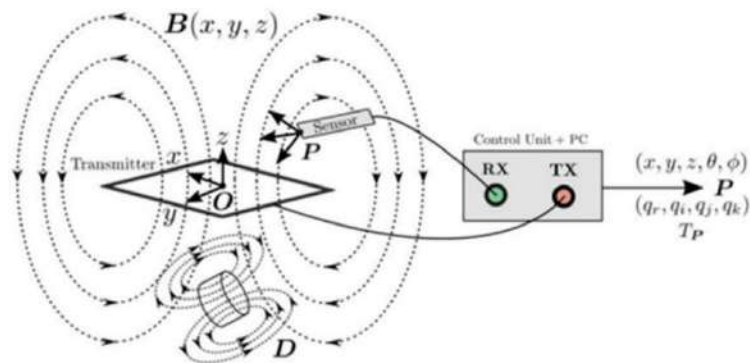


**Figure 10.** Description of the measured parts of the tree: 1—first-order branches, 2—second-order branches, 3—third-order branches.

The Faraday equation states that a time variation of the magnetic field always accompanies a spatial variation in a non-conservative electric field, and vice versa.

The generator of the electromagnetic field (Figure 8) produces a magnetic field constantly, and the moment we press on the stylus, the magnetic field is disturbed. We disrupt it at a certain angle and at a certain place. The coordinates that we entered with the stylus are the coordinates of the location of the disturbed magnetic platform. Since we are working with a magnetic field that is constantly in motion, there must be no metal in our measurement area. It would disturb the correct magnetic field waves, and we would have entered the wrong coordinates for the disturbance.

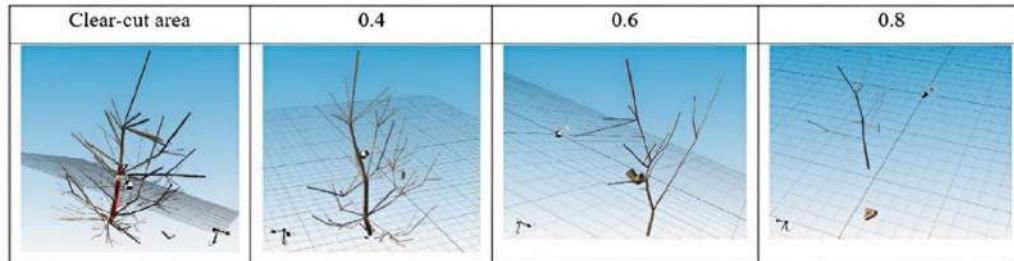
The first magnetic tracking system was developed by Polhemus Navigation Systems [34], which standardized the tracking system topology. An overview of how a typical EMT (electromagnetic tracking) system operates is shown in Figure 11.



**Figure 11.** Universal operation of the magnetic tracking system. The control unit is connected to a transmitter board (TX) and a magnetic sensor (RX). The sensor is induced by the voltage from the time-varying magnetic field  $B$  of the transmitter. The controller measures this voltage and uses this value to determine the position of the sensor  $P$  relative to the origin  $O$ . The orientation component may be expressed as a vector, quaternion, or transformation. Distortions  $D$  in the TX plate region distort the magnetic field and cause errors in the determination of the sensor position [39].

### 2.3. Data Analysis

In total, all 32 pine trees were analyzed (Figure 12) and Appendix A. For better visualization, 3D images of natural regeneration trees were created [12]. Data were processed in Fastrak Digitizer software (version 1.0) [13].



**Figure 12.** Sample of measured 3D models.

To calculate the branch lengths and the sum of the branch lengths of all three orders, the sum of the lengths of individual branch segments was used. The length of each segment was determined using the following formula:

$$L = \sum_{i=1}^n \sqrt{(x_{i-s_1} - x_{i-s_2})^2 + (y_{i-s_1} - y_{i-s_2})^2 + (z_{i-s_1} - z_{i-s_2})^2} \quad (2)$$

where  $L$ —branch length,  $n$ —number of branch segments,  $i$ —order number,  $[X_{i-s_1}, Y_{i-s_1}, Z_{i-s_1}]$ —coordinates of the segment start point,  $[X_{i-s_2}, Y_{i-s_2}, Z_{i-s_2}]$ —coordinates of the segment final point.

Statistical evaluation was performed in R software (version 4.3.1.) [40]. The boxplot function was used for the visual analysis, and a generalized linear model with a Poisson probability distribution (the first variable, in this case, was stand density, and the second variable was total wood biomass) was used for the regression analysis of branching intensity dependence (number of the first-, second-, and third-order branches). The linear model with Gaussian distribution was chosen to analyze the dependence of individual height based on stand density.

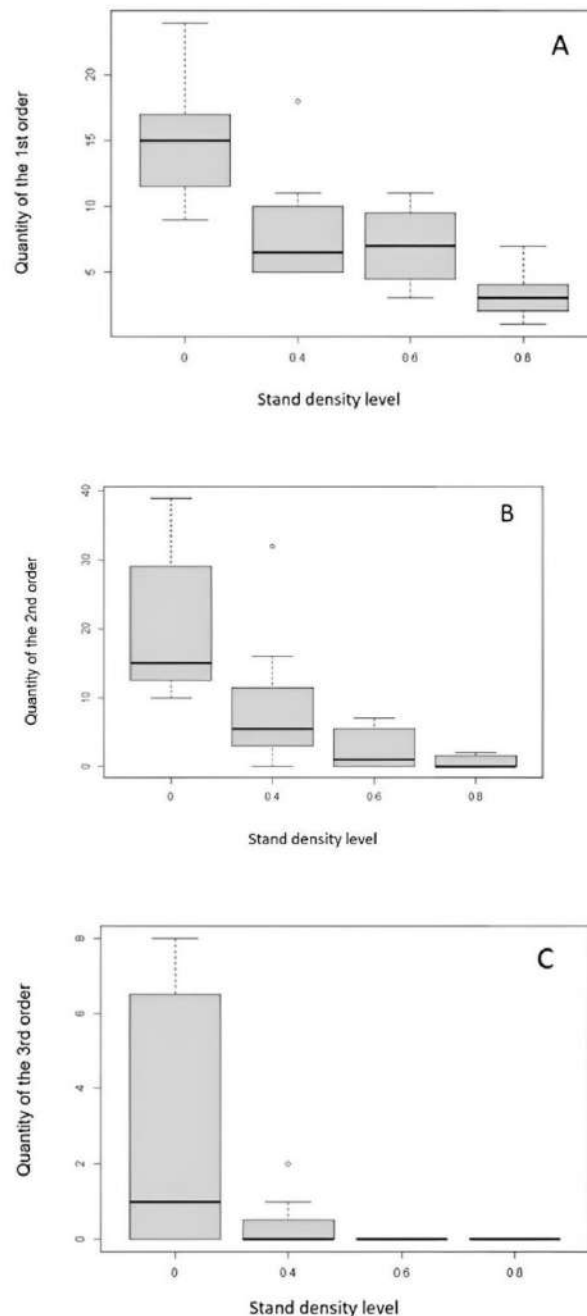
### 3. Results

#### 3.1. Dependence of Branching Regarding Stand Density

The most frequent occurrence of the first-, second-, and third-order branches was found in the clear-cut areas, while the lowest number of the first-, second-, and third-order branches was found in the areas with a stand density of 0.8 (80%). The first order was most frequent in the clear-cut area, while in the plots with a density of 0.4 (40%) and 0.6 (60%), there was no statistically significant difference in the number of occurrences of first-order branches (Figure 13A). The lowest abundance of the first-order branches was evident on a stand density area of 0.8. Similar results were also obtained for the abundance of the second-order branches, and statistically significant differences were observed between the clear-cut area and stand density area of 0.4. Again, the stand density of 0.8 area had the lowest occurrence of the second-order branches (Figure 13B). The third-order branches were, again, most abundant in the clear-cut area and minimal in the stand density of 0.4 area. There were no third-order branches in plots with 0.6 and 0.8 densities (Figure 13C).

Our analysis focused on the effect of stand density on the abundance of each branch order. In the table below, we present the coefficient of the generalized linear model of the relationship between stand density and the abundance of branching order (Table 1). According to the regression coefficient for each linear model (for orders 1, 2, and 3), Table 1 shows that the stand density has a statistically significant effect on the number of individual branch orders. In the case of the first-order branches, the highest number of branches is evident in the clear-cut area, with an average value of 15. The lowest occurrence is on the stand density area of 0.8. In the case of the second order, the highest number of branches is also in the clear-cut area, with an average value of 14. The lowest occurrence of the second-order branches is in the stand density area of 0.8 with an average value of 1, while in the case of the third-order branches, the highest frequency is again in the clear-cut

area (Table 1). Regarding the stand density of 0.4, the third-order branches rarely occur and are completely absent in the stand density of 0.6 and 0.8. The result shows that as stand density increases, the frequency of each order of branches of natural regeneration individuals decreases.



**Figure 13.** Amount of branching of occurrence of the first-(A), second-(B), and third-order branching (C) at different stand densities. The boxplots show the standard deviations (the gray bar), median (the black horizontal line), and minimum and maximum values.



**Table 1.** The effect of stand density on the abundance of branches in each order.

| Coefficients | Intercept | Stock Density (Estimate) | STD     | Error from Value | Pr (>  z )                 |
|--------------|-----------|--------------------------|---------|------------------|----------------------------|
| Order 1      | 2.73680   | −1.62223                 | 0.20893 | −7.765           | $8.19 \times 10^{-15}$ *** |
| Order 2      | 3.11377   | −3.28529                 | 0.24351 | −13.49           | $<2 \times 10^{-16}$ ***   |
| Order 3      | 1.1635    | −6.4741                  | 1.14    | −4.721           | $2.35 \times 10^{-6}$ ***  |

Notes: The results indicate that stand density has a significant effect on the abundance of branches in each order. The intercept represents abundance when stand density is zero. As the order increases, we observe larger changes in the estimated coefficients, which indicates a more complex relationship between stand density and number of orders. All low *p*-values (\*\*\*) that are reported indicate statistical significance of this effect. Our analysis provides evidence that the stand density plays a key role in influencing the abundance of individual orders.

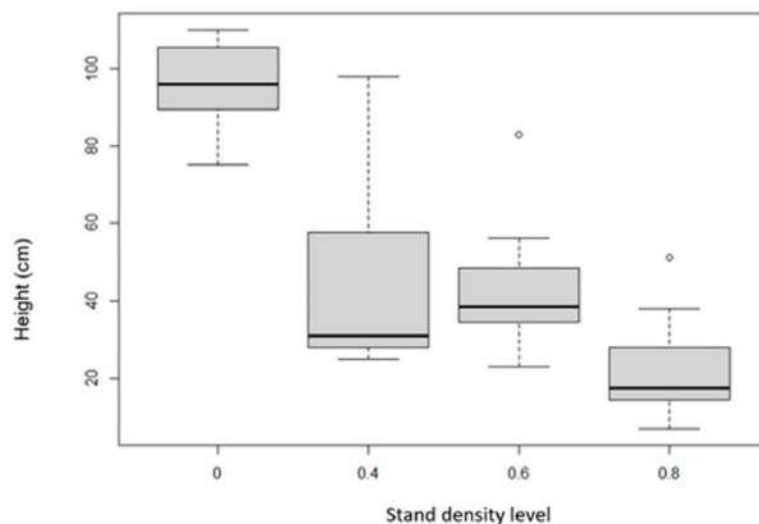
### 3.2. Dependence of Height of Natural Regeneration Individuals on Stand Density

The tallest pine tree was found in the clear-cut area, with an average height of 90 cm, while the smallest pine trees were found in the stand density of 0.8 (15 cm) area. Pines in the stand density of 0.6 (35 cm) area were larger on average than those in the stand density of 0.4 (30 cm) area (Table 2, Figure 14). Based on the values presented, we can confirm the hypothesis that stand density has a statistically significant effect on the height of natural regeneration individuals.

**Table 2.** Dependence of the height of individuals on the density of the parent stand.

| Coefficients        | Estimate | STD     | Error from Value | Pr (>  z )                 |
|---------------------|----------|---------|------------------|----------------------------|
| Intercept           | 2.73680  | 0.09168 | 29.852           | $<2 \times 10^{-16}$ ***   |
| Stand density level | −1.6223  | 0.20893 | −7.765           | $8.19 \times 10^{-15}$ *** |

Notes: Intercept—represents the expected tree height when the stand density is zero. Stand density level—expresses the expected change in the tree height increasing the stand density. \*\*\*—It indicates a higher level of significance, at a significance level of 0.01. The null hypothesis holds, and the probability is less than 1%.

**Figure 14.** Amount of branching of the height of pine trees depending on stand density. The boxplot graph shows the standard deviations (the gray bar), median (the black horizontal line), minima, and maxima.

In the Table 2, we examined the relationship between tree height and the stand density and the density of the parent stand. Below, you will find the interpretation of the individua columns.



The intercept value is 2.73680. We found that this value is statistically significant ( $p$ -value  $< 2 \times 10^{-16}$  \*\*\*), which indicates that we can expect a significantly higher height of individuals even with a low density of the mother stand. The coefficient for “Stand density level” is  $-1.6223$ . A negative sign indicates that the expected tree height decreases with increasing stand density. This coefficient is again statistically significant ( $p$ -value  $8.19 \times 10^{-15}$  \*\*\*), which confirms that the density of the stand has a significant effect on the tree height. This information is key to understanding ecosystem dynamics and may have important implications for forestry and ecological strategies.

### 3.3. Dependence of the Height of Natural Regeneration Individuals on the Biomass of Orders

Our analysis focuses on the relationship between tree height and the total branch biomass of each order. Below, we present the interpretation of the individual columns (Table 3). The dependence of the height of a tree on the total biomass invested in the branches with respect to their order was evaluated. The model’s hypothesis that the natural regeneration of Scots pine increases their height with the same intensity as they increase their branches, i.e., that Scots pine height positively correlates with the number of branches in each order (biomass), was not confirmed (Table 3). In contrast, the statistical model shows that the height of natural regeneration is negatively correlated to the amount of biomass generated from the third-order branches; this finding can also be interpreted to mean that the more biomass a tree stores in the third-order branches, the less height it will attain.

**Table 3.** Dependence of the tree height on the total branch biomass in each order.

| Coefficients | Estimate    | STD      | Error from Value | Pr ( $>  z $ )            |
|--------------|-------------|----------|------------------|---------------------------|
| Order 1      | 0.087987    | 0.016221 | 5.424            | $1.10 \times 10^{-5}$ *** |
| Order 2      | 0.013591    | 0.006651 | 2.043            | 0.05127                   |
| Order 3      | $-0.233641$ | 0.080563 | $-2.900$         | 0.00749 ***               |

“Order 1” is 0.087987, signifying a significant positive effect on individual height with a unit increase in first-order branch biomass ( $p$ -value  $1.10 \times 10^{-5}$  \*\*\*). Order 2: The coefficient for “Order 2” is 0.013591, with a  $p$ -value (0.05127) above the 0.05 significance level, suggesting potential insignificance, though some effect on height may still exist. Order 3: The coefficient for “Order 3” is  $-0.233641$ , indicating a significant negative effect of third-order branch biomass on individual height ( $p$ -value 0.00749 \*\*\*). \*\*\*—It indicates a higher level of significance, at a significance level of 0.01. The null hypothesis holds, and the probability is less than 1%.

### 3.4. Evaluation of the Time and Complexity of Measurements

Every measurement method has advantages and disadvantages. Fastrak digitizer measurements are time-consuming to collect data in the field, but after the data are processed, a field campaign is no longer required. Since the magnetic digitizer needs a power supply for the measurement, it usually has a rule of thumb that a 1 m tall tree takes about 45 min to be measured. Of course, other factors must be taken into account, for example, canopy branching. The data collected can be used to create structural models, which can help to predict the growth of a given tree and evaluate the environmental conditions. For the structural models, the GroIMP software (version 2.0.1) can be used, in which accurate 3D models are necessary in order to simulate growth as accurately as possible, for example. Three-dimensional models measured with Fastrak can therefore be used in GroIMP for growth simulations directly from the measured data without further modifications [41].

## 4. Discussion

### 4.1. Dependence of Branching on Stand Density

Lidar cannot accurately detect branch branching because Lidar cannot measure overlapping branches or branches inside the crown. However, a model canopy structure can be created using Lidar. A method has been developed that overlays a three-dimensional matrix over the forest stand. The [42–44] magnetic digitizer can be used to determine the model canopy structure, but to understand the exact strategy of individual trees, one needs

to know the canopy branching directly. Consistent with our first hypothesis, the number of branch orders was higher in the clear-cut area, while the lowest number was in the areas of 0.8. Differences in the stand density areas of 0.4 and 0.6 were apparent but not statistically significant. The results of our study indicate that if pines grow in a clear-cut area, they will be more branched. While this helps to make the tree more stable, branched crowns may be more susceptible to potential fires [39], especially considering the climatic fluctuations in recent years [45–49]. Models of tree crown architecture in temperate forests are limited to a few studies [50], making it difficult to compare our work's specific methods with similar models. However, for a tree species to survive in a competitive and restrictive environment, its architecture must provide so-called “functional advantages” [51]. For example, when silver birch (*Betula pendula* Roth.) is under severe competitive stress, it invests more in height than in diameter [44]. To a lesser extent, this is also true for Scots pine at young ages [52].

In our study, the crown development was slower in stands with higher stand density than in those with lower stand density. Another study also confirmed, for example, the tendency of Scots pine to develop its crown toward accessible light [53]. For now, however, the question remains how the crown width and the number of orders of existing seedlings will respond to further release of the parent stand. For example, Riikonen et al. [54] showed that Scots pine seedlings respond very well to a reduction in stand density just by increasing crown width. The light plasticity of the crowns of some tree species, i.e., the tendency to achieve a very characteristic crown shape, can then be strongly influenced by the inherited development of the tree [54]. However, our study is consistent with the proposition that crown architecture is crucial for light interception and distribution to each specific photosynthetic unit of the crown. Tree crown architecture can be represented by “models” that delineate basic growth strategies that define successive architectural phases [55], which is also supported by our measurements using the Fastrak Polhemus magnetic digitizer [13].

#### 4.2. Dependence of Height of Natural Regeneration Individuals on Stand Density

As the magnetic digitizer provides accurate 3D models, it is possible to infer about the dependence of the tree height and the stand density. There are many studies that determine the height of vegetation using Lidar data. When measuring with a magnetic digitizer, we do not have to deal with any optimum size as it is based on the magnetic wavelength. The maximum tree height came out with the highest accuracy of 85–90% [56]. However, the accuracy of the magnetic digitizer is 99%, with only a 0.7 mm deviation from the actual tree height.

Consistent with our second hypothesis, the highest pine trees were found in the clear-cut areas, whereas the smallest were found in the areas with a stand density equal to 0.8. No statistically significant differences were found in the stand density areas of 0.4 and 0.6. This result is also confirmed by the study of Brichta et al. [35] that the highest density of pines is in the meadow, where there are also the tallest pines, followed by stand density of 0.4 and stand density of 0.6 and 0.8. Earlier literature also supports the above conclusions, namely that better growth of young pines is evident in areas with lower stand densities [57]. Hence, stand density is also characterized here as a significant indicator directly related to the crown architecture [31]. Another possible negative effect on tree heights in the shelterwood group was the presence of bilberry (*Vaccinium myrtillus* L.) [58,59]. In our plots, bilberry was abundant in the 0.8 stand density level, which also contained the lowest tree of natural pine regeneration. However, data from the study by Brichta et al. [35] suggest a contrary—positive—effect of the bilberry competition on the height of natural regeneration trees. Yet, our study showed that the higher the stand density, the smaller the heights of the trees, i.e., except for the stand density of 0.6, where on average, the trees were taller than in the area with the stand density of 0.4.

The earlier cited exception to this rule could be due to the specific microhabitat conditions at the sampling site. Thus, given the high competition at the herbaceous vegetation



layer, the most critical mechanism seems to be primarily illumination, which influences shelterwood height, and, secondly, the overall architecture of woody plants [60,61]. Only tree growth was considered in our study, but other works have also examined various factors that affect the growth. For example, orthotropy is most commonly associated with conditions of high light intensity, whereas plagiotropy is related to shade conditions. Both orthotropy and plagiotropy are related to certain limiting factors and are viewed as mechanisms that allow synchronization of growth with occasional favorable conditions [62]. However, even the mere consideration of an architectural model is likely insufficient to explain all the links between the ecological status of a species and its architecture. According to Horn [60], architectural models do not directly reflect the adaptive geometry of adult plants. Several species sharing the same architectural model may take on very different shapes. The species model and strategy are only minimally related because the tree shape is flexible [63]. Our results compare favorably with those of another pioneer tree species, namely silver birch (*Betula pendula* Roth.). A study dealing with birch confirmed that birch facing intense light competition is five times smaller than birch with no competition for light [50]. Thus, the latter result also does not contradict our conclusions that natural regeneration pine trees showed the lowest heights only in the area with a stand density of 0.8.

#### 4.3. Dependence of the Height of Natural Regeneration Individuals on the Biomass of Orders

Regarding our third hypothesis, the tree height is correlated only with the first- and second-order branches but not with the third-order branches. However, given the paucity of similar studies, we can relevantly discuss, in particular, why the third order did not affect the height of natural regeneration. Stevens and Perkins [64] mention a correlation between tree height and relative size in this context, but they also question the taxonomic magnitude of this effect. Our data present that the occurrence of third-order branches tended to decrease with increasing stand density. Young pines in open areas invest biomass both in lateral branches and in height growth. Our result further confirms the observation that crown branching is not desirable if the goal is to obtain wood with high quality, which was concluded by researchers investigating the effect of pruning on the tree tissue in the pine forests of Central Europe in a research plot established in 1951 [65]. The results of this work can be compared, for example, with Šebeň et al. [66], who focused on Norway spruce (*Picea abies* L. Karst), where a higher ratio between height increments and lateral branch increments was found exclusively in dominant trees than in non-dominant trees. In this case, height increments were twice as high as lateral increments. In suppressed trees, the ratio of height increments to branch increments was around 1 [66]. It should be added that branching is not very desirable in forestry [67–71]. The latter conclusion implies that in the case of shelterwood management, the regeneration of Scots pine can only be sufficiently rapid, and the quality of the individuals can only be ensured when the stand is considerably thinned.

## 5. Conclusions

This study verified the feasibility of measuring tree architecture using the Fastrak Polhemus magnetic digitizer. It was shown that we can measure even the smallest parts of the tree canopy with this instrument. This is especially important for young individuals, where every small detail is important for understanding their growth strategy. Their measurement is nowadays more and more desirable, especially because woody plants are most productive (in terms of carbon fixation) at a young age, and their formulation is reflected in the future. The measurement of young trees is rare, although important for the future of our forests. To understand the growth strategy of trees as much as possible, we need to know their architecture. It is by using the Fastrak Polhemus magnetic digitizer that we obtain accurate architecture. Currently, the most used method is Lidar; we only compared this method with the help of the literature because using Lidar did not seem practical given the environment, mainly because its use is not effective in young stands.

However, Lidar would be more appropriate if we needed to measure mature trees in the shortest possible time. As mentioned in the above studies, Lidar cannot image all tree stand parts. However, the Fastrak Polhemus magnetic digitizer eliminates this shortcoming because it measures the inner part of the canopy, even where the branches overlap. It is a unique measurement method that, although more time-consuming in the field, has no time requirements for processing results outside the field, unlike other methods. The measurement technique used appears to be suitable for similar analytical studies and, in addition to providing non-destructive measurements, provides clear data in 3D models and is also time-efficient compared to other destructive measurements. We can continue to use these 3D data models for growth models displayed in simulation software like GroIMP to understand tree growth strategies better [41,71–74]. In this study, data on the architecture of the crown and individual branches were obtained using the aforementioned technology to assess the condition and development of Scots pine trees at different stand densities. Based on the analysis of the measured data, it can be concluded that the five-year-old trees of natural regeneration of Scots pine in the clear-cut area are the tallest and have the highest branching density, where the third-order branches are also present. Therefore, it can be concluded that the open, clear-cut area provides the most suitable conditions for the growth of young pines. However, it is interesting to note that the number of third-order branches is not positively correlated with height. Young pines in open areas invest biomass both in lateral branches and in height growth. The present study confirms the importance of sufficient solar radiation for the density and growth of the natural regeneration of Scots pine trees. Because of the limited number of samples evaluated and the lack of similar studies, we recommend that follow-up research be conducted, not only in natural pine habitat conditions.

Our main aim was predominantly to understand growth in general, not an ecological aim, but rather an industrial aim. This study is possibly one of the first research studies of this kind in Central Europe, especially with the use of the Fastrak Polhemus magnetic digitizer. For future studies, an increase in the amount of data is necessary.

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Appendix A

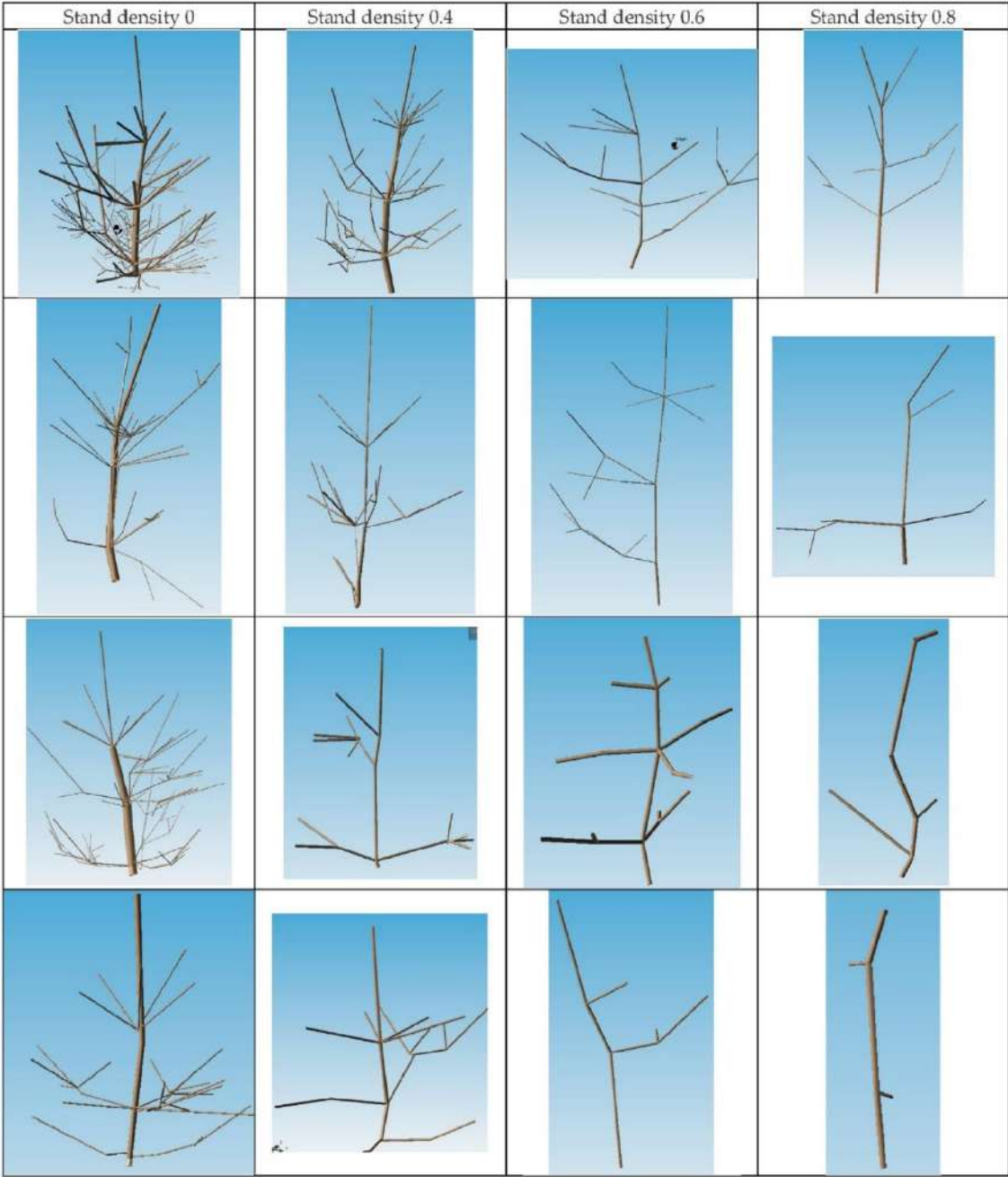
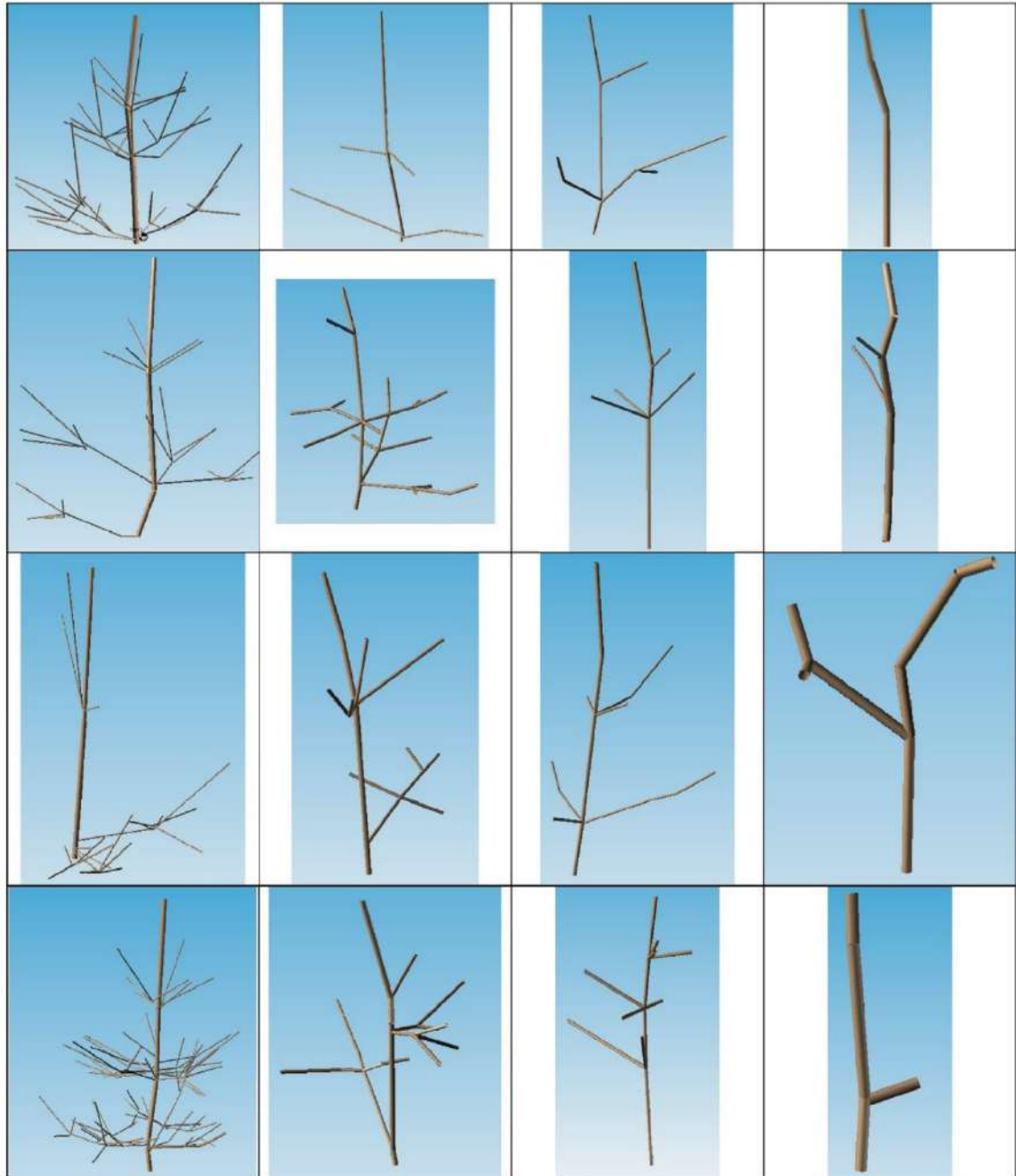


Figure A1. Cont.





**Figure A1.** 3D models of measured Scots pine trees in four different cambered.

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**5.3. Produkce a struktura diferencovaných a smíšených borových porostů,  
vliv vybraných abiotických a biotických faktorů na vitalitu borovice lesní**

**5.3.1 7. publikace: *Dopady změny klimatu na růst borovice lesní (Pinus sylvestris L.)  
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**Souhrn:**

Cílem výzkumu bylo zhodnotit strukturu, produktivitu a zejména radiální růst heterogenních borových porostů v širším evropském měřítku, v kontextu klimatické změny. Dílčím cílem výzkumu pak bylo popsat případné změny přirozené cyklicity v růstu borovice lesní.

Prostřednictvím sběru dat bylo získáno celkem 163 dendrochronologických vzorků z 16 výzkumných ploch v České republice, Polsku, Španělsku a Velké Británii. Vybrané porosty byly v režimu přírodě blízkého hospodaření nebo se jednalo o přírodní rezervace. Měření struktury porostu proběhlo prostřednictvím inventarizace technologií Field-Map, a to na plochách o velikosti 0,25 ha.

Spektrální analýzy studie stanovily podstatné snížení fluktuace růstu letokruhů a ztrátu jejich přirozené růstové cyklicity v posledních třiceti letech. Z výsledků také vyplynulo, že průměrná teplota vzduchu byla nejdůležitějším faktorem ovlivňujícím radiální růst borovice lesní, a to ve srovnání s vlivem srážkových úhrnů. Na základě výsledků, zjištěných v této studii lze zároveň potvrdit, že se borovici daří na srážkově stabilních lokalitách, to naznačují data z Velké Británie. Závěry této studie potvrzují zásadní vliv probíhající globální změny klimatu na dynamiku a růst borových lesů v Evropě.

## Article

# Effects of Climate Change on Scots Pine (*Pinus sylvestris* L.) Growth across Europe: Decrease of Tree-Ring Fluctuation and Amplification of Climate Stress

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**Abstract:** From an economic perspective, Scots pine (*Pinus sylvestris* L.) is one of Europe's most important tree species. It is characterized by its wide ecological adaptability across its natural range. This research aimed to evaluate the forest structure, productivity and especially radial growth of heterogeneous pine stands in 16 research plots in the Czech Republic, Poland, Spain and Great Britain. The study assessed the tree-ring formation and its relationship to climate change for each country, using 163 dendrochronological samples. The stand volume of mature pine forest ranged between 91 and 510 m<sup>3</sup> ha<sup>−1</sup>, and the carbon sequestration in the tree biomass was 40–210 t ha<sup>−1</sup>. The stands had a prevailing random distribution of trees, with a high vertical structure close to selection forests (forest stands with typical very diverse height, diameter and age structure). Spectral analyses showed a substantial decrease in fluctuations in the tree-ring index and a loss in natural growth cyclicity in the last thirty years. The results also evinced that mean air temperature was the most important factor influencing the radial growth compared to precipitation totals. Pine thrives in precipitation-stable locations, as shown by the results from Great Britain. The conclusions of this study confirm the fundamental effect of ongoing global climate change on the dynamics and growth of pine forests in Europe.

**Keywords:** close-to-nature management; forest structure; stand diversity; timber production; carbon sequestration

## 1. Introduction

Climate change in the form of increasing frequency and intensity of long-term droughts, heat waves and other extreme weather events negatively affects forest stands worldwide [1,2]. Climate models for the 21st century predict an increase in the average annual temperature by another 1.5 °C over the next decade, while precipitation will decrease radically [3]. Other scenarios show that the maximum temperature may increase by up to 2.5 °C [4]. In addition, the frequent occurrence of droughts and forest fires [5] decreases the vitality of trees or directly results in the disruption of entire forest stands [6].

Scots pine (*Pinus sylvestris* L.) occupies a dominant position in more than half of European forests [7]. It is considered as one of the tree species most affected by climate change [8–14]. In several alpine areas, drought has already been reported as a major cause of Scots pine decline in the second half of the 20th century [15,16]. Pine stands suffer

considerably from climatic fluctuations, manifested by an unbalanced distribution of wet and dry periods [9,11–13,17]. This has a direct negative impact on the photosynthetic activity of pines [18,19], their cambial growth [20], and their overall resistance against bark beetles [6,21], fungal pathogens [22] and mistletoe (*Viscum album* L.) attack [23–25]. Dry periods also increase the risk of forest fires in pine forests [26]. The vulnerability to various disturbances likely increases with the homogenization of forest stands [27,28].

Changes in management and silvicultural approaches are needed to increase the resilience of forest stands [29–31]. It is accepted that the greater use of natural processes and increased spatial, species and genetic diversity are the main principles of adaptive forest management [32]. In structurally differentiated stands, we generally expect higher stability and an improvement in the possibility of a physiological response to climatic variations [33–35]. Furthermore, refs. [2,8] confirm the influence of the provenance of Scots pine on its adaptability to climate change. Refs. [36,37] point out the relationship between nutrient balance and availability in combination with drought response. Some authors report the essential role of species composition in the drought stress process [38–40] as well as in individual growth trends or habitat conditions [41]. Concerning vulnerability to climate change impact, refs. [42,43] confirm the dependence of tree size, while [44] discuss the influence of competition between tree individuals.

In most of Europe, the productive silviculture of pine forests is mainly based on clear cutting or shelter systems. This reflects the ecological requirements of Scots pine as a light-demanding tree species with a tendency to create asymmetric crowns in lower stand densities [45]. The resulting homogenous even-aged forest stands usually require subsequent manipulation of stand density by thinning to increase their resistance to damaging factors [46–49]. Although close-to-nature forest management methods have been used for more than 100 years [50], there are still significant knowledge gaps in the silviculture of structurally differentiated pine stands. Stands with higher structural differentiation allow low-intensity management and are expected to better adapt to climate change [28,51–55].

Climate change negatively affects tree growth, while recent years indicate the phenomenon of a divergence problem between drought with high temperature and irregular precipitation distribution in Europe. The beginning of this divergence can be considered as starting from the 1980s [56,57].

This research evaluates production, structural and especially dendrochronological parameters of heterogenous Scots pine forest stands in the Czech Republic (CZ), Spain (SP), Poland (PL) and Great Britain (GB). The specific objectives of this study were to determine (i) the stand forest production parameters, biomass potential and carbon sequestration of pine stands in four different countries across Europe; (ii) the spatial pattern, structural differentiation and total diversity of tree layers; (iii) the dynamics of radial growth and cyclicity of the tree-ring width index of Scots pine from the 1951 to 2016 in two periods before and during the more noticeable dynamic climate change using the threshold year of 1986; and (iv) the effect of climatic factors (temperature and precipitation) on radial growth in relation to climate change.

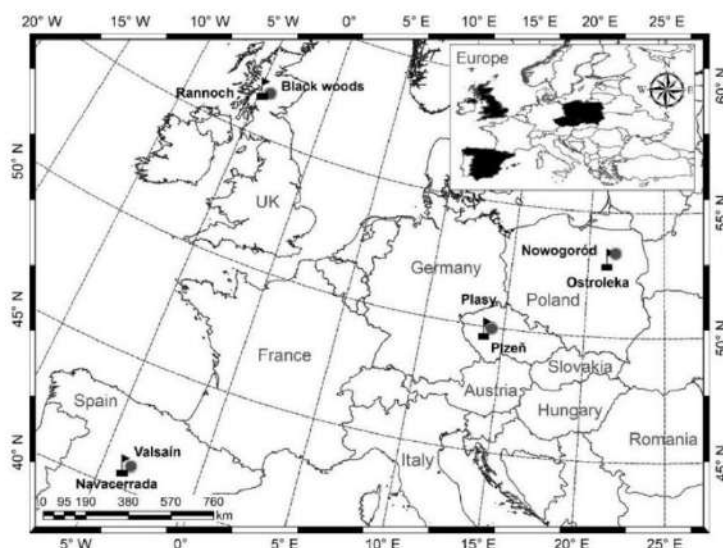
## 2. Materials and Methods

### 2.1. Study Areas

This study evaluated Scots pine stands in four locations in four European countries representing different climatic and geographic zones: the Czech Republic (CZ), Spain (SP), Poland (PL) and Great Britain (GB) (Figure 1). The forest stands from the Czech Republic are located in the Western Bohemia Uplands; the studied forest stands in Spain are located in the central part of the Sierra de Guadarrama; the study area in NE Poland is in the northwest of the city of Nowogoród, in the catchment of Narew River; and the Scots pine stands in Great Britain are located in the sub-central part of the Scottish Highlands, on the south shore of Loch Rannoch, within the Black Wood complex of native pine stands [58,59] in the Tummel Valley, Perthshire. The studied pine forests represent heterogeneous stands due to close-to-nature management (CZ—Czech Republic, PL—



Poland, ES—Spain) or natural dynamics without interventions (GB—Great Britain) for several decades. In the case of the Black Wood of Rannoch, the last extensive felling occurred in 1940–1941, when only the best trees were removed [59]. Before World War II, the harvesting of trees occurred probably via selective logging [58]. In Spain, the stands represent one of the most productive Scots pine forests, with highly valued wood. Since the 1980s, an irregular shelterwood system has been applied, with a greater emphasis on the environmental functions and services of the forest [60,61]. Since 2013, the areas have been part of Sierra de Guadarrama National Park. A felling policy with different intensities was carried out on sites in CZ and PL, with close-to-nature management to support natural regeneration and create complex forest structures. In general, clear-cuts and further release cuts were rejected. The tree species composition is formed by monospecific Scots pine with mixed Norway spruce (*Picea abies* [L.] Karst.) (<5%) and silver birch (*Betula pendula* Roth.) (<5%). In terms of phytocoenology, the pine stands in Poland and the Czech Republic belong prevalently to the vegetation association *Vaccinio vitis-idaea-Quercetum* Oberdorfer 1957 and the vegetation association *Vaccinio myrtilli-Pinetum sylvestris* Juraszek 1928. According to [62], the Scottish pinewoods belong to the *Pinus-Hylocomium* type, while in Spain, the represented association is *Senecioni carpetani-Cytisetum oromediterranei* R. Tx. and Oberdorfer 1958 corr. Rivas-Martinez (ca. 1991).



**Figure 1.** Location of research plots (dots) and adjacent location of sites for which meteorological data were derived (flags).

In Table 1, all research plots (RPs), with their location and overview of basic site parameters, are listed; other basic climate characteristics for all study areas are shown in Table 2. Climatic regions of the study areas were determined according to the Köppen–Geiger climate classification [63]. Long-term climate characteristics for all study areas were focused on two periods—Period 1: 1951–1985 and Period 2: 1986–2016. The division into two periods was implemented to cover the growth of pine before the most intense climate changes and during climate changes. The rationale for splitting this time series was the growth divergence of tree rings caused by higher average temperatures, leading to increased growth variability and the emergence of the “divergence” issue, where tree-ring growth does not mirror climate fluctuations with the same trend [64–66]. The period of the onset of divergence can be considered the period from the 1980s, when a gradual temperature increase began, with precipitation levels remaining around the same threshold, leading to divergence between these observed factors [56]. In our study, the cutoff for the



onset of climate change is set at 1986, marking the period of the beginning of divergence and also half of the period of our observed climate data. When comparing these periods, air temperature in the growing season increased in all studied countries meanly by 0.95 °C, and no changes were observed for the overall precipitation (mean increase by 1.8 mm for all countries; decrease only in the case of Great Britain). The April to September growing season was an intentional choice of a seasonal window, aimed to reduce variability in the start and end of the growing season. The data assessed within this timeframe represents the nearest real vegetation period shared across all research plots (Figure 2).

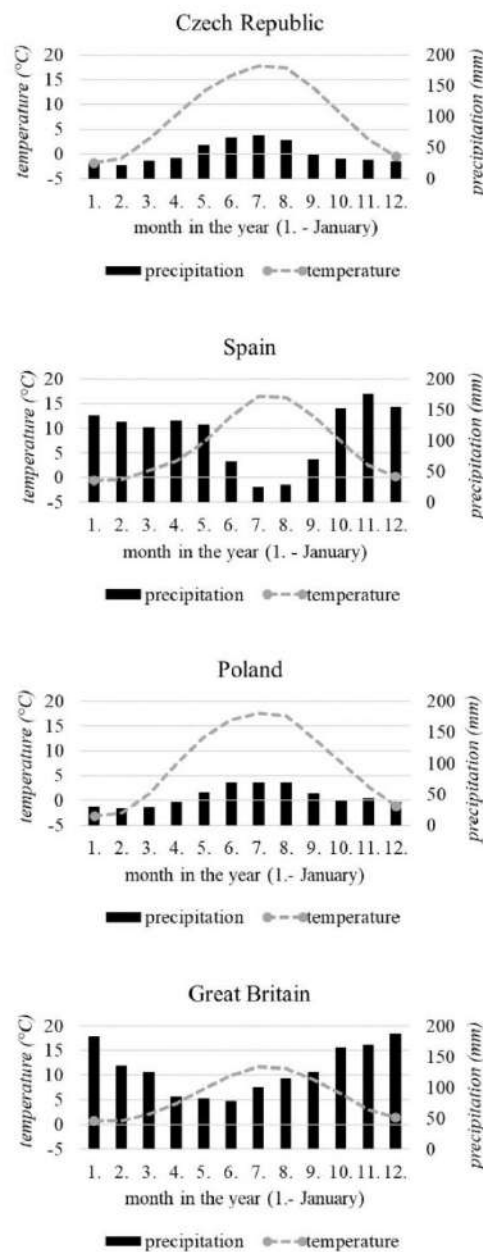
**Table 1.** Location and overview of basic site parameters of research plots.

| RP ID | Country        | GPS Latitude (WGS84) | GPS Longitude (WGS84) | Altitude (m) | Slope | Expo-Sure | Soil Type                    |
|-------|----------------|----------------------|-----------------------|--------------|-------|-----------|------------------------------|
| CZ_1  | Czech Republic | 49°54'35.653" N      | 13°11'59.617" E       | 600          | -     | -         | Gleyic Podzol                |
| CZ_2  | Czech Republic | 49°54'15.779" N      | 13°12'30.546" E       | 580          | 4°    | E         | Gleyic Podzol                |
| CZ_3  | Czech Republic | 49°54'19.548" N      | 13°12'17.456" E       | 600          | 4°    | E         | Gleyic Podzol                |
| CZ_4  | Czech Republic | 49°55'37.037" N      | 13°14'16.646" E       | 580          | 4°    | E         | Gleyic Podzol                |
| SP_1  | Spain          | 40°49'2.102" N       | 3°59'8.730" W         | 1580         | 11°   | SE        | Cambisol—<br>Ferric Luvisols |
| SP_2  | Spain          | 40°48'56.365" N      | 3°58'58.343" W        | 1670         | 13°   | SE        | Cambisol—<br>Ferric Luvisols |
| SP_3  | Spain          | 40°48'52.132" N      | 3°58'44.223" W        | 1780         | 20°   | SE        | Cambisol—<br>Ferric Luvisols |
| SP_4  | Spain          | 40°48'58.747" N      | 3°58'55.331" W        | 1670         | 17°   | SE        | Cambisol—<br>Ferric Luvisols |
| PL_1  | Poland         | 53°19'12.130" N      | 21°40'19.159" E       | 130          | -     | -         | Arenic Podzol                |
| PL_2  | Poland         | 53°19'25.408" N      | 21°40'17.895" E       | 130          | -     | -         | Arenic Podzol                |
| PL_3  | Poland         | 53°19'17.887" N      | 21°39'46.918" E       | 130          | -     | -         | Arenic Podzol                |
| PL_4  | Poland         | 53°19'23.354" N      | 21°39'13.084" E       | 130          | -     | -         | Arenic Podzol                |
| GB_1  | Great Britain  | 56°40'29.170" N      | 04°20'51.520" W       | 250          | 4°    | NW        | Gleyic Podzol                |
| GB_2  | Great Britain  | 56°40'29.170" N      | 04°20'51.520" W       | 250          | 4°    | NW        | Gleyic Podzol                |
| GB_3  | Great Britain  | 56°40'19.748" N      | 04°20'32.942" W       | 280          | 4°    | NW        | Gleyic Podzol                |
| GB_4  | Great Britain  | 56°40'19.748" N      | 04°20'32.942" W       | 280          | 4°    | NW        | Gleyic Podzol                |

**Table 2.** Long-term climate characteristics for all study areas (Period 1: 1951–1985; Period 2: 1986–2016).

|                                                           | Czech Republic | Spain   | Poland | Great Britain |
|-----------------------------------------------------------|----------------|---------|--------|---------------|
| Köppen–Geiger climate classification                      | Dfb            | Csb     | Dfb    | Cfb           |
| Annual average air temperature (°C)                       | 7.95           | 6.55    | 7.34   | 5.67          |
| Growing season average air temperature (°C)               | 13.98          | 9.02    | 14.18  | 11.30         |
| Growing season average air temperature: Period 1 (°C)     | 12.63          | 8.79    | 13.73  | 10.68         |
| Growing season average air temperature: Period 2 (°C)     | 13.64          | 9.29    | 14.68  | 12.03         |
| Annual average total precipitation (mm)                   | 492.28         | 1325.71 | 553.18 | 1552.24       |
| Growing season average total precipitation (mm)           | 351.22         | 553.51  | 340.57 | 445.38        |
| Growing season average total precipitation: Period 1 (mm) | 350.66         | 533.08  | 325.24 | 478.06        |
| Growing season average total precipitation: Period 2 (mm) | 351.87         | 577.35  | 357.94 | 407.27        |

Notes: Köppen–Geiger climate classification: Cfb—oceanic climate; Csb—Warm-summer Mediterranean climate; Dfb—humid continental climate.



**Figure 2.** Average air temperatures (°C) and average total precipitation (mm) in individual months for the period 1951–2016 for the monitored countries: Czech Republic, Spain, Poland and Great Britain.

## 2.2. Data Collection

Field-Map technology (IFER-Monitoring and Mapping Solutions Ltd., Jilové u Prahy, Czech Republic) was used to determine the tree layer structure and production parameters in RPs (Research Plots) in 2015–2016. Four 50 × 50 m (0.25 ha) RPs were established in each country (Czech Rep., Spain, Poland and Great Britain; a total of 16 RPs). The positions of all individuals of the tree layer with a diameter at breast height (DBH) ≥ 8 cm were recorded. The height of trees, height of the live crown base and the crown projection were

measured in at least four directions perpendicular to one another. The diameter of tree layer individuals was measured by a Mantax Blue metal caliper (Haglöf, Långsele, Sweden) with an accuracy of 1 mm, and heights were measured using a Vertex laser hypsometer (Haglöf, Sweden) with an accuracy of 0.1 m.

Dendrochronological samples were taken from codominant and dominant trees, according to the classification described by [67], for significant growth response (compared to subdominant and suppressed trees) [68]. We collected a total of 163 dendrochronological samples, with a minimum of 34 samples on the research plot and a maximum of 47, with one sample drilled from a single tree. The core samples were taken with Pressler auger at BH (Breast Height), perpendicular to the axis of the tree along/against the slope. The dendrochronological samples were glued to boards and carefully ground and polished, so that it was possible to measure the distances between the annual rings, as polishing also highlights the anatomical structure of the annual rings. The tree-ring width was measured (accuracy 0.01 mm) using an Olympus binocular magnifying glass on a LinTab measurement table and registered using the TSAP-Win software (version 4.64, RINNTECH, Heidelberg, Germany).

Climatic data for the Czech Republic were obtained from the Czech Hydrometeorological Institute (CHMI)—meteorological station Kralovice (49°58′54.522″ N, 13°29′38.331″ E; altitude 318 m; distance to RPs 22.4 km); for Poland from the Institute of Meteorology and Water Management (IMGW)—meteorological station Ostrołęka (53°04′59.9″ N 21°34′00.3″ E; altitude 94 m; distance to RPs 27.2 km); for Great Britain from the Met Office Integrated Data Archive System—the gridding process accounts for effects such as latitude, longitude, altitude, coastal influence, and the effect of urban land through the use of normalization with respect to monthly 1961–1990 climate normals, and in the case of some variables a regression model [69]. For more details about the construction, see [70]. Climatic data for Spain were obtained from the State Meteorological Agency (AEMET)—meteorological station Puerto de Navacerrada (40°47′18.863″ N, 4°0′12.158″ W; altitude 1860 m; distance to RPs 3.1 km).

### 2.3. Data Processing

The basic structure, diversity and production characteristics of the tree layer were evaluated by the SIBYLA Triquetra 10 forest growth simulator [71]. For the evaluation of the spatial pattern, the aggregation index [72] was calculated. Structural diversity was evaluated by the Arten-profile index [73], diameter and height differentiation [74], crown differentiation, vertical diversity and total stand diversity [75] (see Table 3). The stand volume of pine was calculated according to [76]. Tree biomass was derived from the above-ground biomass (stem, branches and needles) and below-ground biomass (roots and snags). The above-ground biomass of pine in dry matter was derived from the model from [77]. The biomass of pine roots was calculated using a model from [78]. The content of carbon (C) in pine trees was calculated following the research of [79] using the unit content of elements in 10 mg kg<sup>−1</sup> of dry matter. The relative stand density index (SDI) [80] and the canopy closure [81] were observed for each plot.

Dendrochronological analysis was performed in R (version 4.3.1) software [82]. Each dendrochronological tree-ring series were detrended through a two-step process. First, a negative exponential detrending function was applied, followed by a 67% insertion cubic smoothing spline detrending, as per the 'dplR' instructions, to the original tree-ring series [83,84]. Detrending removes the age trend by preserving low-frequency climate signals [85–88]. The time frame of the dendrochronological data was divided into two periods (Period 1: 1951–1985, Period 2: 1986–2016) to evaluate the Scots pine response to changing climatic conditions. The DendroClim 2002 program was used to analyze dendrochronological curves with monthly climatic data, using the 'response and correlation' function from April of the preceding vegetation season to September of the current vegetation season [89]. Spectral analyses and a Simple Linear Correlation (Pearson *r*) table were used for the indexed (detrended) radial growth of Scots pine, using Statistica 13 software [90].



The calculation was conducted with the ‘Single Furier (Spectral) Analysis’ function for the evaluation of fluctuations in tree-ring growth variability, using the output ‘Periodogram’ plot by ‘Period’ [90].

**Table 3.** Overview of indices describing the stand diversity and their common interpretation.

| Criterion                 | Quantifier          | Label    | Reference                          | Evaluation                                                                                                                                         |
|---------------------------|---------------------|----------|------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------|
| Horizontal structure      | Aggregation index   | R (C&Pi) | Clark and Evans (1954) [72]        | mean value R = 1 (random distribution); aggregation R < 1; regularity R > 1                                                                        |
| Vertical structure        | Arten-profile index | A (Pri)  | Pretzsch (2006) [73]               | range 0–1; balanced vertical structure A < 0.3, inhomogeneous structure A = 0.3–0.6, multi-layered structure A = 0.6–0.9, selection forest A > 0.9 |
|                           | Vertical diversity  | S (J&Di) | Jaehne and Dohrenbusch (1997) [75] | low S < 0.3, medium S = 0.3–0.5, high S = 0.5–0.7, very high diversity S > 0.7                                                                     |
| Structure differentiation | Diameter dif.       | TMd (Fi) | Füldner (1995) [74]                | range 0–1; low TM < 0.3, medium TM = 0.3–0.5, high TM = 0.5–0.7, very high differentiation TM > 0.7                                                |
|                           | Height dif.         | TMh (Fi) |                                    |                                                                                                                                                    |
|                           | Crown dif.          | K (J&Di) | Jaehne and Dohrenbusch (1997) [75] | low K < 1.0, medium K = 1.0–1.5, high K = 1.5–2.0, very high differentiation K > 2.0                                                               |
| Complex diversity         | Stand diversity     | B (J&Di) | Jaehne and Dohrenbusch (1997) [75] | monotonous structure B < 4, even structure B = 4–6, uneven structure B = 6–8, diverse structure B = 8–9, very diverse structure B > 9              |

The dendrochronological indices were computed using the tutorial methods of [83,84]. The detrended ring-width data of Scots pine were used to calculate the EPS (expressed population signal). The EPS indicates the reliability of a chronology as a fraction of the joint variance of the theoretical infinite tree population. We used the ‘EPS cutoff’ to increase the quality of dendrochronological data, and therefore, the time series was shortened to the time period 1951–2016 for all variants so that EPS > 0.85 [83,84]. This time period was defined as the intersection of data availability due to the availability of comparable precipitation and temperature forecasts. We also calculated the SNR (signal-to-noise ratio), which evaluates the signal strength of chronology and R-bar (inter-series correlations) [86,91]. The indicators EPS, SNR, R-bar, and AR1 were computed using the ‘dplr’ guidelines [83,84], which are based on standard principles of dendrochronology [85,86,91]. Information on dendrochronological indicators can be found in Table 4.

**Table 4.** Characteristics of tree-ring chronologies of Scots pine for the period 1951–2016 in research plots.

| Country        | No. Trees | Age Mean | Sampling Year | Increment (mm) | Increment Min–Max (mm) | Std.  | R-Bar | SNR    | EPS   |
|----------------|-----------|----------|---------------|----------------|------------------------|-------|-------|--------|-------|
| Poland         | 40        | 125      | 2016          | 1.25           | 0.67–2.44              | 0.618 | 0.234 | 9.005  | 0.900 |
| Czech Republic | 42        | 132      | 2015          | 0.95           | 0.47–1.61              | 0.494 | 0.247 | 11.186 | 0.917 |
| Spain          | 47        | 119      | 2015          | 1.33           | 0.73–1.92              | 0.664 | 0.314 | 19.172 | 0.950 |
| Great Britain  | 34        | 117      | 2016          | 2.22           | 0.82–4.85              | 1.017 | 0.385 | 8.254  | 0.887 |

Notes: No. Trees—number of trees; Age mean—mean sample age in years; Sampling year—year of dendrochronological sampling; Increment—average annual increment in tree-ring width; Increment min-max—the range of minimum and maximum growth of the tree ring; Std.—standard deviation; R-bar—inter-series correlation; SNR—signal-to-noise ratio; EPS—expressed population signal.

The analysis of negative pointer years (NPyS) was performed according to [92,93]. For each tree, the pointer year was set as an extremely narrow tree ring that does not reach 40% of the increment average from the four preceding years. The occurrence of the negative year was proven if a strong reduction in increment occurred at least in 20% of the trees on the plot.



Principal component analysis (PCA) in CANOCO 5 [94] was used to analyze the relationships between timber production, stand structure and diversity on RPs and also radial growth (tree-ring width index) and climate factors (temperature and precipitation) in relation to climate change for all countries. Data were log-transformed, centered and standardized before the analysis. The results of PCA were exported into the form of an ordination diagram. The situation map was made in ArcGIS 10 software (Esri, Redlands, CA, USA).

### 3. Results

#### 3.1. Stand Structure and Production

The DBH and height range was 18.2–50.4 cm and 10.88–27.36 m, respectively, across all RPs (Table 5). The number of trees was in the range from 144 trees ha<sup>−1</sup> on RP GB\_1 to 768 trees ha<sup>−1</sup> on PL\_1. Similarly, the highest basal area (47.6 m<sup>2</sup> ha<sup>−1</sup>) and stand volume (510 m<sup>3</sup> ha<sup>−1</sup>) was observed on RP PL\_1 with the highest stocking (SDI). The highest ever carbon sequestration (210 t/ha) was also found at PL\_1. This index, influencing the overall production of the stand, ranged between 0.31 and 0.93. In terms of average values for all RPs and countries, the average basal area reached 30.6 m<sup>2</sup> ± 10.7 SD, stand volume 303 m<sup>3</sup> ha<sup>−1</sup> ± 129 m<sup>3</sup> ha<sup>−1</sup> and carbon sequestration in biomass 123 t ha<sup>−1</sup> ± 52 SD. Overall, the average annual radial growth in Table 4 best reflects the production in each RP. The highest increment was recorded in GB (2.26 mm), followed by SP (1.33 mm), and PL (1.25 mm), with the lowest mean annual increments recorded in CZ (0.95 mm).

**Table 5.** Basic stand characteristics on RPs in the Czech Republic (CZ\_1–CZ\_4), Spain (SP\_1–SP\_4), Poland (PL\_1–PL\_4) and Great Britain (GB\_1–GB\_4).

| RP   | DBH  | H     | v                 | N                         | BA                                 | V                                  | HDR  | SDI  | CC   | BIO                   | Carbon                |
|------|------|-------|-------------------|---------------------------|------------------------------------|------------------------------------|------|------|------|-----------------------|-----------------------|
|      | (cm) | (m)   | (m <sup>3</sup> ) | (trees ha <sup>−1</sup> ) | (m <sup>2</sup> ha <sup>−1</sup> ) | (m <sup>3</sup> ha <sup>−1</sup> ) |      |      | (%)  | (t ha <sup>−1</sup> ) | (t ha <sup>−1</sup> ) |
| CZ_1 | 25.8 | 17.15 | 0.439             | 596                       | 31.2                               | 261                                | 66.5 | 0.62 | 75.8 | 213                   | 111                   |
| CZ_2 | 18.2 | 16.95 | 0.215             | 424                       | 11.0                               | 91                                 | 93.1 | 0.26 | 59.2 | 76                    | 40                    |
| CZ_3 | 23.2 | 15.22 | 0.372             | 368                       | 15.5                               | 137                                | 65.6 | 0.33 | 47.6 | 110                   | 58                    |
| CZ_4 | 34.5 | 25.43 | 1.061             | 316                       | 29.6                               | 335                                | 73.7 | 0.48 | 62.4 | 236                   | 124                   |
| SP_1 | 28.2 | 16.13 | 0.663             | 556                       | 34.7                               | 369                                | 57.2 | 0.68 | 74.9 | 286                   | 150                   |
| SP_2 | 27.4 | 14.19 | 0.496             | 752                       | 44.5                               | 373                                | 51.8 | 0.88 | 75.8 | 293                   | 154                   |
| SP_3 | 24.9 | 14.55 | 0.436             | 740                       | 36.1                               | 323                                | 58.4 | 0.74 | 81.5 | 257                   | 135                   |
| SP_4 | 24.7 | 10.88 | 0.335             | 676                       | 32.2                               | 227                                | 44.0 | 0.67 | 76.4 | 180                   | 94                    |
| PL_1 | 28.1 | 19.73 | 0.664             | 768                       | 47.6                               | 510                                | 70.2 | 0.93 | 84.1 | 401                   | 210                   |
| PL_2 | 27.6 | 18.92 | 0.683             | 716                       | 42.8                               | 489                                | 68.6 | 0.85 | 74.7 | 381                   | 200                   |
| PL_3 | 31.7 | 19.68 | 0.973             | 384                       | 30.2                               | 374                                | 62.1 | 0.55 | 69.0 | 281                   | 147                   |
| PL_4 | 38.0 | 27.36 | 1.496             | 304                       | 34.5                               | 455                                | 72.0 | 0.60 | 69.0 | 346                   | 181                   |
| GB_1 | 43.6 | 15.39 | 1.326             | 144                       | 21.4                               | 191                                | 35.3 | 0.35 | 56.4 | 144                   | 75                    |
| GB_2 | 50.4 | 19.12 | 1.928             | 196                       | 39.0                               | 378                                | 37.9 | 0.61 | 77.3 | 282                   | 148                   |
| GB_3 | 34.8 | 13.02 | 0.826             | 248                       | 23.5                               | 205                                | 37.4 | 0.41 | 70.8 | 159                   | 83                    |
| GB_4 | 29.7 | 14.28 | 0.571             | 232                       | 16.1                               | 132                                | 48.1 | 0.31 | 62.2 | 105                   | 55                    |

Notes: DBH—mean quadratic diameter at breast height; H—mean height; v—mean stem volume; N—number of trees per hectare; BA—basal area; V—stand volume; HDR—height to diameter ratio; SDI—stand density index; CC—canopy closure; BIO—biomass in dry matter; Carbon—carbon sequestration in biomass.

#### 3.2. Diversity of Tree Layer

The horizontal structure of the tree layer was random in most RPs, aggregated in the case of three RPs and regular on PL\_4. The vertical structure shows a monotonous to very high diversity, approaching a selection forest. According to both evaluation indices, vertical diversity reached the highest values in Spain. On the other hand, the lowest vertical diversity was on the RPs in Great Britain. Similarly, the highest diameter, height and crown differentiation was observed in the case of plots in Spain. However, the structure differentiation of stands was generally low to medium for all RPs. Total diversity, describing

the complex diversity of forest stands, ranged from  $B = 3.936$  on RP GB 2 (monotonous structure) to  $B = 7.051$  on CZ\_1 (uneven structure) (Table 6).

**Table 6.** Diversity of tree layers on permanent research plots in the Czech Rep. (CZ\_1–CZ\_4), Spain (SP\_1–SP\_4), Poland (PL\_1–PL\_4) and Great Britain (GB\_1–GB\_4).

| RP   | Horizontal Structure | Vertical Structure | Vertical Diversity | Diameter Differen. | Height Differen. | Crown Differen. | Total Diversity |
|------|----------------------|--------------------|--------------------|--------------------|------------------|-----------------|-----------------|
| CZ_1 | 1.119                | 0.369              | 0.795              | 0.314              | 0.207            | 1.868           | 7.051           |
| CZ_2 | 0.957                | 0.455              | 0.827              | 0.300              | 0.228            | 1.993           | 6.684           |
| CZ_3 | 1.078                | 0.383              | 0.742              | 0.254              | 0.206            | 1.618           | 5.346           |
| CZ_4 | 1.104                | 0.674              | 0.484              | 0.200              | 0.125            | 1.101           | 5.134           |
| SP_1 | 0.926                | 0.904              | 0.903              | 0.428              | 0.372            | 1.568           | 5.274           |
| SP_2 | 0.943                | 0.789              | 0.875              | 0.327              | 0.243            | 1.926           | 5.548           |
| SP_3 | 0.904                | 0.909              | 0.829              | 0.392              | 0.303            | 1.603           | 5.032           |
| SP_4 | 0.797A               | 0.967              | 0.814              | 0.339              | 0.234            | 2.642           | 6.046           |
| PL_1 | 1.079                | 0.398              | 0.786              | 0.367              | 0.227            | 1.791           | 5.995           |
| PL_2 | 1.075                | 0.499              | 0.720              | 0.355              | 0.256            | 1.506           | 5.210           |
| PL_3 | 0.875                | 0.631              | 0.812              | 0.423              | 0.351            | 2.142           | 6.124           |
| PL_4 | 1.191R               | 0.168              | 0.805              | 0.217              | 0.136            | 2.095           | 5.957           |
| GB_1 | 0.799A               | 0.251              | 0.781              | 0.391              | 0.252            | 1.535           | 4.823           |
| GB_2 | 0.863                | 0.469              | 0.432              | 0.269              | 0.122            | 1.705           | 3.936           |
| GB_3 | 0.655A               | 0.425              | 0.834              | 0.400              | 0.252            | 1.797           | 6.279           |
| GB_4 | 0.811                | 0.487              | 0.737              | 0.324              | 0.201            | 1.956           | 6.166           |

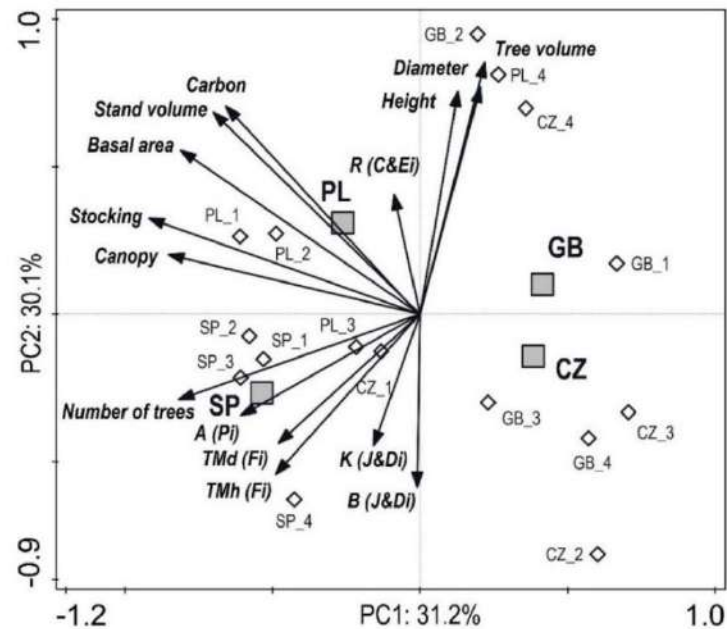
Notes: A/R—statistically significant ( $p < 0.05$ ) for horizontal structure (A—aggregation, R—regularity).

### 3.3. Interactions between Production, Structure and Diversity

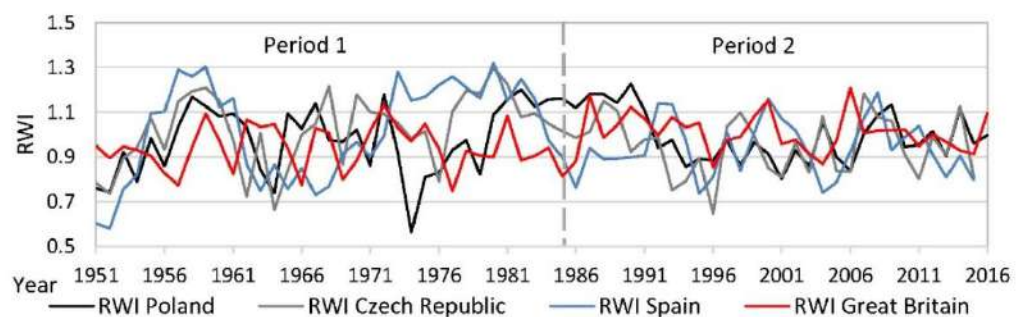
The PCA results are presented in an ordination diagram in Figure 3. The first ordination axis explains 31.2% of data variability, the first two axes combined explain 61.3% and the first four axes 87.2%. The  $x$ -axis illustrates the canopy closure and stocking (stand density index), and the  $y$ -axis represents the mean height and aggregation index with total diversity. Tree characteristics (tree volume, diameter, height) were positively correlated with the aggregation index (tendency to regularity), while these parameters were negatively correlated with structural diversity indices. Total diversity and crown differentiation decreased with the increasing mean height and diameter of trees. Stand volume was positively correlated with the carbon sequestration in biomass, basal area, stocking and canopy. Vertical structure and structural (height and diameter) differentiation increased with the increasing number of trees. The aggregation index was the lowest explanatory variable in the ordination diagram. Differences between all studied parameters (stand characteristics, structural diversity indices) in the ordination diagram in Figure 3 were remarkable for countries, as symbols (■) from each record were relatively distant from one another, except for Great Britain and the Czech Republic (similarity between the two countries). The lower part of the diagram was typical for stands with high structural and overall diversity, while the upper part of the graph represents areas with a high production potential and carbon sequestration.

### 3.4. Dynamics and Spectral Analysis of Radial Growth

The detrended ring-width chronologies in Figure 4 show that the difference between Periods 1 and 2 is mainly in the growth variability continuity of the curves. The period 1951–1985 was characterized by more significant fluctuations in detrendable growth than in Period 2; however, a slight exception is the samples from Great Britain, where both periods are almost identical. The most incoherent growth took place in Period 1 in Poland and Spain. Samples from the Czech Republic in Period 1 show smaller differences compared to plots from Poland. The later Period 2 shows a gradual synchronization of the growth of Scots pine across all studied habitats, especially in the period since 2000.



**Figure 3.** Ordination diagram focused on the species and environmental variables shows results of the principal component analysis of relationships between stand characteristics (Stand volume, Carbon—sequestration in biomass, Tree volume, Basal area, Diameter, Height, Number of trees, Canopy closure, Stocking—stand density index), structural diversity (R (C&Ei), A (Pi), TMd (Fi), TMh (Fi), K (J&Di), B (J&Di); see Table 3), and countries (CZ—Czech Republic, PL—Poland, GB—Great Britain, SP—Spain). Symbols indicate  $\blacksquare$  countries and  $\diamond$  permanent research plots (label: country + number of plot).



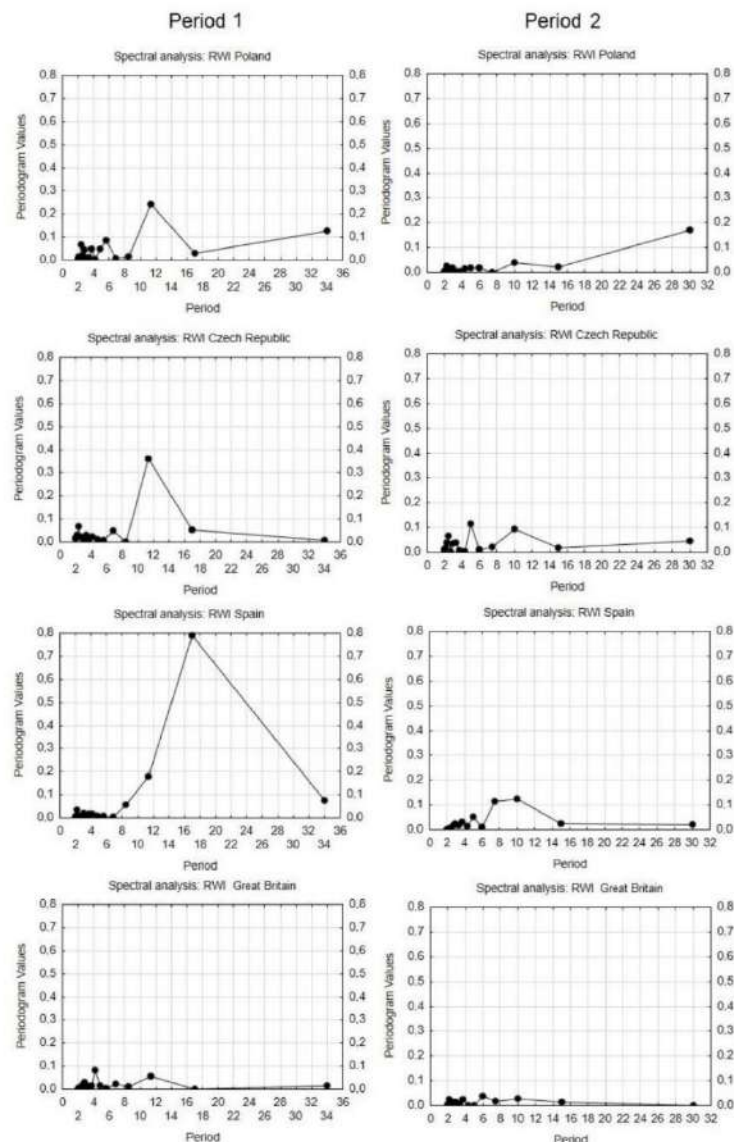
**Figure 4.** Detrended ring-width chronologies of Scots pine in Periods 1 and 2. Period 1 for 1951–1985, and Period 2 for 1985–2016. RWI means ring-width index.

In terms of NPYs, in Spain, extreme radial growth decline was seen in 1963, 1986, 1995 and 2004; in the conditions of the Czech Republic, these were the years 1962 and 1996. In Poland, a significant decline in increase was observed in 1964 and 1974. No NPYs were observed for Great Britain.

The spectral analyses of detrended data in Figure 5 show that there is a difference between Period 1 and Period 2, chiefly in the ‘Periodogram values’, where in Period 1 there are higher values than in Period 2. Larger data values in the ‘Periodogram values’ suggest more differences between cycles. Areas in Spain go through the most visible cyclical



fluctuations during Period 1, where Scots pine has the most significant cycles from 8 to 34 years according to the periodogram values. In contrast, the smallest cyclical fluctuations are in areas in Great Britain, where the ‘Periodogram values’ are the lowest of our variants, and there is not much difference between Periods 1 and 2. Overall, Period 1 shows the greatest cyclical fluctuations at all research sites. In contrast, Period 2 shows smaller cycles in the radial growth of pine, as confirmed by Figures 4 and 5.



**Figure 5.** Spectral analysis ‘Periodogram’ of RWI for Poland, Czech Republic, Spain and Great Britain in Periods 1 and 2. Period 1 is calculated for 36 cases (1951–1985), and Period 2 is calculated for 32 cases (1986–2016). RWI means ring-width index.

Cyclical fluctuations of detrendable growth in the Czech Republic and Poland share nearly the same ‘Periodogram values’; in the Czech Republic, there are slightly higher differences between growth cycles than in Poland. The same growth periods in the Czech



Republic and Poland also occur, with 11-year cycles in Period 1 having the greatest value. In Period 2, the 5- and 11-year cycles are more pronounced. In contrast to Poland, the 30-year cycles are more pronounced for the Czech Republic in Period 2, according to the periodogram values, in contrast to Period 1. Furthermore, there are 4- and 11-year cycles in Great Britain in Period 1, but in Period 2, there are fewer 6-year cycles. In Period 2, 7- to 10-year cycles are the highest in Spain. Overall, it can be said that in six variants of eight, there are 11-year periods.

### 3.5. Effect of Temperature and Precipitation on Radial Growth

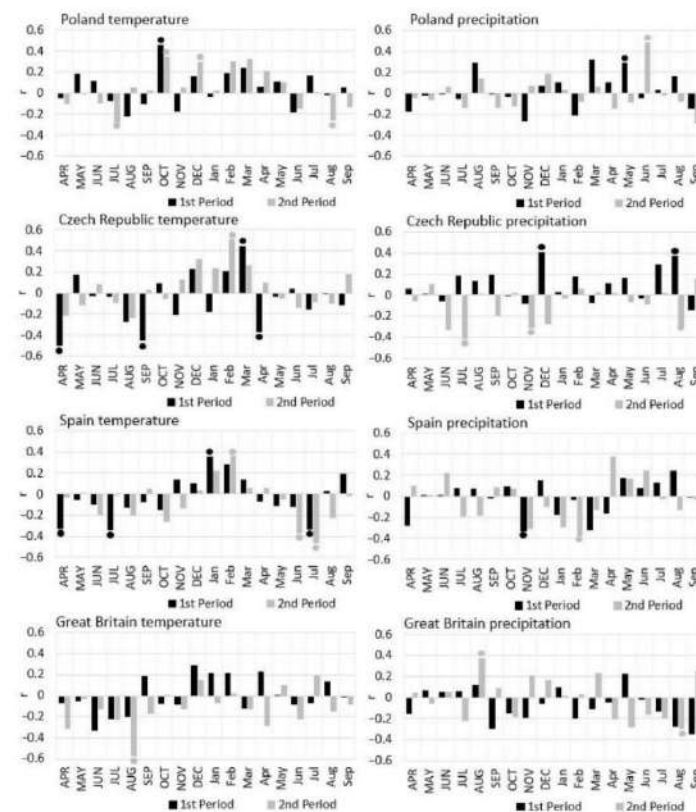
Correlation coefficients (Table 7) describe the correlations between the ring-width index and average temperature and precipitation sums in the vegetation season and average annual temperature and annual precipitation sums. The correlations between the temperatures and ring-width index do not show statistically significant values ( $p < 0.05$ ). However, the highest correlation with temperatures can be seen in the Czech Republic for temperatures in the vegetation season ( $r = -0.29$ ) in Period 1. Spain shows a high correlation with temperature in the vegetation season in Period 2 ( $r = -0.27$ ). Tree rings of pine show a higher correlation of annual temperature compared to temperatures in the vegetation season, which show lower correlations, with the two exceptions already mentioned above. Precipitation totals have mostly negative correlations with the ring-width index, but all statistically significant values are positive. Higher correlations are shown in vegetation season precipitation with tree-ring growth. Significant correlations are for Period 1 tree-ring growth with precipitation in the vegetation season ( $r = 0.40$ ) and annual precipitation ( $r = 0.38$ ). Spain also shows a significant correlation, where Period 2 is positively correlated with precipitation in the vegetation season ( $r = 0.39$ ). The most negative correlations between precipitation and the growth of tree rings are evident for values from Great Britain. Correlations between growth in Periods 1 and 2 tend to be negative. These correlations are positive in the case of the average annual temperature for locations in Poland, and only slightly negative in the Czech Republic. The correlation trend for precipitation totals is also negative between Periods 1 and 2, except for Spain, where values show a transition from lower correlations to higher positive correlations.

**Table 7.** Correlation coefficients of ring-width index (RWI) with temperature in the vegetation season, annual temperature, seasonal precipitation and annual precipitation. Values in bold are statistically significant ( $p = 0.05$ ).

| Plot Name          | Time Period/Year   | Temperature in Veg. Season | Annual Temperature | Precipitation in Veg. Season | Annual Precipitation |
|--------------------|--------------------|----------------------------|--------------------|------------------------------|----------------------|
| RWI Poland         | Period 1/1951–1985 | 0.03                       | 0.15               | 0.21                         | −0.02                |
|                    | Period 2/1986–2016 | 0.01                       | 0.18               | −0.01                        | −0.12                |
| RWI Czech Republic | Period 1/1951–1985 | −0.29                      | −0.01              | <b>0.40</b>                  | <b>0.38</b>          |
|                    | Period 2/1986–2016 | −0.07                      | 0.19               | −0.13                        | −0.06                |
| RWI Spain          | Period 1/1951–1985 | −0.07                      | 0.12               | 0.02                         | −0.16                |
|                    | Period 2/1986–2016 | −0.27                      | −0.16              | <b>0.39</b>                  | −0.02                |
| RWI Great Britain  | Period 1/1951–1985 | 0.09                       | 0.16               | −0.26                        | −0.27                |
|                    | Period 2/1986–2016 | −0.03                      | −0.07              | −0.23                        | −0.09                |

Comparing both time periods, the radial growth of pine was more affected by monthly air temperature and the overall precipitation in the second period across all RPs (Figure 6). Overall, a higher number of significant correlation coefficient ( $p < 0.05$ ) months affecting growth were found, in six cases in the second period (eight significant values for all plots). In one case in the first period, we observed less frequent significant correlation values with temperature on all plots (six significant values) for temperatures in CZ, and in one case, equalized for temperatures in Spain. Generally, precipitation had a lower effect (12 significant correlation coefficients in different months—12 months) on radial growth in all

research plots than temperature (16 months). Both studied climate factors had the same effect on radial growth in the previous year (April to December—14 significant moths), such as in the current year (January to September—14 significant moths). The climate in August of the current year had the highest effect on radial growth (4× significant values).

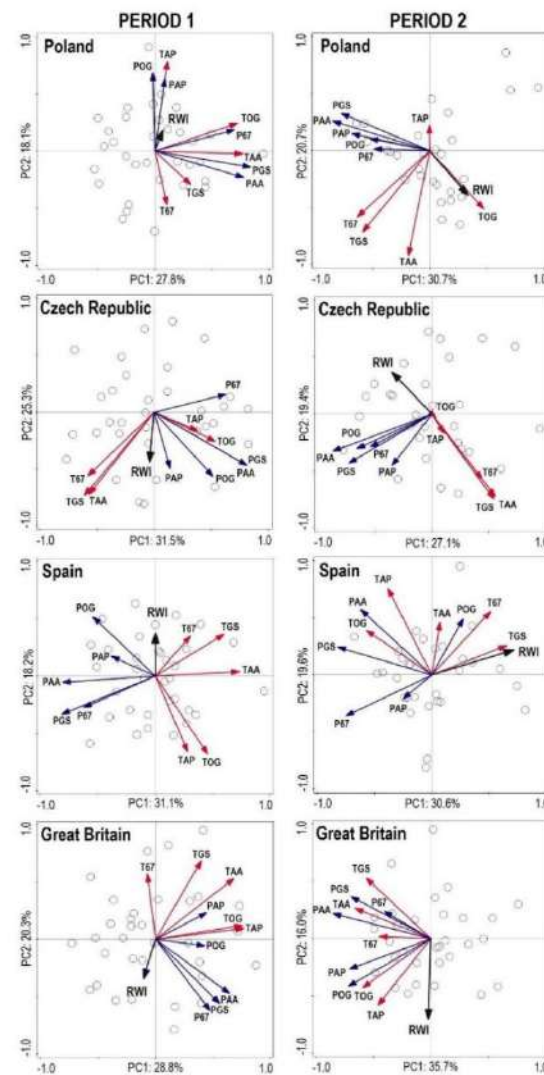


**Figure 6.** The correlation coefficients of ring-width index values for Scots pine monthly temperatures and precipitation from April (capital letter) of the previous year to September of the current year (lowercase letter). Values are divided into Period 1 (1951–1985) and Period 2 (1986–2016). Statistically significant values ( $p < 0.05$ ) are marked with a round/circle symbol.

In terms of individual countries, the lowest influence of climate factors on radial growth was recorded in Great Britain (3 significant months), followed by Poland (6 months; Figure 6). Conversely, the most sensitive pine forest to climate factors was in the Czech Republic (10 months) and in Spain (9 months). In Poland, the main limiting factor for radial growth was low temperature from October to December of the previous year, while in the case of the Czech Republic it was the period from February to March of the current year. In Spain, the main limiting factor for growth of pine was low temperature from February to March together with high temperature in June and July of the current year. Precipitation and temperature in August of the previous year played a major role in the case of Great Britain.

Interactions between the radial growth of pine and climate factors (temperature and precipitation) in different periods are presented by PCA in an ordination diagram in Figure 7 for all countries and both periods. All four ordination axes explain 71.1–79.2%, while in all cases (except the Czech Republic), there was a higher explanation of climate factors in relation to ring-width index in the second period. The diagram shows that the influence of climatic factors (precipitation vs. temperature) and its intensity on radial growth has

changed over time. Radial growth was more affected by climate factors in the second period in all four countries.



**Figure 7.** Ordination diagrams focused on the species and environmental variables show results of the principal component analysis of relationships between radial growth of pine (black color: RWI), temperature indicators (red color: TAA—annual temperature of the current year, TAP—annual temperature of the previous year, TGS—temperature in growing season of the current year, TOG—temperature outside growing season, T67—temperature in June and July of the current year) and precipitation indicators (blue color: PAA—annual precipitation of the current year, PAP—annual precipitation of the previous year, PGS—precipitation in the growing season of the current year, POG—precipitation outside growing season, P67—precipitation in June and July of the current year). Values are divided into Period 1 (1951–1985) and Period 2 (1986–2016) and countries (Czech Republic, Poland, Great Britain, Spain). Symbol ○ indicates years.



## 4. Discussion

### 4.1. Stand Production

The stand volume of the studied heterogeneous pine forests covered a broad range, from 91 to 510 m<sup>3</sup> ha<sup>-1</sup>, and a basal area from 11 m<sup>2</sup> ha<sup>-1</sup> to 47.6 m<sup>2</sup> ha<sup>-1</sup>. The stand summary characteristics were variable in each country. The high variability of stand characteristics was also confirmed in other studies, both from the conditions of native Scots pine woodlands and from managed stands [58,95,96]. The lowest production parameters were observed on RP CZ\_2, CZ\_3 and GB\_4, with natural dynamics since the 1940s [57]. Comparable stand volumes (88–176 m<sup>3</sup> ha<sup>-1</sup>) were observed in semi-natural pine stands in the Czech Republic [96]. On the other side, [97] showed very high volumes of monospecific pine stands, of 714 m<sup>3</sup> ha<sup>-1</sup>, and even 874 m<sup>3</sup> ha<sup>-1</sup> for mixed ones. The authors of [98] reported similar results from pure pine stands, with a volume of up to 714 m<sup>3</sup> ha<sup>-1</sup>.

The biomass of RP pine stands varies from 71 to 401 t ha<sup>-1</sup>, and carbon sequestration from 40 to 210 t ha<sup>-1</sup>. The high productive potential and carbon sequestration of Scots pine compared to other native or introduced tree species have also been documented in several studies in Europe [99–101]. According to [100], Scots pine stands show significantly higher values of carbon sequestration compared to spruce, Douglas fir or larch tree. Conversely, [102] and [29] state that in the conditions of European beech forests, carbon sequestration is up to twice as high as in the case of Scots pine stands, with a higher primary production. The highest increment of codominant and dominant trees in our case is evident in Great Britain (average annual increment in tree-ring width of 2.22 mm), the lowest in the Czech Republic (0.95 mm), while intermediate increment rates were evidenced in Spain (1.33 mm) and Poland (1.25 mm). The highest carbon sequence was recorded in Poland stands, probably due to the larger volume of recorded RPs. The stand volume has a positive effect on tree-stand biomass, which is related also with tree-stand age and height [103].

### 4.2. Stand Structure

The horizontal structure of the tree layer individuals was random in most RPs, aggregated in the case of three RPs, and regular only in the case of one plot PL\_4. The authors of [27] confirm that in Scots pine stands with a limited regime of silvicultural interventions, an aggregated distribution of trees is visible, while in typical production forests the distribution of individuals is regular. The random horizontal structure of individuals in heterogeneous stands was also shown by [95], where younger trees formed in such stand aggregations, while older individuals were distributed regularly. Based on the spatiotemporal analysis, [104] observed in uneven-aged Scots pine-dominated forests a shift from a random to a clumped pattern of pine trees with forest ageing, while for oak trees, the spatial pattern developed toward uniform structures.

The vertical structure was relatively low in the case of Great Britain and high in the case of Spain, with values typical for selection forests. This is also the case for the diameter, height and crown differentiation. However, the structural differentiation of stands was generally low to medium for most RPs. Higher structural differentiation of Scots pine stands in Spain can be explained by the typical mountain environment, management history [59,60] and significant pine mortality due to climate change in the entire Valsaín region, including the studied site [61]. According to studies dealing with water stress [15,105], we can assume that the lack of moisture was the reason for significant changes in the structure of pine stands also in this case. The study in [106] mentions that diameter differentiation is significantly higher in heterogeneous stands, but based on [73], the diameter differentiation in RPs (index values 0.200–0.428) was low to medium. The same applies to the height differentiation (index values: 0.122–0.372). For example, the authors of [107] claim that height differentiation in heterogeneous stands with a limited economic regime tends to be significantly greater. However, in their conclusions based on comparable conditions, [106] mentions a similar range of height differentiation in Scots pine stands as in our study. The crown differentiation index amounted to 1.101–2.642, indicating low to high differentiation [74]. These values are comparable to [27].



#### 4.3. The Effect of Climate on the Radial Growth of Pine

We found a significant effect of climatic factors on radial growth, where temperature and precipitation affected pine growth significantly more in the second period (1986–2016) of ongoing climate change compared to the first one (1951–1985). Climate change is behind the widespread dieback of pine forests in almost all of Europe. The main abiotic factors causing pine dieback are the lack of precipitation and the increase in temperature [8–13,108–110]. Dry periods also greatly affect the radial growth of Scots pine. Low correlation coefficients ( $r = 0.3$  to  $-0.3$ ) were observed between monthly precipitation values and temperature and tree-ring growth. The lowest radial growth was observed in pine trees at sites in Great Britain. A minimal correlation between the increment and precipitation is reported, for example, by a study from Sweden; [111] claims that, on the contrary, it is the temperature that significantly affects the radial growth of pine. The results show the negative impact of rainfall on pine trees in Spain, where there is an uneven distribution of precipitation during the vegetation season. Their study also mentions the effect of temperature on the radial growth of pine. While warming has a noticeable negative impact on growth [110], statistically, the authors are not able to confirm this effect. The absence of correlations between precipitation and temperature and the increase of tree-ring width at sites in Great Britain can be partly explained by the presence of the Gulf Stream, which ensures a significant warming of the western shores of Europe, especially in winter, thus maintaining a mild climate [112] and reducing the frequency of extreme weather fluctuations [113]. However, we are aware that the possibility of influencing the growth of trees by the Gulf Stream can be called into question by the location of the research sites, i.e., inland with an altitude of 250–280 m a.s.l.

Overall, concerning all the investigated sites, monthly precipitation showed less significant correlation with increment than monthly temperatures, except for the locations in Great Britain, where more significant correlations with precipitation were found. This finding is surprising given the claims of other authors [114], who found in the climatic conditions of Great Britain that temperature has a greater influence on the increment than the total precipitation. Similarly, [114] and [115] report that the lack of precipitation affects the diameter increment of pine trees. The results of our study confirm that temperature is the main factor determining the radial growth of pine, which is shown by the higher correlations of monthly temperatures to radial growth. However, it is also necessary to add that the growth of Scots pine, as well as other trees, could also be affected by air pollution in the last century [116–118].

#### 4.4. Cyclic Tree-Ring Growth of Pine Trees

Spectral analyses showed a difference between Period 1 and Period 2. A substantial decrease in fluctuations in the tree-ring index and loss in the growth cyclicality of pine was observed in the second period, likely affected by ongoing climate change. The explanation for this phenomenon may be a smaller effect of winter temperatures on pine, which was described in Estonia [119]. Moreover, the effect of winter temperatures is positively correlated with pine RWI at three research sites, with the exception of the UK research plot.

The high-frequency oscillations in 2 to 7 years on Scots pine might be associated with the frequent changing in the temperature and precipitation [120,121]. However, these high-frequency signals in RWI are lesser compared to the lower oscillations (larger RWI cycles). Moreover, it was shown that in six out of eight cases, in the spectral analyses for the research plots, there was a repetition of a 9- to 11-year period. This cycle can be linked with the influence of the solar cycle that has been described for precipitation and temperature across Europe [122,123] and can be observed in the tree-ring series of many tree species. The 11-year growth cycle has been recorded on forest tree rings throughout Europe, on European beech, for example, in the Czech Republic, Italy [124–126], and Bulgaria [127]. Scots pine forests also reflected solar cycles, for example, in western Russia [87,88,120]. The solar cycle is involved in weather that is either stale or changeable [122,128]. Overall,

the cyclical processes of radial growth of pine may vary, but across the results, it is the aforementioned 11-year cycle that can be found as a common factor in our results.

## 5. Conclusions

Scots pine forests representing a close-to-nature management approach (Czech Republic, Poland and Spain) and semi-natural forests in Great Britain showed high diversity and vertical structure. These forest stands also reached high potential in terms of carbon sequestration and biomass productivity. In all study sites, close-to-nature management and natural development have led to high variability of stand structures, which is desirable for increasing the resilience of forest stands. Tree-ring analyses from all four countries showed a difference in the fluidity of radial increment curves in Period 1 (1951–1985) and Period 2 (1986–2016). Data reveal the presence of 11-year growth cycles in Period 1, while Period 2 was characterized by the prevailing loss of these cycles. On the contrary, the effect of climate factors and stress was significantly higher in Period 2 compared to Period 1. The results also partially confirm that temperature is the main factor influencing the radial growth of pine, rather than precipitation totals. Locations in Great Britain are an exception, where a mild relationship between precipitation and temperature and tree growth was recorded. Scots pine thrives in sites with balanced precipitation and moderate temperatures, characteristic of an oceanic climate. The highest average annual increment of dominant and codominant trees in Great Britain also demonstrated this. Scots pine's reaction to climatic variables was more sensitive in Mediterranean and continental climate conditions. Forest management affects the structural and production characteristics of pine stands, and the growth of pine itself changes as a result of climate change, including climate resistance and cyclicity dynamics.

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**Data Availability Statement:** The data presented in this study are available on request from the corresponding author.

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### 5.3.2 1. publikace: *Přirozená dynamika v porostech borovice lesní jako model zvyšování její adaptability?*

**Originální název:** Stand dynamics in natural Scots pine forests as a model for adaptation management?

**Časopis:** Dendrobiology (časopis zařazen do databáze SCOPUS a WOS, aktuálně IF – 1.4, Q2)

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#### **Souhrn:**

Cílem výzkumu bylo popsat charakter přirozeného vývoje porostů borovice lesní na přirozených borových stanovištích, a to ve vztahu k jejich ekologické stabilitě, adaptabilitě na klimatické změny a imisnímu poškození.

Během hodnocení porostů bez přímého vlivu člověka byla v letech 2006 a 2016 posuzována jeho horizontální a vertikální struktura a druhová diverzita. Inventarizace se zabývala jedinci stromového patra, mrtvým dřevem a přirozenou obnovou každé z celkem 6 výzkumných ploch (0,25 ha) na území Přírodní rezervace (PR) Kostelecké bory (ČR). Na zájmových plochách bylo také odebráno vždy 25 dendrochronologických vzorků (celkem tedy 150 vzorků) pro následnou dendrochronologickou analýzu s cílem zjištění šířky jednotlivých letokruhů.

Šířka letokruhů byla korelována s klimatickými údaji (srážky, teplota) v jednotlivých letech, zároveň také s údaji o imisích SO<sub>2</sub> (SO<sub>2</sub> z let 1988–2015, NO<sub>x</sub> a AOT40F – expozice ozónu z let 1992–2015). Opakovaná inventarizace porostů potvrdila, že se od roku 2006 do roku 2016 zvýšila zásoba porostu o 26,0 %, tedy na 136 m<sup>3</sup>/ha (108 m<sup>3</sup>/ha v roce 2006), zároveň se zvýšil také objem mrtvého dřeva o 127,2 %, tedy na 27 m<sup>3</sup>/ha (12 m<sup>3</sup>/ha v roce 2006). Horizontální struktura stromového patra a přirozené obnovy byla převážně agregovaná až zcela náhodná. Výraznější změny v biodiverzitě a charakteru struktury porostu byly zjištěny především u přirozené obnovy (21,5 %) oproti stromovému patru (2,8 %). Souhrnně lze tvrdit, že významný nedostatek vláhy ve vegetačním období a zároveň velmi vysoké teploty z předchozího podzimu a zimy byly limitujícími faktory pro radiální růst dospělých jedinců borovice lesní. Radiální růst negativně koreloval s koncentracemi SO<sub>2</sub> (P < 0,01) a expozicí ozónu (P < 0,05). Koncentrace NO<sub>x</sub> měly nicméně nízký vliv na radiální růst. Lze také potvrdit, že přirozená dynamika lesa zde měla pozitivní vliv na biodiverzitu stromového patra, stejně jako na množství mrtvého dřeva ve zdejších borových porostech. Samovolný vývoj porostu v tomto případě představuje vhodný vzor pro management obdobných porostů.



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## Stand dynamics in natural Scots pine forests as a model for adaptation management?

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**Abstract:** The paper deals with the dynamics of structure, diversity and growth of natural pine stands without direct human impact during the ten-year period in Nature Reserve (NR) Kostelecké bory, Czech Republic. The objective was to determine the main characteristics of the spontaneous development of Scots pine (*Pinus sylvestris* L.) forest stands in relation to their naturalness, ecological stability and adaptation to climate change and air pollution stress.

Horizontal and vertical structure and species diversity of the tree layer, dead wood and natural regeneration of each permanent research plot (PRP) were evaluated ( $n = 6$ ,  $50 \times 50$  m /0.25 ha/, Northern Bohemia, 410–425 m above sea level). The average ring series of PRPs were correlated with the climatic data (precipitation, temperature) according to individual years from the Doksy climatic station, and the air pollution data ( $\text{SO}_2$  in 1988–2015,  $\text{NO}_x$  and AOT40F – ozone exposure in 1992–2015) from Radimovice station. In 2016, the stand volume increased by 26.0% to  $136 \text{ m}^3 \text{ ha}^{-1}$  ( $108 \text{ m}^3 \text{ ha}^{-1}$  in 2006) and the volume of dead wood increase by 127.2% to  $27 \text{ m}^3 \text{ ha}^{-1}$  ( $12 \text{ m}^3 \text{ ha}^{-1}$  in 2006). The horizontal structure of tree layer and natural regeneration was predominantly aggregated to random. More distinct changes in biodiversity and structural characteristics occurred in the natural regeneration (21.5%) compared to tree layer (2.8%). The precipitation had a significantly higher effect on radial growth compared to temperature. The lack of precipitation in growing season and high temperature in previous autumn and winter were limiting factors for growth. Climatic factors had significant effect on diameter increment in July of the current year ( $P < 0.01$ ) and June of the current and previous year ( $P < 0.05$ ). Radial growth was negatively correlated with  $\text{SO}_2$  concentrations ( $P < 0.01$ ) and ozone exposure ( $P < 0.05$ ).  $\text{NO}_x$  concentrations had low effect on radial growth. The natural stand dynamics had positive effect on biodiversity and functional integrity of natural pine ecosystems.

**Keywords:** *Pinus sylvestris*, forest dynamics, stands structure, air pollution, climatic factors, Central Europe

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## Introduction

Autochthonous Scots pine (*Pinus sylvestris* L.) occurs in the Czech Republic in vegetation zones from the lowlands to the mountains. Its ecotypes are based on populations that survived the last glacial in various isolated refuges (Pefina, 1960). Contemporary autochthonous pine and pine-oak stands are the results of the vegetation development of predominantly the last 10,000 years in the postglacial period (Mikeska & Vacek, 2008). These are azonal communities which gradually evolved from the preboreal and have been preserved only in extreme habitats with the limited competitiveness of other species (Matuszkiewicz et al., 2013). We naturally find these on a large scale in the Czech Republic only on poor and dry sandy soils. In other places, its natural appearance is bound to the relatively smaller extreme locations such as the rock outcrops and the edges of the crystalline and carbonate rocks and the sandstone rock towns (Kučera, 1999; Bohn et al., 2003; Vacek et al., 2017). Among the most important works characterizing these communities in Europe belong Passarge (1963), Lilja and Kuuluvainen (2005), Rouvinen and Kuuluvainen (2005), Gaudio et al. (2011), Matuszkiewicz et al. (2013).

Scots pine is considered to be an undemanding tree with pioneer strategy (Lanier et al., 1986; Zadworny et al., 2016). Apart from the mountain ecotypes, however, it is very demanding on light (De Chantal et al., 2003; Dehlin et al., 2004; Gaudio et al., 2011). At the same time, it is highly tolerant to drought (Picon-Cochard et al., 2006; Sanchez-Gomez et al., 2006). Many of its ecotypes are adapted to the entire range of habitats (Richardson, 2000; Medail, 2001; Ostonen, 2007; Sterck et al., 2012; Reich, 2014; Uriá-Diez et al., 2017). Due to this, it is able to survive practically in any environment from waterlogged areas to xerothermic sites (Mikeska & Vacek, 2008; Zadworny et al., 2017).

Pine as important commercial tree species has expanded significantly beyond its natural habitats in Europe in the last few centuries (Zerbe & Brande, 2003; Mirschel et al., 2011). In addition to the increase of forest production, this change in species composition has led to a range of ecological problems, especially in monoculture stands (Kazda & Pichler, 1998; Zaitsev et al., 2014). Recently, there is an evident trend to transform artificial forest into ecosystems with higher degree of naturalness (Zerbe, 2002; Schou et al., 2012; Hlásny et al., 2017) and higher resistance and resilience (Déchéne & Buddle, 2010; Griess et al., 2012; Neuner et al., 2014; Allen et al., 2002; Reynolds et al., 2013; Salamon et al., 2008; Zaitsev et al., 2014). In addition, in less productive pine forests, reduction in active management has occurred in recent decades, which may also result

in positive successive changes (Vacek et al., 2017). Since 2006 the monitored stands and the whole Nature Reserve (NR) Kostecké bory have been left to spontaneous development (Vacek et al., 2012). Practically, however, these stands have not been actively managed since the 1970s.

As such, the forests left to spontaneous development can be an important source of information for understanding natural processes and deriving procedures of close-to-nature silviculture (Burrascano et al., 2011; Petritan et al., 2014; Puettmann et al., 2015; Bílek et al., 2016). Understanding the forest development in response to natural disturbances and changing environmental conditions is very important for the setting of management approaches and measures (Pham et al., 2004; Dobrowolska & Veblen, 2008; Durak & Durak, 2015).

The aim of this paper is to evaluate the structure and development of selected stands of relict pine stands left to spontaneous development in the period from 2006 to 2016. The structure of forest stands can be defined on the basis of a number of parameters (Spies & Franklin, 1991; Poage & Tappeiner, 2005). The structure includes both the vertical and the horizontal components and the species arrangement (Maltamo et al., 2005; Vacek et al., 2017). Since the relict pine stands left to spontaneous development have been scarcely explored from this point of view in Central Europe, we have focused on all the above-mentioned attributes in this paper. The basic scientific questions were as follows:

1. What are the main characteristics of the spontaneous development of natural pine forest under the given conditions?
2. Do these changes lead to higher naturalness and ecological stability of the studied stands?
3. Is the spontaneous development of pine stands on edaphically extreme sites a suitable adaptation measure to the ongoing climate change?

## Materials and Methods

### Study Area

The Kostecké bory Nature Reserve, with an area of 51.2 hectares, was declared in 2003 and forms rock crests under the hill Kostelec (433 m above sea level). The geological bedrock is formed of the Mesozoic rectangular sandstone of the middle Turon. The most widespread soil type in the area is the arenic Podzol together with the arenic Cambisol on the sandstone slopes. The predominantly sandy soils are mineral poor and low in humus content. Climatically, the NR territory is classified according to Quitt (Quitt, 1971) as a slightly warm area MT9. The average annual temperature is approximately 7.5 °C and

the average annual rainfall is around 650 mm (Tolasz, 2007). The vegetation is formed by acidophilus forest communities. The *Dicrano-Pinetum* forest types (*Pinetum relictum humile saxatile*; Preising et Knapp ex Oberdorfer 1957) are bound to the ridges and rocky edges with a shallow layer of soil, and the cranberry pine-oak forests of *Vaccinio vitis-idaeae-Quercetum roboris* forest type (Oberdorfer 1957) are found marginally on the less exposed habitats. The tree layer of both communities is dominantly formed by pine (Chytrý et al., 2010; AOPK, 2014). The herb layer consists mainly of blueberry, cranberry, and several other acidophytes. Only in extreme locations in the pine stands, a more pronounced moss and lichen layer has developed. Among the most important plant species are the Morrison spurrey (*Spergula morisonii* Boreau) and the chickweed wintergreen (*Trientalis europaea* L.) – (AOPK, 2014).

The permanent research plots (PRP) are situated in altitude 410–425 m above sea level with south-east exposition and mean slope of 5 degrees. The location of PRPs 1–6 50 × 50 m is shown in Fig. 1. According to the forest management plan (2017–2026) the

mean stand age of upper layer is 179 years, respectively 40 years of lower layer. Stand volume is 139 m<sup>3</sup> ha<sup>-1</sup> with 99% share of Scots pine and 1% of Norway spruce (*Picea abies* /L./ Karst.).

## Data Collection

To determine the tree layer structure and natural regeneration, FieldMap technology (IFER-Monitoring and Mapping Solutions Ltd.) was used to establish 6 permanent research plots (PRPs) of 50×50 m (0.25 ha) size in 2006. The same technology was used for repeated measurements of these PRPs in 2016. The positions of all individuals of the tree layer with a diameter at breast height (DBH) ≥ 4 cm were recorded. The height, height of the live crown base, and the crown projection were measured, at least in four directions perpendicular to each other. The diameter of the trees was measured with a metal calliper (accuracy 1 mm) and the heights were measured using a Vertex laser hypsometer (accuracy 0.1 m). From 25 dominant trees on each PRP, the core samples were randomly (RNG Excel) taken with Pressler

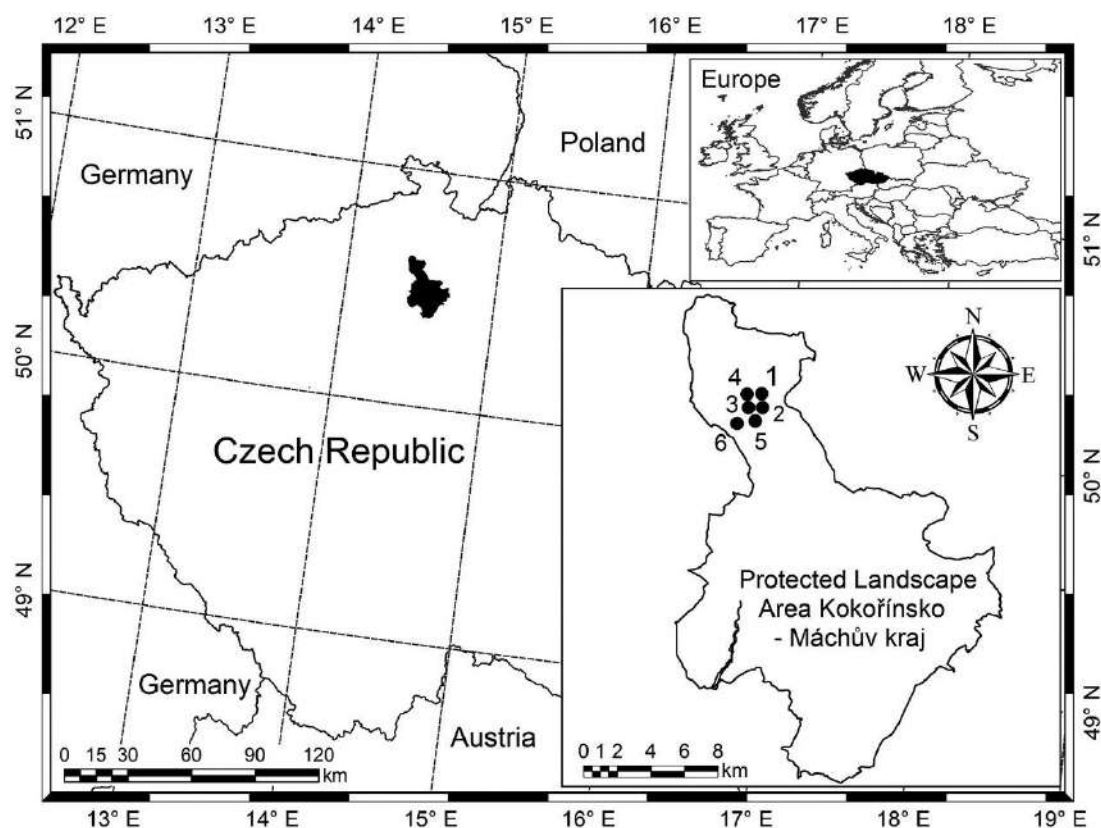


Fig. 1. Location of permanent research plots (PRP) 1–6 with natural pine forest stands in Nature Reserve Kostecké bory in Protected Landscape Area Kokořínsko – Máchův kraj

auger at DBH perpendicular to the axis of the tree along/against the slope. The annual ring width was measured (accuracy 0.01 mm) using an Olympus binocular magnifying glass on a LINTAB measurement table and registered using the TSAPWin software (www.rinntech.com).

For dead wood, the degrees of decomposition (five-point scale: 1 – undisturbed trunk, 5 – final decay phase; the scale adjusted according to Spetich et al. (2001)), its volume and share in the total stand volume were examined. The natural regeneration was measured in 2006 and in 2016 on individual PRPs at 10 × 50 m transects that are representative from the point of regeneration. The following characteristics were measured for the natural regeneration: the position, the height, the height of live crown base and the width of the crown with height gauge rod (1 cm accuracy).

## Data processing

Horizontal and vertical structure and species diversity of the tree layer, dead wood and natural regeneration of each PRP were evaluated. The basic stand characteristics of the tree layer were evaluated using the simulator SIBYLA Triquetra 10 (Fabrika & Pretzsch, TUZVO). The PointPro 2.1 (Zahradnik & Pus, CULS) program was used to calculate the characteristics of the horizontal layout of the individuals on the plot. The test of the significance of deviations from the values expected for the random arrangement of the points was made using Monte Carlo simulations. For the evaluation of biodiversity, the following indices were computed: index of non-randomness (Mountford, 1961), aggregation index (Clark & Evans, 1954), index of cluster size (David & Moore, 1954), indexes of diameter and height differentiation (Füldner, 1995), species richness index (Margalef, 1958), species heterogeneity index (Shanon, 1948), species evenness index (Pielou, 1959), Arten-profile

index and total stand diversity index (Jachne & Dohrenbusch, 1997) (Table 1). Further, the stand density index (SDI), the crown closure (CC) and crown projection area (CPA) were calculated.

The annual growth ring width series were individually cross-dated (error correction associated with the absence of missing rings) using statistical tests in the PAST application (Knibbe, 2007) and subsequently subjected to visual inspection according to Yamaguchi (Yamaguchi, 1991). If a missing tree ring was found, a tree ring with a width of 0.01 mm was inserted in its place. The individual curves from the PRP were further de-trended in a standard way and the average annual series was created in the AR-STAN program (Laboratory of Tree-Ring Research). The 30-year spline was applied (Grissino-Mayer et al., 1992). Negative significant pointer years were analyzed according to Schweingruber (Schweingruber et al., 1990). For each tree, a significant year was identified as an extremely narrow tree ring, which did not reach 40% of the average tree ring widths from the previous 4 years. The occurrence of the negative year was proven if the strong reduction in growth occurred in at least 20% of the trees in the area. The average ring series of PRPs were correlated with the climatic data (precipitation, temperature) according to individual years from the Doksy station (1948–2016; 284 m a.s.l.), and the air pollution data (SO<sub>2</sub> in 1988–2015, NO<sub>x</sub> and AOT40F – ozone exposure in 1992–2015) from Radimovice station (378 m a.s.l.). DendroClim software (Biondi & Waikul, 2004) was used to model the diameter increment depending on climatic characteristics.

In order to analyze the effect of overall meteorological conditions on the growth, Sielianinov hydrothermal coefficient (*K*) was used (Radzka & Rymuza, 2015). To determine the combined effect of average annual temperature and an annual sum of precipitation on diameter increment of pine, correlation quadratic model was used.

Table 1. Overview of the indexes describing the stand diversity and their common interpretation

| Criterion                 | Quantifiers             | Label           | Reference                     | Evaluation                                                                                 |
|---------------------------|-------------------------|-----------------|-------------------------------|--------------------------------------------------------------------------------------------|
| Horizontal structure      | Index of non-randomness | $\alpha$ (P&Mi) | Mountford (1961)              | mean value $\alpha = 1$ ; aggregation $\alpha > 1$ ; regularity $\alpha < 1$               |
|                           | Aggregation index       | $R$ (C&Ei)      | Clark and Evans (1954)        | mean value $R = 1$ ; aggregation $R < 1$ ; regularity $R > 1$                              |
|                           | Index of cluster size   | CSI (D&Mi)      | David and Moore (1954)        | mean value CSI = 0; aggregation CSI > 0; regularity CSI < 1                                |
| Vertical diversity        | Arten-profile index     | $A$ (Pri)       | Pretzsch (2006)               | range 0–1; balanced vertical structure $A < 0.3$ ; selection forest $A > 0.9$              |
| Structure differentiation | Diameter dif.           | $TM_d$ (Fi)     | Füldner (1995)                | range 0–1; low $TM < 0.3$ ; very high differentiation $TM > 0.7$                           |
|                           | Height dif.             | $TM_h$ (Fi)     |                               |                                                                                            |
| Species diversity         | Richness                | $D$ (Mai)       | Margalef (1958)               | minimum $D = 0$ , higher $D$ = higher values                                               |
|                           | Heterogeneity           | $H'$ (Shi)      | Shannon (1948)                | minimum $H' = 0$ , higher $H'$ = higher values                                             |
|                           | Evenness                | $E$ (Pii)       | Pielou (1975)                 | range 0–1; minimum $E = 0$ , maximum $E = 1$                                               |
| Complex diversity         | Stand diversity         | $B$ (J&Di)      | Jachne and Dohrenbusch (1997) | monotonous structure $B < 4$ ; uneven structure $B = 6–8$ ; very diverse structure $B > 9$ |



Table 2. Basic stand characteristics of pine forest on individual permanent research plots 1–6 in 2006 and 2016

| PRP | Year | Age<br>y | dbh<br>cm | h<br>m | v<br>m <sup>3</sup> | N<br>trees ha <sup>-1</sup> | BA<br>m <sup>2</sup> ha <sup>-1</sup> | V<br>m <sup>3</sup> ha <sup>-1</sup> | HDR  | MAI<br>m <sup>3</sup> ha <sup>-1</sup> y <sup>-1</sup> | CC<br>% | CPA<br>ha | SDI  |
|-----|------|----------|-----------|--------|---------------------|-----------------------------|---------------------------------------|--------------------------------------|------|--------------------------------------------------------|---------|-----------|------|
| 1   | 2006 | 195      | 21.1      | 11.1   | 0.230               | 624                         | 21.8                                  | 143                                  | 52.6 | 0.73                                                   | 77.0    | 1.47      | 0.48 |
|     | 2016 | 201      | 22.9      | 11.9   | 0.281               | 624                         | 25.8                                  | 176                                  | 52.0 | 0.88                                                   | 78.1    | 1.52      | 0.55 |
| 2   | 2006 | 201      | 19.6      | 10.5   | 0.205               | 720                         | 21.6                                  | 148                                  | 53.6 | 0.74                                                   | 78.5    | 1.54      | 0.49 |
|     | 2016 | 206      | 21.4      | 11.2   | 0.252               | 724                         | 26.0                                  | 183                                  | 52.3 | 0.89                                                   | 80.2    | 1.62      | 0.57 |
| 3   | 2006 | 183      | 19.4      | 12.4   | 0.221               | 560                         | 16.5                                  | 124                                  | 63.9 | 0.67                                                   | 72.3    | 1.29      | 0.36 |
|     | 2016 | 187      | 21.3      | 13.3   | 0.274               | 560                         | 19.9                                  | 153                                  | 62.4 | 0.82                                                   | 74.2    | 1.35      | 0.42 |
| 4   | 2006 | 172      | 22.0      | 12.7   | 0.295               | 316                         | 12.0                                  | 93                                   | 57.7 | 0.54                                                   | 57.8    | 0.86      | 0.25 |
|     | 2016 | 178      | 23.7      | 13.5   | 0.352               | 324                         | 14.2                                  | 114                                  | 57.0 | 0.64                                                   | 57.9    | 0.86      | 0.29 |
| 5   | 2006 | 154      | 17.3      | 8.5    | 0.134               | 572                         | 13.4                                  | 76                                   | 49.1 | 0.49                                                   | 66.8    | 1.10      | 0.31 |
|     | 2016 | 159      | 18.8      | 9.3    | 0.165               | 608                         | 16.9                                  | 100                                  | 49.5 | 0.64                                                   | 71.3    | 1.25      | 0.38 |
| 6   | 2006 | 163      | 13.7      | 7.9    | 0.074               | 836                         | 12.2                                  | 62                                   | 57.7 | 0.38                                                   | 68.3    | 1.15      | 0.32 |
|     | 2016 | 165      | 14.7      | 8.4    | 0.088               | 996                         | 17.0                                  | 88                                   | 57.1 | 0.53                                                   | 74.1    | 1.35      | 0.43 |

Notes: age – weighted arithmetic mean of ages of the trees forming the particular stand component, dbh – mean quadratic breast height diameter, h – mean height, v – average tree volume, N – number of trees per hectare, BA – basal area, V – stand volume, HDR – slenderness ratio, MAI – mean annual increment, CC – canopy closure, CPA – crown projection area, SDI – stand density index.

In order to determine the response of the stand health status to site conditions, the climatic data (the sum of precipitation and mean temperatures in the current and previous year), air pollution factors ( $\text{SO}_2$  concentrations,  $\text{NO}_x$  concentration, AOT40F) and radial growth were tested for correlations in the software Statistica 12 (StatSoft). Unconstrained principal component analysis (PCA) in Canoco 5 program (Šmilauer & Lepš, 2014) was used to analyze the relationships among climatic data,  $\text{SO}_2$  concentrations,  $\text{NO}_x$  concentration, ozone exposure and the ring width. The data were log-transformed, centered and standardized before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram.

## Results

### Tree Layer Structure and Production

In 2006, the stand density ranged from 316 to 836 trees ha<sup>-1</sup> (for pine it was 224–756 trees ha<sup>-1</sup>) with a stand density index (SDI) of 0.25–0.49 (Table 2). The stand volume was 62–148 m<sup>3</sup> ha<sup>-1</sup>, of which 61–147 m<sup>3</sup> ha<sup>-1</sup> were pines, 8–9 m<sup>3</sup> ha<sup>-1</sup> were spruces (PRP 3–5 only) and the rest was formed by silver birch (*Betula pendula* Roth). The highest stand volume was found on PRP 2, where it reached 148 m<sup>3</sup> ha<sup>-1</sup> and the lowest on PRP 6, 62 m<sup>3</sup> ha<sup>-1</sup>. The highest stand volume of pine was also found on PRP 2 (147 m<sup>3</sup> ha<sup>-1</sup>) and the lowest on PRP 6 (61 m<sup>3</sup> ha<sup>-1</sup>). The stand basal area ranged from 12.0–21.8 m<sup>2</sup> ha<sup>-1</sup> (pine

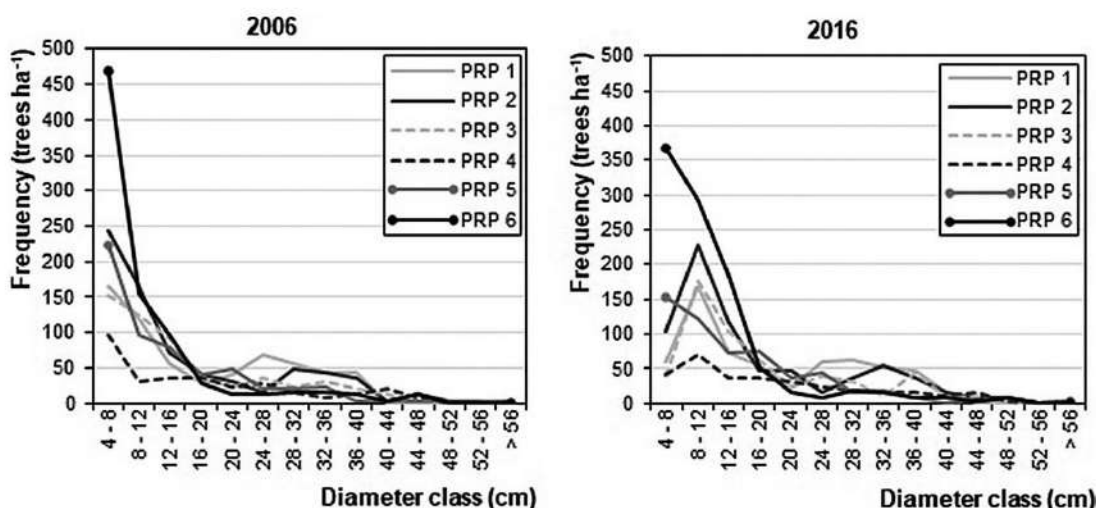


Fig. 2. Histograms of diameter structure of the tree layer on permanent research plots 1–6 Kostelecké bory in 2006 and 2016

9.1–21.4 m<sup>3</sup> ha<sup>-1</sup>) and the mean annual increment was 0.4–0.7 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup> (pine 0.4–0.7 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup>).

In 2016, number of live trees ranged from 324 to 996 trees ha<sup>-1</sup> (pine 224–884 trees ha<sup>-1</sup>) with SDI of 0.29–0.57 (Table 2). The stand volume was 88–183 m<sup>3</sup> ha<sup>-1</sup>, of which 84–182 m<sup>3</sup> ha<sup>-1</sup> were pines, 12–14 m<sup>3</sup> ha<sup>-1</sup> spruces (PRP only 3–5), and the rest was formed by birch. The highest stand volume was found on PRP 2 with 183 m<sup>3</sup> ha<sup>-1</sup> (pine 182 m<sup>3</sup> ha<sup>-1</sup>) and the lowest on PRP 6 with 88 m<sup>3</sup> ha<sup>-1</sup> (84 m<sup>3</sup> ha<sup>-1</sup>). The stand basal area ranged from 14.2 to 26.0 m<sup>2</sup> ha<sup>-1</sup> (pine 10.5–25.7 m<sup>2</sup> ha<sup>-1</sup>) and the mean annual increment was 0.5–0.9 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup> (the pine is 0.4–0.9 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup>). In 2016, the canopy classification ranged from 0.58 to 0.80 in crown closure and from 0.86 to 1.62 in crown area. Comparing year 2006 and 2016, the highest increase was observed in stand volume (+26.0%) and in basal area (+22.9%), while it was the lowest in crown closure (+3.6%), followed by number of trees (+5.7%).

The highest pine trees reached a height of 20–23 m. The highest individuals of admixed spruce on PRPs 3 and 4 reached 20–22 m, but spruce mostly occurred in the middle storey. The birch was predominantly in the middle storey with the highest individuals between 13–15 m. In the course of 10 years, the average height increase of pine and spruce was up to 1.0 m, in case of birch, it was 1.2–1.8 m. In terms of the diameter structure, the diameter class of 4–8 cm prevailed in 2006, only on the PRP 3 prevailed the diameter class of 8–12 cm (Fig. 2). The average DBH of the trees at the PRP was 21.3–23.7 cm, in case of pine, it was 21.6–24.41 cm and the spruce 14.4–17.9 cm.

### Tree Layer Biodiversity

In 2016, the vertical structure according to A index was moderately diverse (index values 0.55–0.62)

on PRPs 1–5 and highly varied on PRP 6 (0.72; Table 3). Diameter differentiation  $TM_d$  was predominantly medium (0.29–0.35) and height differentiation  $TM_h$  was low on PRPs 1–4 and 6 (0.22–0.29), only on PRP 5 it was medium (0.33). In terms of species diversity according to  $H'$  entropy, the species heterogeneity was very low on PRPs 1 and 2 (0.03–0.08), low on PRPs 3, 5 and 6 (0.11–0.23) and PRP 4 had medium biodiversity (0.37). On the basis of species evenness  $E$ , PRPs 1 and 2 had low diversity (0.10–0.27), PRPs 3, 5 and 6 had medium diversity (0.35–0.47) and PRP 4 was of high biodiversity (0.61). The total complex diversity  $B$  indicated uneven stand structure (6.34–7.10), only PRP 6 has even stand structure (5.9). The biodiversity of the tree layer changed between 2006 and 2016. Generally, biodiversity increased during the time on PRPs (+2.8%), especially in species heterogeneity  $H'$  (+5.1%) and height differentiation  $TM_h$  (+3.3%). In total diversity  $B$ , as the only one, increase was monitored on all PRPs (+1.2%).

The horizontal structure of the tree layer in 2006 and 2016, according to valuated  $\alpha$ ,  $R$  and  $CSI$  indices, is predominantly random on PRPs (Table 3, Fig. 3). An exception is PRP 2 and 6 with the highest stand density, where the distribution of trees was aggregated. During stand dynamics, the horizontal structure of the tree layer changed only slightly with no apparent trend to clustering or more regular horizontal structure (Table 3).

### Interactions of Radial Growth, Climate Factors and Air Pollution

The average tree ring width in the years 1800–2016 on PRP 1 was 0.65 mm ( $\pm 0.5$  SD), PRP 2 0.77 mm ( $\pm 0.3$  SD), PRP 3 0.68 mm ( $\pm 0.4$  SD), PRP 4 values 0.77 mm ( $\pm 0.3$  SD), PRP 5 values of 0.96

Table 3. Biodiversity indices of pine forest stands on permanent research plots 1–6 in 2006 and 2016

| PRP | Year | A     | $TM_d$ | $TM_h$ | $H'$  | E     | $\alpha^*$         | $R^*$              | $CSI^*$            | B     |
|-----|------|-------|--------|--------|-------|-------|--------------------|--------------------|--------------------|-------|
| 1   | 2006 | 0.556 | 0.291  | 0.243  | 0.078 | 0.253 | 0.943              | 1.063              | 0.058              | 6.273 |
|     | 2016 | 0.573 | 0.297  | 0.255  | 0.081 | 0.269 | 0.970              | 1.040              | 0.053              | 6.366 |
| 2   | 2006 | 0.566 | 0.321  | 0.288  | 0.026 | 0.091 | 1.343 <sup>A</sup> | 0.933 <sup>A</sup> | 0.372 <sup>A</sup> | 6.461 |
|     | 2016 | 0.551 | 0.315  | 0.278  | 0.029 | 0.096 | 1.332 <sup>A</sup> | 0.941 <sup>A</sup> | 0.358 <sup>A</sup> | 6.483 |
| 3   | 2006 | 0.557 | 0.378  | 0.293  | 0.229 | 0.457 | 1.337              | 0.982              | 0.229              | 6.382 |
|     | 2016 | 0.583 | 0.351  | 0.287  | 0.212 | 0.444 | 1.303              | 0.998              | 0.212              | 6.500 |
| 4   | 2006 | 0.605 | 0.337  | 0.261  | 0.342 | 0.601 | 1.123              | 1.014              | 0.056              | 7.063 |
|     | 2016 | 0.624 | 0.351  | 0.287  | 0.365 | 0.606 | 1.102              | 1.030              | 0.065              | 7.104 |
| 5   | 2006 | 0.613 | 0.347  | 0.318  | 0.203 | 0.452 | 1.243              | 0.938              | 0.216              | 6.841 |
|     | 2016 | 0.631 | 0.373  | 0.333  | 0.225 | 0.472 | 1.267              | 0.980              | 0.206              | 6.964 |
| 6   | 2006 | 0.703 | 0.264  | 0.203  | 0.101 | 0.338 | 2.502 <sup>A</sup> | 0.853 <sup>A</sup> | 1.799 <sup>A</sup> | 5.798 |
|     | 2016 | 0.720 | 0.286  | 0.215  | 0.106 | 0.352 | 2.538 <sup>A</sup> | 0.886 <sup>A</sup> | 1.860 <sup>A</sup> | 5.853 |

Notes: A (Pri) – Arten-profile index,  $TM_d$  (Fi) – diameter differentiation,  $TM_h$  (Fi) – height differentiation,  $H'$  (Shi) – species heterogeneity,  $E$  (Pii) – species evenness,  $\alpha$  (P&Mi) – index of non-randomness,  $R$  (C&Ei) – aggregation index,  $CSI$  (D&Mi) – index of cluster size,  $B$  (J&Di) – total stand diversity.

\*statistically significant for horizontal structure (<sup>A</sup> – aggregation, <sup>R</sup> – regularity); changes: \ – decrease, / – increase.

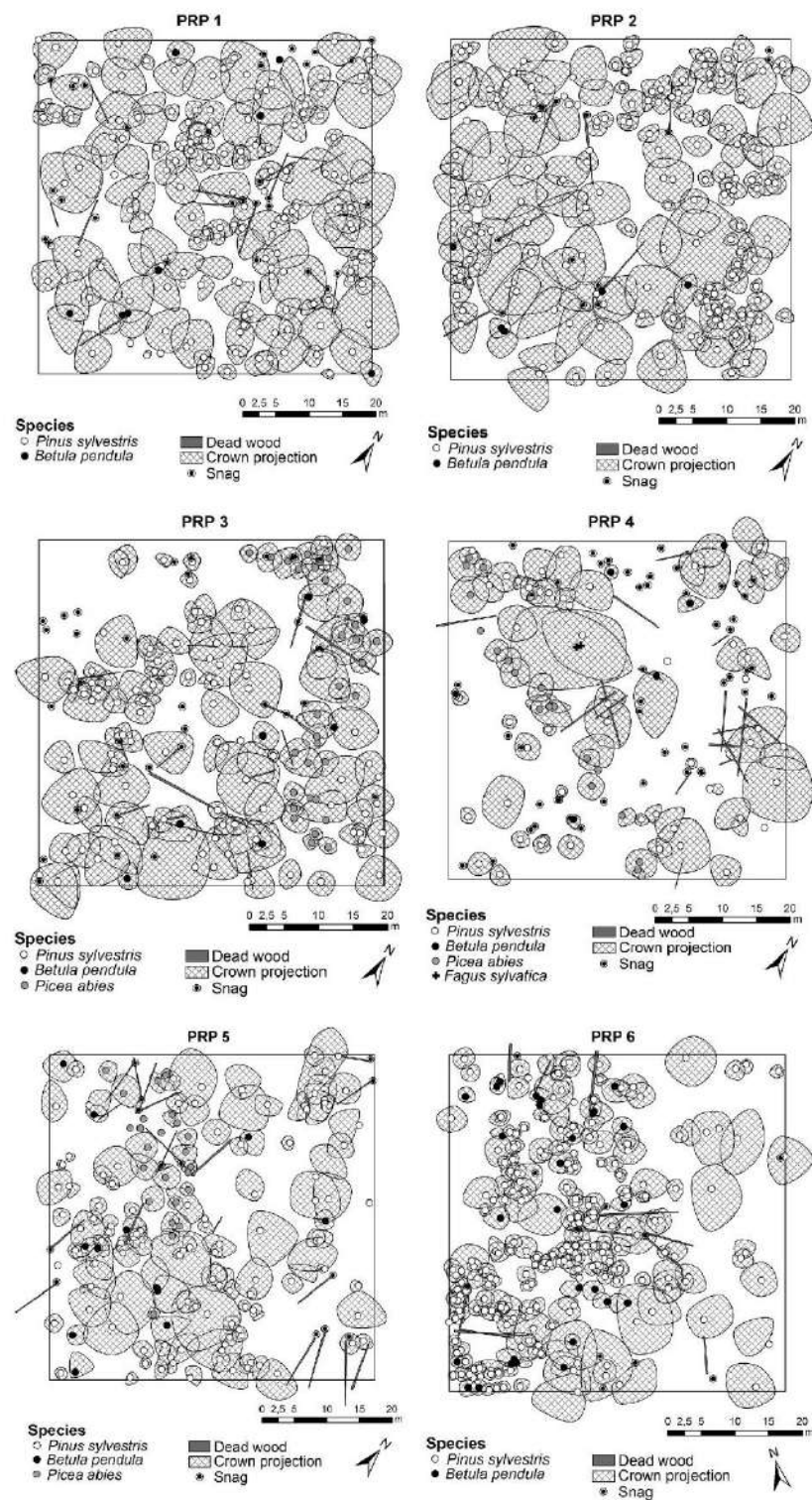


Fig. 3. Horizontal structure of natural pine stands on permanent research plots 1–6 in Kostelecké bory in 2016

mm ( $\pm 0.3$  SD), and PRP 6 values of 0.72 mm ( $\pm 0.4$  SD). Comparison of the average ring-width curves for individual PRPs showed their high reliability of synchronization. From the regional standardized dendrochronology, there is obvious a relatively heterogeneous radial growth in the years 1800–2016 (Fig. 4). The age of the upper layer pine trees was between 237–264 years. The years 1976 were analysed as negative pointer years for low radial growth of pine (January–July precipitation amount 161 mm, mean 340 mm in 1948–2016).

Correlations of diameter increment with the average monthly temperatures and precipitation in 1948–2016 indicated some statistically significant values from software Dendroclim (Fig. 5). There were significant negative correlations of diameter increment with temperature in September of the previous year ( $r = -0.29$ ) and in January of the current year ( $r = -0.23$ ). Conversely, precipitation amount had a predominantly significant positive effect on radial growth, especially in June and July of the previous year ( $r = 0.22$  and  $0.27$ ) and from May to July of the current year ( $r = 0.22$ – $0.34$ ). The negative effect

of the precipitation was observed only in November of the previous year ( $r = -0.22$ , Fig. 5).

The main factor influencing the diameter increment of pine in the study area was identified as the precipitation (Fig. 6). Diameter increment only slightly increased with increasing annual mean temperature, while the considerable increase of growth was observed with increasing annual sum of precipitation. According to hydrothermal index  $K$ , climate (combination of temperature and precipitation) had significant positive impact on radial growth in July of the current year ( $r = 0.37$ ,  $P < 0.01$ ) and June of the current and previous year ( $r = 0.24$ – $0.29$ ,  $P < 0.05$ ).

In addition to climatic factors, air pollution had significant effect on radial growth. Diameter increment was significantly negatively correlated with  $\text{SO}_2$  concentrations (1988–2015), especially in growing season ( $r = -0.56$ ,  $P < 0.001$ ). In terms of month  $\text{SO}_2$  concentrations, there was no significant correlation of radial growth with December, January, and February ( $P > 0.05$ ), while significant negative correlation was observed in all other months with the highest negative effect in July ( $r = -0.58$ ,  $P < 0.001$ ).

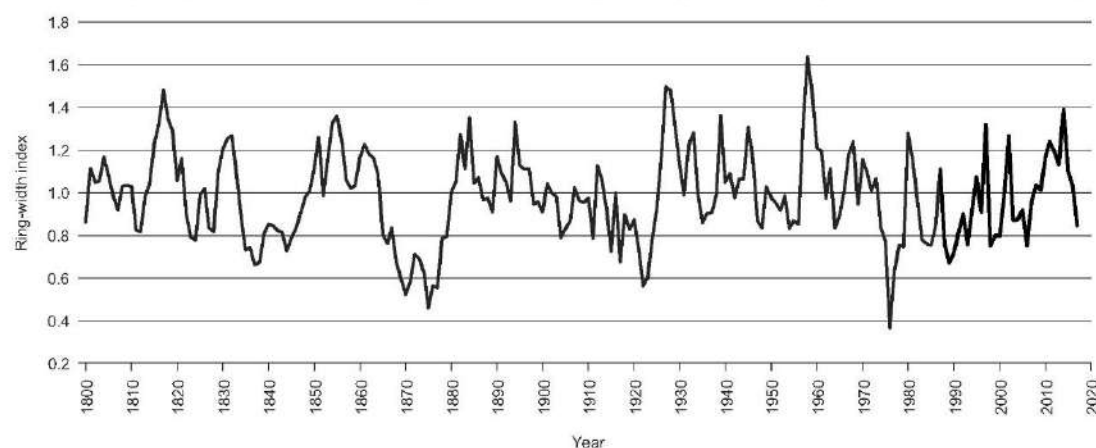


Fig. 4. Standardized average ring width chronology for pine after age detrending in period 1800–2016

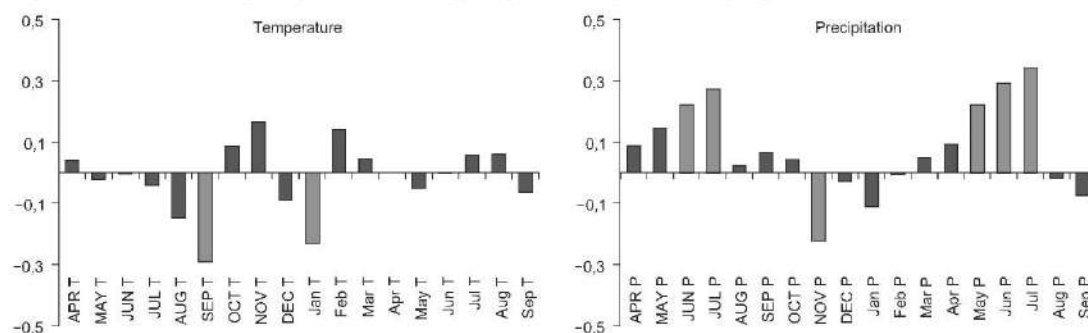
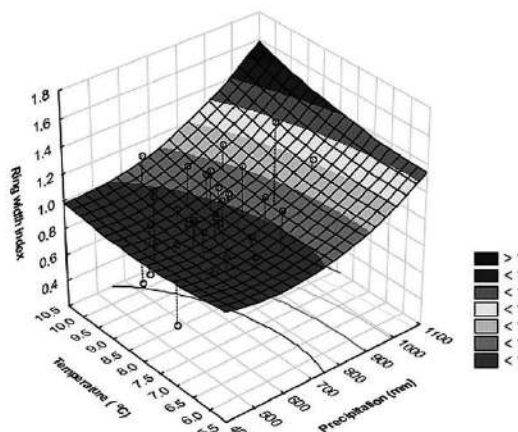
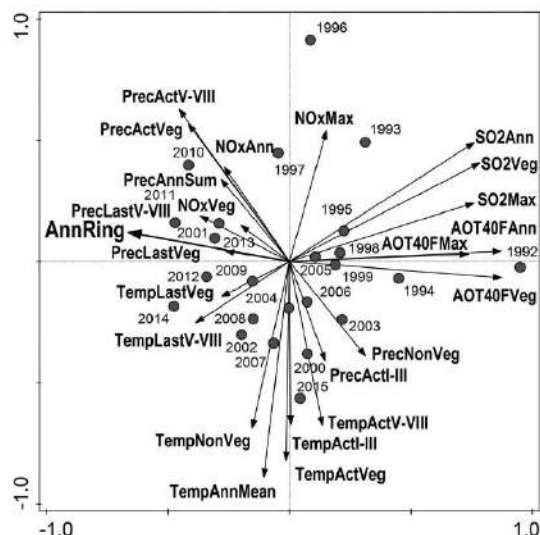


Fig. 5. The values of correlation coefficients of the regional residual index tree ring chronology with the monthly temperatures and precipitation (period 1948–2016) from May of the previous year (capital letter) to September of the current year (small letters). Significant values are displayed by light grey colour ( $\alpha = 0.05$ )





Results of the PCA are presented in an ordination diagram in Fig. 7. The first ordination axis explains 23.7% of the variability in the data, the first two axes together 43.4% and the first four axes together 69.9%. The first axis  $x$  represents annual ring width, the sum of precipitation in growing season of the previous year with ozone exposure. The second axis  $y$  represents  $\text{NO}_x$  concentrations with mostly temperature indicators. Radial growth was positively correlated with precipitation in growing season and from May to



August of the previous and current year, while these parameters were negatively correlated with  $\text{SO}_2$  concentrations and ozone exposure.  $\text{NO}_x$  concentrations had low effect on radial growth. With respect to time, radial growth during the first third of the investigated period (the 1990s) was related more to strong air pollution ( $\text{SO}_2$  concentrations and ozone exposure), whereas during the second part of the investigated period (2000s, 2010s) it was related more to climatic factors. The lowest contribution of interactions was observed in  $\text{NO}_x$  concentrations in growing season.

Notes:  $SO_2Veg$  – mean  $SO_2$  concentrations in vegetation season,  $SO_2Ann$  – mean annual  $SO_2$  concentrations,  $SO_2Max$  – maximal annual  $SO_2$  concentrations,  $NO_3$  –  $NO_3$  concentrations,  $AOT40F$  – ozone exposure,  $TempActAnn$  – mean annual temperature,  $TempActVeg$  – mean temperature in the current vegetation season,  $TempLastVeg$  – mean temperature in the previous vegetation season,  $TempActV-VIII$  – mean temperature in May–August of the given year,  $TempLastV-VIII$  – mean temperature in May–August of the previous year,  $TempActI-III$  – mean temperature in January–March of the given year,  $TempNonveg$  – mean temperature in the non-vegetation season (from October of the previous year to March of the given year),  $Prec$  – sum of precipitation.

The dynamics of parameters in the course of 24 years was remarkable especially for the period from 1992 to 1998 as marks of each record are relatively distant from one another whereas marks after the year 1998 were relatively closer together in the diagram.

### Structure and Dynamics of Dead wood

The volume of dead wood ranged in 2016 between 15.8–39.3 m<sup>3</sup> ha<sup>-1</sup> (Table 5). Dead wood volume accounts for 8.0–25.6% of the total wood volume (live and dead trees). The percentage of lying dead wood ranged between 22.0–58.2% (41.9% on average) of the total dead wood volume. Overall, the share of standing dead wood prevailed (58.2%). Dead wood consisted of pine (93.4%), spruce (4.7%) and birch (1.9%). Of the lying dead wood, there were 56.3% in the 4<sup>th</sup> stage of decay, 25.4% in the 3<sup>rd</sup> stage, 11.7% in the stage 5, 5.7% in stage 2 and 0.9% in stage 1 (Table 5).

The proportion of standing dead wood ranged from 41.8–78.0% of the total dead wood volume. Standing dead wood was mainly pine (96.5%) and the rest was spruce. The most volume of dead wood was in the 2<sup>nd</sup>

degree of decomposition (61.8%), in the 3<sup>rd</sup> degree it was 26.0%, in the 1<sup>st</sup> degree 11.6% and in the 4<sup>th</sup> degree 0.6%. The horizontal structure of the standing and lying dead wood was random on all PRPs.

The total volume of dead wood in 2006 was significantly lower in comparison with 2016 (7.2–21.4 m<sup>3</sup> ha<sup>-1</sup>; Table 5). During 10 years, volume of dead wood increased by 127.2%. Dead wood accounted for 3.9–13.2% of the total wood volume (live and dead trees). The share of lying dead wood prevailed slightly (53.7%), while standing dead wood prevailed in 2016 (58.4%). Moreover in 2006, dead wood of birch was not found. Nearly no changes occurred in the proportion of dead wood in the individual stages of decomposition.

### Structure, Dynamics and Game Damage of Natural Regeneration

The number of individuals of natural regeneration ranged from 1,700 (PRP 5) to 10,250 (PRP 2) recruits ha<sup>-1</sup> in 2006 (Table 6). In the course of 10 years, the PRPs 2–6 had seen an increase in the

Table 5. The volume of standing, lying and total dead wood differentiated by the degrees of decomposition on permanent research plots 1–6 in 2006 and 2016

| PRP | Year | Degrees of decomposition of dead wood (m <sup>3</sup> ha <sup>-1</sup> ) |      |     |     |       |                 |     |     |      |     |       | Total |
|-----|------|--------------------------------------------------------------------------|------|-----|-----|-------|-----------------|-----|-----|------|-----|-------|-------|
|     |      | Standing dead wood                                                       |      |     |     |       | Lying dead wood |     |     |      |     |       |       |
|     |      | 1.                                                                       | 2.   | 3.  | 4.  | Total | 1.              | 2.  | 3.  | 4.   | 5.  | Total |       |
| 1   | 2006 | 2.4                                                                      | 5.2  | 2.3 | 0.0 | 9.9   | 0.0             | 0.3 | 1.0 | 0.0  | 0.0 | 1.3   | 11.2  |
|     | 2016 | 3.1                                                                      | 12.3 | 6.2 | 0.0 | 21.6  | 0.0             | 0.1 | 1.4 | 4.2  | 0.4 | 6.1   | 27.7  |
| 2   | 2006 | 0.5                                                                      | 2.3  | 3.5 | 0.1 | 6.4   | 0.0             | 0.4 | 0.4 | 0.0  | 0.0 | 0.8   | 7.2   |
|     | 2016 | 1.7                                                                      | 1.8  | 8.0 | 0.0 | 11.5  | 0.4             | 0.1 | 0.8 | 3.0  | 0.0 | 4.3   | 15.8  |
| 3   | 2006 | 0.2                                                                      | 2.8  | 2.2 | 0.1 | 5.3   | 0.0             | 2.1 | 1.4 | 0.7  | 0.0 | 4.2   | 9.5   |
|     | 2016 | 1.2                                                                      | 4.9  | 4.7 | 0.6 | 11.4  | 0.0             | 0.4 | 4.8 | 6.7  | 1.4 | 13.3  | 24.7  |
| 4   | 2006 | 6.3                                                                      | 9.0  | 0.0 | 0.0 | 15.3  | 0.1             | 1.4 | 3.7 | 0.9  | 0.0 | 6.1   | 21.4  |
|     | 2016 | 0.6                                                                      | 23.2 | 1.1 | 0.0 | 24.9  | 0.2             | 0.0 | 4.4 | 7.0  | 2.8 | 14.4  | 39.3  |
| 5   | 2006 | 2.4                                                                      | 2.9  | 0.0 | 0.0 | 5.3   | 0.7             | 3.1 | 1.3 | 0.0  | 0.0 | 5.1   | 10.4  |
|     | 2016 | 4.4                                                                      | 9.2  | 0.0 | 0.0 | 13.6  | 0.0             | 3.3 | 3.5 | 5.7  | 2.0 | 14.5  | 28.1  |
| 6   | 2006 | 0.5                                                                      | 6.2  | 1.4 | 0.1 | 8.2   | 0.2             | 0.5 | 2.8 | 0.6  | 0.0 | 4.1   | 12.3  |
|     | 2016 | 0.0                                                                      | 7.1  | 4.6 | 0.0 | 11.7  | 0.0             | 0.0 | 2.6 | 12.2 | 1.5 | 16.3  | 28.0  |

Table 6. Number and share of natural regeneration and mean recruit height differentiated by tree species in 2006 and 2016

| PRP | Year | Density              |       |                      |     |                      |      |                      |     | Mean height          |       |       |        |       |
|-----|------|----------------------|-------|----------------------|-----|----------------------|------|----------------------|-----|----------------------|-------|-------|--------|-------|
|     |      | Pinus                |       | Picea                |     | Betula               |      | Fagus                |     | Total                | Pinus | Picea | Betula | Fagus |
|     |      | pcs ha <sup>-1</sup> | %     | pcs ha <sup>-1</sup> | %   | pcs ha <sup>-1</sup> | %    | pcs ha <sup>-1</sup> | %   | pcs ha <sup>-1</sup> | cm    | cm    | cm     | cm    |
| 1   | 2006 | 8,250                | 94.2  | 250                  | 2.9 | 250                  | 2.9  | –                    | 0.0 | 8,750                | 137   | 14    | 6      | –     |
|     | 2016 | 7,750                | 100.0 | –                    | 0.0 | –                    | 0.0  | –                    | 0.0 | 7,750                | 280   | –     | –      | –     |
| 2   | 2006 | 9,750                | 95.2  | 250                  | 2.4 | 250                  | 2.4  | –                    | 0.0 | 10,250               | 89    | 12    | 7      | –     |
|     | 2016 | 11,500               | 97.9  | 250                  | 2.1 | –                    | 0.0  | –                    | 0.0 | 11,750               | 255   | 57    | –      | –     |
| 3   | 2006 | 7,000                | 70.0  | 250                  | 2.5 | 2,250                | 22.5 | 500                  | 5.0 | 10,000               | 92    | 16    | 61     | 29    |
|     | 2016 | 9,750                | 56.5  | 500                  | 2.9 | 6,500                | 37.7 | 500                  | 2.9 | 17,250               | 147   | 53    | 122    | 82    |
| 4   | 2006 | 6,500                | 72.2  | –                    | 0.0 | 2,500                | 27.8 | –                    | 0.0 | 9,000                | 94    | –     | 70     | –     |
|     | 2016 | 9,500                | 66.7  | –                    | 0.0 | 4,750                | 33.3 | –                    | 0.0 | 14,250               | 153   | –     | 142    | –     |
| 5   | 2006 | 1,400                | 82.4  | 100                  | 5.9 | 200                  | 11.7 | –                    | 0.0 | 1,700                | 70    | 13    | 12     | –     |
|     | 2016 | 3,900                | 100.0 | –                    | 0.0 | –                    | 0.0  | –                    | 0.0 | 3,900                | 95    | –     | –      | –     |
| 6   | 2006 | 1,300                | 72.2  | 100                  | 5.6 | 300                  | 16.6 | 100                  | 5.6 | 1,800                | 73    | 10    | 25     | 132   |
|     | 2016 | 2,800                | 93.3  | –                    | 0.0 | 100                  | 3.3  | 100                  | 3.3 | 3,000                | 109   | –     | 105    | 240   |

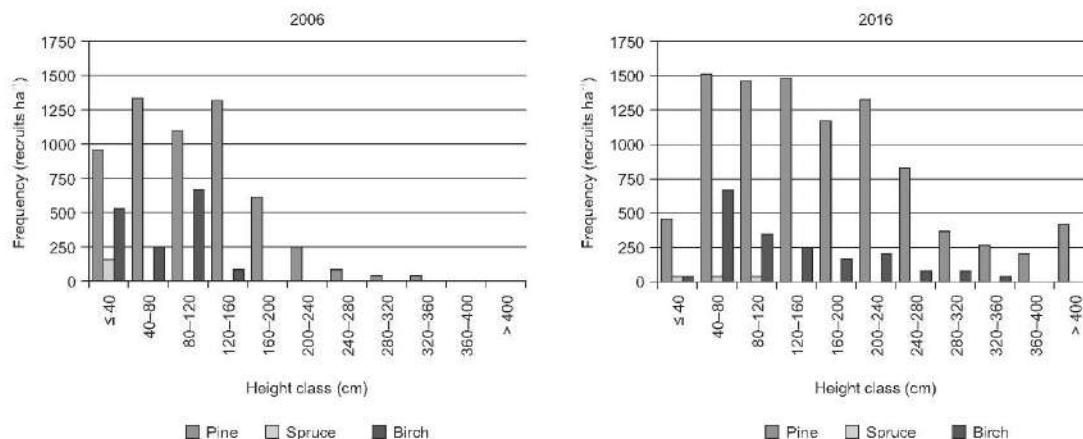


Fig. 8. The average height structure of natural regeneration on permanent research plots differentiated by tree species in 2006 and 2016

number of regeneration individuals, with only PRP 1 slightly decreasing. There occurred a significant shift towards the maturity of natural regeneration on all the PRPs (Fig. 8). In 2016, the number of natural regeneration ranged from 3,000 (PRP 6) to 17,250 (PRP 3) recruits  $\text{ha}^{-1}$  (Table 6). On average, pine represented 78.1%, spruce 1.3%, birch 19.6%, and European beech (*Fagus sylvatica* L.) 1.0% of all regeneration individuals. The average height of the pine regeneration was 95–280 cm, of spruce 53–57 cm, of birch 105–142 cm and of beech 82–240 cm (Table 6).

In 2016, the share of individuals with the terminal shoot damaged by browsing was low (pine 1.6%, spruce 8.7%, birch 0.2%), only in case of beech it was high (36.2%). The most affected were individuals with a height of 20–80 cm. Compared to 2016, the damage was significantly higher in 2006 (pine 12.2%, spruce 19.4%, birch 2.3%, beech 92.5%).

The species richness  $D$  was medium on PRP 3 and low on remaining PRPs. The species heterogeneity

according to the  $H'$  entropy index was low on PRPs 1, 2 and 5 and medium to high on PRPs 3, 4 and 6. The species evenness of regeneration according to the index  $E$  was low on PRPs 1, 2 and 5, medium to high on PRPs 3 and 6 low and very high on PRP 4. On PRPs 2 and 4, the situation was similar in 2016 and 2006. The decrease in biodiversity in the monitored years was observed on PRPs 1, 5 and 6, but it increased significantly only on PRPs 3.

The spatial pattern of the regeneration was significantly aggregated on PRPs except PRP 2 and 4 according to monitored indices in 2016 (Table 7). The clustering of the regeneration individuals according to their distance (spacing) arises also from the Ripley  $L$ -function (Fig. 9). The distinctly clustered natural regeneration pattern was on PRPs 5 and 6, slightly clustered on PRP 3. On PRP 4, the horizontal structure of the regeneration was between the clustered and random spacing. On PRPs 1 and 2, a clustered regeneration was to the distance of 0.5 m and then

Table 7. Biodiversity indices of natural regeneration on permanent research plots 1–6 in 2006 and 2016

| PRP | Year | $D$   | $H'$  | $E$   | $\alpha^*$         | $R^*$              | CSI*               |
|-----|------|-------|-------|-------|--------------------|--------------------|--------------------|
| 1   | 2006 | 0.220 | 0.157 | 0.143 | 1.709              | 0.898 <sup>A</sup> | 0.565 <sup>A</sup> |
|     | 2016 | 0.000 | 0.000 | 0.000 | 1.532              | 0.912              | 0.330              |
| 2   | 2006 | 0.217 | 0.138 | 0.126 | 2.348 <sup>A</sup> | 0.822 <sup>A</sup> | 0.306              |
|     | 2016 | 0.107 | 0.103 | 0.149 | 1.668              | 0.868 <sup>A</sup> | 0.253              |
| 3   | 2006 | 0.312 | 0.342 | 0.247 | 3.307 <sup>A</sup> | 0.748 <sup>A</sup> | 0.509 <sup>A</sup> |
|     | 2016 | 0.326 | 0.896 | 0.646 | 2.401 <sup>A</sup> | 0.780 <sup>A</sup> | 0.406 <sup>A</sup> |
| 4   | 2006 | 0.110 | 0.591 | 0.852 | 2.703 <sup>A</sup> | 0.911              | 0.409 <sup>A</sup> |
|     | 2016 | 0.109 | 0.637 | 0.918 | 2.907 <sup>A</sup> | 0.933              | 0.285              |
| 5   | 2006 | 0.269 | 0.327 | 0.297 | 4.056 <sup>A</sup> | 0.872 <sup>A</sup> | 0.961 <sup>A</sup> |
|     | 2016 | 0.000 | 0.000 | 0.000 | 3.538 <sup>A</sup> | 0.871 <sup>A</sup> | 0.818 <sup>A</sup> |
| 6   | 2006 | 0.271 | 0.429 | 0.390 | 2.664 <sup>A</sup> | 0.624 <sup>A</sup> | 0.844 <sup>A</sup> |
|     | 2016 | 0.250 | 0.291 | 0.265 | 1.762              | 0.599 <sup>A</sup> | 0.991 <sup>A</sup> |

Notes:  $D$  (Mai) – species richness,  $H'$  (Shi) – species heterogeneity,  $E$  (Pii) – species evenness,  $\alpha$  (P&Mi) – index of non-randomness,  $R$  (C&Ei) – aggregation index, CSI ( $D$ &Mi) – index of cluster size

\*statistically significant for horizontal structure (<sup>A</sup> – aggregation, <sup>R</sup> – regularity); changes: \ – decrease, / – increase.

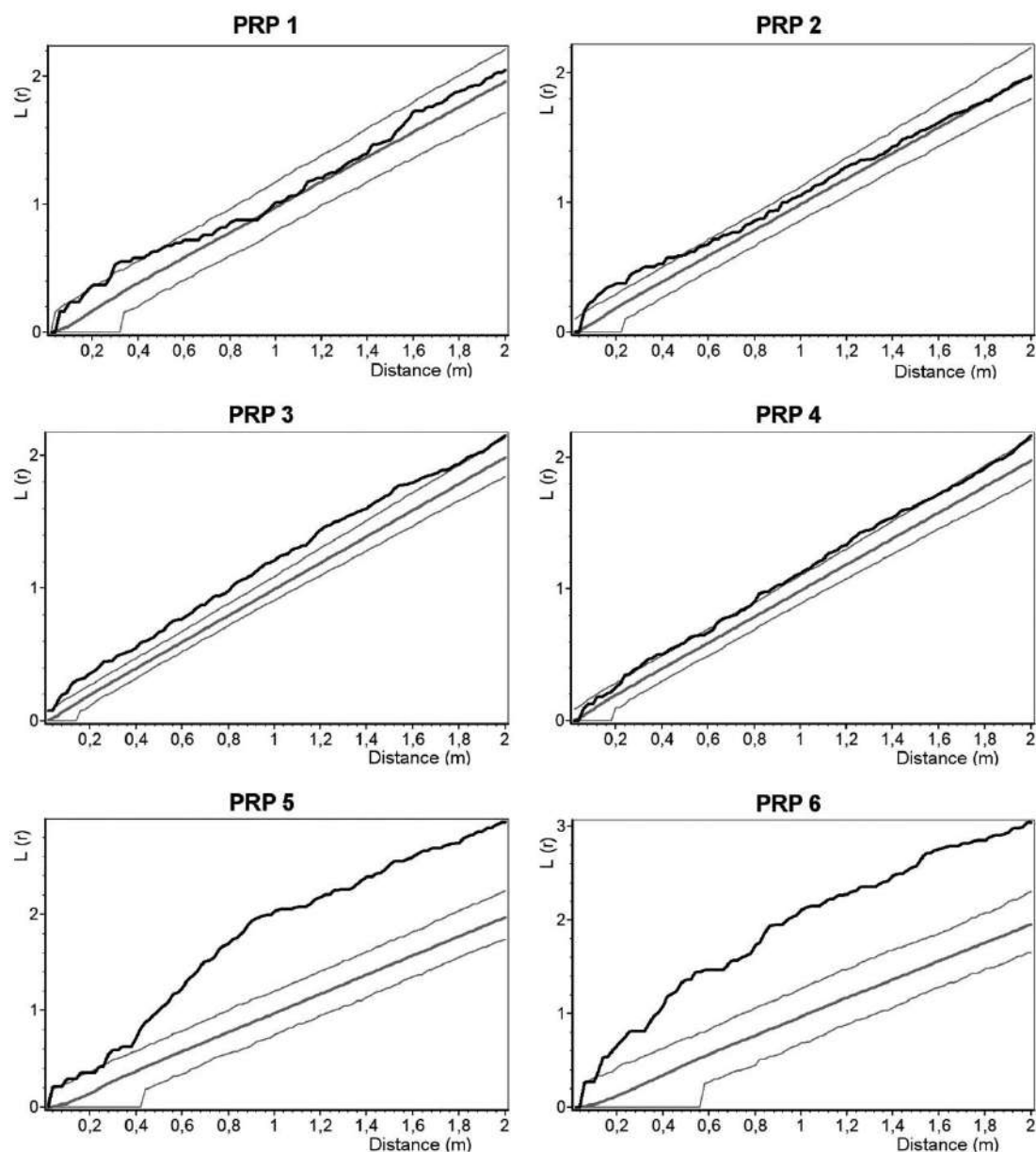


Fig. 9. The spatial pattern of natural regeneration on permanent research plots 1–6 expressed by  $L$ -function in 2016; the black line represents the  $L$ -function for real distances of recruits; the bold grey line represents the mean course for random spatial distribution and the two thinner central curves represent 95% interval of reliability; when the black line of recruits distribution on the plots is under (below) this interval, it indicates a tendency of recruits toward aggregation (regular) distribution

the distribution was random. In 2006 on the PRPs 1–6, there was found clustered distribution of natural regeneration. During the monitored period, on PRPs horizontal structure was more aggregated in 2006 compared to 2016, only on PRP 4 distribution of recruits was more regular.

## Discussion

As part of the ongoing climatic changes (Knoke et al., 2008; Bošela et al., 2016; Dyderski et al., 2018), and in the context of often borderline habitat conditions for the forest existence, natural pine



ecosystems are rightfully receiving more and more attention (Popa et al., 2017; Wang et al., 2017). The structure and growth of pine stands in the Czech Republic were dealt with by Bílek et al. (2016); Vacek et al. (2016) or Sharma et al. (2017). The dynamics of relict pine stands in relation to environmental conditions were dealt with in the Czech Republic by Bílek et al. (2016) and Vacek et al. (2017).

The main characteristics of spontaneous development of natural pine stands in given conditions are high age of individual trees in the upper story, extraordinary regeneration capacity with predominantly clustered spatial distribution of seedlings and saplings, and a significant increase of dead wood during the monitoring period. The summary stand characteristics on PRPs such as tree density, basal area and growing stock have mostly increased over the monitored period and can be regarded as balanced. Generally, we assume that these structural attributes contribute to higher naturalness, heterogeneity and ecological stability of the studied stands, and thus can be considered as a possible mitigation measure to ongoing global climate change. Nevertheless, in the case of the studied areas, and also in comparison with other authors, the variability of the results is generally high. This is due to the interaction of numerous factors such as the growth characteristics of each species, climatic and edaphic habitat conditions, the structure of the stands and the previous management (Forrester, 2014; Bauhus et al., 2017).

According to Forrester et al. (2017), for example, mixed and unmixed stands can vary considerably in the productivity, function, and stability, the extent and direction of these differences being very heterogeneous. In the context of higher structural diversity, correlation with the production of above-ground biomass has been confirmed for the pine stands (Balvanera et al., 2006; Szwagrzyk & Gazda, 2007; Ercanli & Kahrman, 2015). The diameter structure on individual plots remained almost unchanged during the period under review and is markedly left-tailed with the Liocourt curve character. This arrangement is usually the result of the opening of the canopy cover when a relatively rapid onset of natural regeneration takes place (Franklin et al., 2002; Zeibig et al., 2005). The diameter structure in the shape of the Liocourt curve is also referred to as typical for the close to nature stands of other tree species (Král et al., 2010; Sagheb-Talebi et al., 2015). A similar left-tailed distribution as on our plots reported Szmyt and Tarasiuk (2018) from the pine forests in Poland. Their work shows clearly the increase in the thickness of the individuals on the research plots during the 14-year period, which correlates with the decrease of their number.

For the natural regeneration and the tree layer, there is a predominant random to cluster spatial

distribution, while the horizontal structure has changed only slightly with no prevailing trend. A cluster distribution is typical for areas with more extreme habitat conditions (Šerá et al., 2000; Bulušek et al., 2016) and also results from the establishment and growth of natural regeneration in gaps of the parent stand (Bolte et al., 2014). This is the preference of a micro-site with better light conditions. On the contrary, the mortality of individuals in the case of increasing stand density (Getzin et al., 2006; Das et al., 2011), or in the absence of openings in the stand (Haase et al., 1996; Uriá-Diez & Pommerening, 2017) contributes to the regularity of the spatial distribution. In connection with this, Szmyt & Tarasiuk (2017) confirm the change in the stand structure during the stand development from random to regular. In the pine stands, a cluster arrangement (Brown et al., 2015; Tuten et al., 2015) and regular arrangement (Li et al., 2012) were confirmed according to various authors.

The tree ring analyses show that the age of the upper layer of the studied stands was in case of pine between 237–264 years. Precipitation had significantly higher effect on radial growth compared to temperature. Especially precipitation in June and July of the previous year and in May–July of the current year influenced radial growth positively. Similarly, the precipitation in May, June and July significantly positively influenced the radial growth of Scots pine trees in the Kuyavian-Pomerania region in Poland, while there was positive effect of the mean monthly temperature for February and March of the current year (Koprowski et al., 2012). Also study from Latvia showed, that the air temperature from the second half of January to the first half of April of the same year has significant effect on radial growth of pine (Zunde et al., 2008). In the relict pine stands in the national nature reserve (NNR) Adršpach-Teplice Rocks in the Czech Republic, the statistically important correlations of radial growth with the temperature in December of the previous year and in March and August of the current year were recorded. Similarly, significant positive correlations were found with the precipitation amount in July of the previous year and in June of the current year (Vacek et al., 2017). In natural lowlands in eastern Bohemia, radial growth was positively correlated with the temperature in March of the current year and precipitation in November and December of the previous year and February, March and April of the current year (Vacek et al., 2016). Also, other studies from the Mediterranean area (Augustaitis et al., 2007; Oberhuber et al., 2007; Bogino et al., 2009) suggest that drought is a decisive factor for the radial growth of Scots pine. Similarly, in the northeastern lowlands of Brandenburg (Germany), a sufficient amount of precipitation in the autumn of the previous year and summer

precipitation of the current year are very important for foliage formation and radial growth. According to the work of Insinna et al. (2007), the temperature has less influence on growth processes than precipitation. From the regional standardized ring chronology, there is a relatively unstable radial growth between 1800–2017. Years with a low radial increase were in 1922, 1976, and 1998. Especially negative pointer year 1976 was the driest year since 1959 (annual precipitation 492 mm, long-term average 620 mm), the monthly rainfall in June reached only 22 mm (average 69 mm) with high temperatures in the growing season (1.2 °C above the long-term average). Similarly, in 1998, when the very beginning of the growing season was marked by very high temperatures and minimal precipitation (April temperature +2.1 °C and rainfall only 41% of the average).

In accordance with other studies (Vacek et al., 2017; Wilczyński, 2006), radial growth was negatively correlated with  $\text{SO}_2$  concentrations and ozone exposure.  $\text{NO}_x$  concentrations had low effect on radial growth, while in other studies from natural pine stands in the Czech Republic mean  $\text{NO}_x$  concentrations affected the radial growth positively (Vacek et al., 2016). On the other hand, high concentrations of  $\text{NO}_x$  and  $\text{SO}_2$  in combination with severe climate events can lead to serious defoliation (Vacek et al., 2016) with further degradation of the forest stands.

Dead wood as an important component of natural forest ecosystems (Odor et al., 2006; Jakoby et al., 2010) occurred in the studied locality in 2016 in the range of 15.8–39.3  $\text{m}^3 \text{ha}^{-1}$ . During the research period, the volume of dead wood increased significantly (by 127.2%) compared to 2006 (7.2–21.4  $\text{m}^3 \text{ha}^{-1}$ ). Within natural forest dynamics steep increase of dead wood volumes is mainly related to the degradation phase of the tree layer. Some authors also refer to spatial relationships and mutual competition of trees as important factors in relation to mortality (LeMay et al., 2009; Larson et al., 2015). Significantly higher volume of dead wood in pine primary forests in North America in the range of 37.2–124.1  $\text{m}^3 \text{ha}^{-1}$  are reported by Silver et al. (2013). Uotila et al. (2001) report in the pine primary forests in Finland and Russian Karelia 66.7  $\text{m}^3 \text{ha}^{-1}$ . On the contrary, similar results are presented from the relict pine forests of the NNR of the Adršpach-Teplice Rocks by Vacek et al. (2017) with an average dead wood stock of 33.1  $\text{m}^3 \text{ha}^{-1}$ . The standing and lying dead wood ratio on studied plots was consistent with the Karjalainen & Kuuluvainen (2002), which presents a substantially identical standing (39%) and lying dead wood (61%) ratio.

Our results also show a significant regeneration capacity of researched pine stands. This is very important from the point of view of natural dynamics since natural regeneration is an important component of

natural forest ecosystems (Petritan et al., 2007; Pardos et al., 2008; Dovčiak & Brown, 2014). The number of natural regeneration individuals ranged from 3,000 to 17,250 recruits  $\text{ha}^{-1}$ . This density is substantially higher in comparison with another relict pine forest in Czech Republic, (Vacek et al., 2017). During the monitored period, a rather significant increase (by 55.0%) in the number of natural regeneration was recorded, with the exception of one PRP, but Martín-Alcón et al. (2015) presents the opposite trend. The works by Šticha et al. (2010) and Prévosto et al. (2012) then present the competition of grass vegetation as a possible negative impact on natural regeneration. Other works present browsing as a negative effect for natural regeneration, especially for the attractive tree species (Ammer, 1996; Čermák et al., 2009). Even though in 2006 the game was damaging also other species, beech has to be judged as the most attractive tree species for ungulates in the studied locality.

## Conclusion

During the monitored years 2006–2016, the changes in the diversity of the relict pine stands were generally low, while significant changes occurred in the development of natural regeneration. Under a reduced pressure of the ungulates, the development of the stand goes to greater spatial diversity and to a larger proportion of admixed trees such as birch, spruce, and beech. We conclude that natural stand dynamics characterised by gap formation and following regeneration process had positive effect on functional integrity of natural pine ecosystems. Under similar conditions, active management of forest stands should aim to achieve these attributes that are specific to natural pine stands. If passive management scenarios are preferred, control methods analysing the regeneration process and vitality of parent trees are needed. With respect to observed changes in the stand structure (success of natural regeneration and related increase in tree species diversity, balanced growing stock and dead wood, vertical and horizontal heterogeneity), spontaneous development on the stand level and in given temporal frame can be judged as suitable adaptation measure to ongoing climate change.

## Author Contributions

S.V., Z.V. and J.R. planned and designed the experiment; Z.V., J.K., D.B. collected stand data, I.H. provided and processed meteorological data; Z.V. and J.K. analysed data; S.V., Z.V., J.B. and L.B. interpreted the results and wrote the paper; all authors reviewed and edited the manuscript.

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## Conflicts of Interest

The authors declare no conflict of interest.

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### 5.3.3 6. publikace: *Potenciál smíšených porostů smrku ztepilého [Picea abies (L.) Karst.] a borovice lesní (Pinus sylvestris L.) v nižších polohách středních Čech*

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#### **Souhrn:**

Cílem níže popsané studie bylo zjistit vliv smíšení smrku ztepilého [*Picea abies* (L.) Karst.] a borovice lesní (*Pinus sylvestris* L.) na produkci, strukturu, diverzitu a růst smíšených porostů v nižších polohách České republiky. Cílem práce také bylo stanovit vliv klimatických faktorů na radiální růst těchto dřevin.

Zájmovou lokalitou byl lesní úsek Klokočná (Lesy ČR, s. p., LZ Konopiště), jehož porosty jsou v režimu přeměny na výběrné hospodářství. Celkem 5 trvalých výzkumných ploch (25 m × 50 m) bylo navrženo tak, aby zastoupení dřevin na ploše bylo následující: (i) borovice 92,5–100 % (borovice 100 %), (ii) 75 ± 7,5 % borovice a 25 ± 7,5 % smrk (borovice 75 %), (iii) 50 ± 7,5 % borovice a 50 ± 7,5 % keře (borovice 50 %), (iv) 25 ± 7,5 % borovice a 75 ± 7,5 % smrk (borovice 25 %) a (v) 92,5–100 % smrk (smrk 100 %). S využitím technologie Field-Map byla zaznamenávána poloha všech jedinců s DBH ≥ 7 cm, u kterých byly dále zjišťovány jejich dendrometrické charakteristiky.

Výsledky studie prokázaly vyšší produkci porostů smíšených, a to o 29,8 % ve srovnání se smrkovými a borovými monokulturami. Smrk ztepilý dosahoval vyššího radiálního růstu, nicméně variabilita radiálního růstu byla vyšší než u borovice, jejíž letokruhy byly z hlediska tloušťky více pravidelné. Teplota měla ve srovnání se srážkami větší vliv na radiální růst obou dřevin, zejména ve vegetačním období. Zjištěná data také potvrdila, že ve srovnání s nesmíšenými porosty smrku a borovice dosahovaly smíšené porosty výrazně vyšší strukturní diferenciaci a celkové diverzity.



## Potential of mixed *Picea abies* (L.) Karst. and *Pinus sylvestris* L. forests in lowland areas of Central Bohemia

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**Abstract:** Mixed forests play a key role in terms of stability, production potential, and adaptation to climate change. In addition, the studied Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) belong to the most economically important tree species in Europe. The objectives were to determine the effect of the species composition of these two tree genera on the production, structure, diversity, and growth of mixed stands at lower elevations in the Czech Republic. Based on dendroecological samples, research was also carried out on the influence of climatic factors and climate change on the radial growth of these trees of interest. Mixed forests showed higher timber production by 29.8% compared to spruce and pine monocultures. The production of mature stands ranged from 328 to 479 m<sup>3</sup>·ha<sup>-1</sup>. Spruce achieved higher radial growth, but its growth variability was higher than that of pine. Compared to precipitation, temperatures had a greater influence on the radial growth of both tree species, especially in the growing season. In terms of diversity, mixed stands achieved significantly higher structural differentiation and overall diversity compared to monospecific variants. Mixed stands can achieve higher production potential, diversity, and especially resistance to climatic extremes in the lowland regions of the Czech Republic. The differences between mixed stands and monocultures, i.e. the effect of tree species mixing, depend on the appropriate proportions of tree species and their spatial pattern.

**Keywords:** climate change; dendrochronology; Norway spruce; productivity; Scots pine

Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) are the most economically important tree species in Europe (Eckenwalder 2009; Krakau et al. 2013; O'Reilly-Wapstra et al. 2014; Sevik, Topacoglu 2015; Caudullo et al. 2016; Brichta et al. 2023). From the point of view of their prosperity in the conditions of global climate change (Vacek et al. 2016, 2023; Usoltsev et al. 2022), their origin (Taeger et al. 2013; Leštianska et al. 2023), the habitat, and stand conditions are important (Mikulenka et al. 2020; Gallo et al. 2021; Kovalevskii et al. 2022). Due to their high production, Nor-

way spruce and Scots pine were planted in different habitat conditions, including outside their natural distribution (Mikeska et al. 2008; Poleno et al. 2009; Caudullo et al. 2016; Durant et al. 2016) where they are often affected by various disturbances (Caudullo et al. 2016; Hlásny et al. 2019, 2021; Šimůnek et al. 2020; Sydorenko et al. 2021). It is primarily true of richer habitats of Scots pine (Mikeska et al. 2008; Brichta et al. 2023), and in the case of Norway spruce, not lower than in the 5<sup>th</sup> forest vegetation zone unless the habitats are affected by water (Vacek et al. 2007; Poleno et al. 2009).

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Currently, as a result of global climate change, the main threat to spruce and pine stands is primarily drought and, in connection with that, attacks by insect pests (especially bark beetles *Ips typographus*, *Ips acuminatus*, *Ips sexdentatus*, *Pityogenes chalcographus*), and fungal pathogens such as *Heterobasidion* spp., *Fomes* spp., and *Armillaria* spp., etc. (Komonen et al. 2011; Gao et al. 2017; Buras et al. 2018; Barta et al. 2019; Čermák et al. 2019; Holuša et al. 2019; Knížek et al. 2021). It is precisely periods of climatic stress that negatively affect the photosynthetic activity of Norway spruce and Scots pine, and there is an increase in defoliation and a decrease in radial growth (Flexas, Medrano 2002; Reddy et al. 2004; Vacek et al. 2023). Rising air temperatures, together with low water availability, are responsible for several other diseases and also for the reduced defense capacity of trees against insect pests (Allen et al. 2015; Hlásný et al. 2019, 2021; Knížek et al. 2021; Haberstroh et al. 2022).

Drought is, therefore, a significant and frequent predisposing factor for forest decline and disturbances (Hlásný et al. 2021; Knížek et al. 2021). The resistance of the forest to drought depends primarily on the intensity of the drought but also on specific functional properties (Greenwood et al. 2017) and can also vary among individuals of the same species (Gazol et al. 2017; Camarero et al. 2018). Compared to Scots pine, Norway spruce is one of the most drought-sensitive European trees (van der Maaten-Theunissen et al. 2013; Hartl-Meier et al. 2014; Leuschner, Ellenberg 2017; Čermák et al. 2019), because it is a species demanding on rainwater or soil moisture and has a shallow root system (Horgan et al. 2003; Johnson, More 2006; OECD 2006; Farjon 2010). In contrast, Scots pine has a deep root system and can obtain water from significantly greater depths than Norway spruce (Praciak et al. 2013). For these reasons, it is advisable to grow spruce and pine in a two-story high forest (Poleno et al. 2009).

In connection with global climate change, the distribution areas of these tree species are also changing. Both Norway spruce and Scots pine are significantly retreating in the more southerly areas of their ranges and at lower altitudes, and, on the contrary, increasing their range at higher altitudes and in their northern locations (Benito Garzón et al. 2008; Reich, Oleksyn 2008; Matias, Jump 2012; Hanewinkel 2013; Vacek et al. 2023). The management strategy of these stands is consequently changing in an attempt to increase their adaptabil-

ity to climate change (Vacek et al. 2022). In spruce stands at lower elevations, their transformation into mixed stands corresponds in composition to stands close to nature (Hanewinkel, Pretzsch 2000; Spiecker et al. 2004; Teuffel et al. 2005; Souček, Tesař 2008; Poleno et al. 2009; Švec et al. 2015). In Scots pine stands, existing clearings and clearings created during stand regeneration are shrinking, and natural regeneration methods are increasingly applied as part of shelterwood methods of management (Bielak et al. 2014; Spathelf et al. 2015; Bílek et al. 2016; Drössler et al. 2018; Aleksandrowicz-Trzcińska et al. 2017, 2018; Brichta et al. 2020). The shelterwood method of natural regeneration is more favourable concerning the nature of microhabitats during the ongoing global climate change (Matias, Jump 2012; Aleksandrowicz-Trzcińska et al. 2014, 2017, 2018; Vítámvás et al. 2019; Brichta et al. 2020). In Scots pine stands in richer habitats, rebuilding is also occurring, from both economic and ecological points of view (Čížek et al. 1959; Souček et al. 2018). Considerable areas of these stands are potentially threatened by widespread damage of both abiotic and biotic nature, so it is imperative to look for suitable management alternatives using methods of close-to-nature silviculture (Plíva 2000; Průša 2001). Therefore, it is necessary to implement changes in the species composition aimed at structuring mixed stands with Scots pine, which will better fulfil all the required functions of the forest (Andrzejczyk 2006; Bielak et al. 2014). Mixed stands with varying degrees of structuring ensure higher stability and diversity (Bauhus et al. 2017; Vacek et al. 2021b). The replacement of existing monocultures with mixed stands fulfils the goals of the current forestry policy (Poleno et al. 2009; Novák et al. 2017). In addition, mixed stands, in comparison to monocultures, can achieve higher production potential and carbon sequestration in the context of climate change mitigation (del Río et al. 2016; Pretzsch, Schutze 2016; Vacek et al. 2023). Modifying the species composition towards species mixtures with a higher potential to mitigate the negative effect of climate change is one of the basic silvicultural measures (Füst et al. 2007; Podrázský, Remeš 2010; Remeš et al. 2020).

This research aims to evaluate the degree of stability and the possibility of adaptability of stands of Norway spruce and Scots pine in the lower areas of Central Bohemia. The specific objectives are to determine (i) the production potential of mixed spruce stands, (ii) the structure and diversity of the

studied stands, and (iii) the effect of precipitation, temperature, and climate change on the radial growth of Scots pine and Norway spruce.

## MATERIAL AND METHODS

**Study area and natural conditions.** The area of interest is managed by the Forests of the Czech Republic, a state enterprise (Lesy ČR, s.p.), and is part of the Konopiště forest enterprise and the Říčany forest district. The forest block has a size of 3.2 km<sup>2</sup> (GPS: 49°58'29"N, 14°43'05"E). The altitude of the studied area ranged from 430 m a.s.l. to 480 m a.s.l. with a characteristic flat relief in the 3<sup>rd</sup> and 4<sup>th</sup> forest vegetation zone (Remeš, Kozel 2006). From a typological point of view, these are mainly groups of forest types 3K – *Querceto-Fagetum acidophilum* and 4P – *Querceto-Abietum variohumidum acidophilum* (Viewegh et al. 2003). The predominant soil types are cambisol, pseudogley, and luvisol, with long-term considerable soil acidification (Podrázský et al. 2005; Podrázský, Remeš 2007). The average temperature of the area of interest is 7.5 °C, the total annual precipitation is 600 mm, less than 400 mm in the growing season, and the length of the growing season is about 150 days (Švec et al. 2015). According to the Forest Management Plan, the age of the upper tree layer of the investigated forest stands is in the range of 87–117 years. The investigated mature stands are mixed and made up of two main tree species – Norway spruce and Scots pine. Other admixed tree species are silver fir (*Abies alba* Mill.) and Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco].

**Forest management.** These are close-to-nature forest stands during the conversion to the shelterwood system, with the application of selection principles, which has been continuous since 1993. The reason for the change in forest management was mainly due to frequent wind damage to spruce or breakage of pine caused by wet snow, under the former clear-cut regimen. The spruce and pine stands that had been destroyed in the past were not reconstructed but were left to develop spontaneously, which allowed natural regeneration to occur, creating large differences in height and thickness between the surviving trees. These sites are now managed according to selection principles, making maximum use of natural regeneration. Artificial regeneration is used only to introduce native tree species that almost disappeared from the area under the previous management. The main criterion for harvesting specific trees is their target

diameter (diameter at breast height – *DBH*), not the age of the stand (Remeš, Kozel 2006).

**Data collection.** The study area was conducted on five rectangular plots of 25 m × 50 m (the size of one plot was 1 250 m<sup>2</sup>) in 2022. The permanent research plots (PRPs) were divided into five variants by species composition: (i) 92.5–100% pine (pine 100%), (ii) 75 ± 7.5% pine and 25 ± 7.5% spruce (pine 75%), (iii) 50 ± 7.5% pine and 50 ± 7.5% spruce (pine 50%), (iv) 25 ± 7.5% pine and 75 ± 7.5% spruce (pine 25%), and (v) 92.5–100% spruce (spruce 100%), see Vacek et al. (2021b). FieldMap technology (EMU; IFER, Czech Republic) recorded the positions of individual trees with *DBH* ≥ 7 cm, and their crown projection was measured in four directions. Boundary trees with more than half of their *DBH* lying inside a PRP were counted in. The *DBH* was measured with a Mantax Blue caliper (Haglöf, Sweden) with an accuracy of 1 mm, and the height of the individual trees and the height of the live crown with a Vertex laser hypsometer (Haglöf, Sweden) with an accuracy of 0.1 m.

For the analysis of radial growth, core samples were obtained from the trees with a Pressler auger (Haglöf, Sweden) at the height of 1.3 m in the direction north/south. From each tree species, 30 samples of Norway spruce and 30 of Scots pine from the dominant and co-dominant trees according to the Kraft classification (Kraft 1884) were randomly [RNG function, MS Excel (Version 365, 2023)] taken as the significant growth response (compared to subdominant and suppressed trees; Remeš et al. 2015). All these selected trees only come from the upper tree story with a registration value of *DBH* over 30 cm. The annual increments of the tree rings were then measured with an accuracy of 0.01 mm using an Olympus binocular microscope (SZ51; Olympus, Japan) on a LINTAB measuring table (6d; Rinntech, Germany) and recorded in TsapWin software (Version Professional 4.82b2, 2022). Climate data were taken from the nearest Czech Hydrometeorological Institute (CHMI) station, Ondřejov (49°54'36"N, 14°46'48"E) for the period 1962–2021.

**Data analyses.** The basic structure, diversity, and production characteristics of the tree layer were calculated by the SIBYLA Triquetra software (Version 10.0 alpha, 2015) using a tree-level and spatially explicit data set (Fabrika, Ďurský 2005) based on our measurements. All collected dendrometric parameters of individual trees (see the Data collection section) were used as input data (tree spe-

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cies, coordinates, height, *DBH*, crown width, live crown base, and age). The crown width was derived from the measured area of the crown projection. The PointPro program (Version 2.2, 2010) (Zahradník, Puš, ČZU) was used to calculate the characteristics of the horizontal layout of the trees on PRPs using the Clark and Evans (1954) aggregation index. The tree volume was calculated by the volume equations published in Petráš and Pajtlík (1991). Crown closure (Crookston, Stage 1999) and the relative stand density index (Reineke 1933) were then calculated from the measured stand density indicators. The relative *SDI* (stand density index) was calculated as the ratio of the actual value of the stand density index to its maximum value. The stand density index represents the theoretical number of trees per ha if the mean quadratic diameter of the stand component is equal to 25 cm (Reineke 1933). The maximum *SDI* value was derived from the model of yield tables (Halaj 1987). Standard deviations (SD) were calculated for the mean quadratic *DBH* and mean height. Tree biomass was derived according to Petráš et al. (1985), Petráš and Pajtlík (1991), and Ledermann and Neumann (2005). The biomass of the roots was calculated using a model by Drexhage and Colin (2001). The content in trees was determined following the research of Bublinec (1994) using the unit content of elements in 10 mg·kg<sup>-1</sup> of dry matter.

Structural diversity was evaluated based on the horizontal structure (Clark, Evans 1954), the ver-

tical structure using the Arten-profile index (Pretzsch 2006) and vertical diversity index (Jaehne, Dohrenbusch 1997), the structural differentiation of the stand using the indices of diameter and height differentiation (Füldner 1995), and crown differentiation (Jaehne, Dohrenbusch 1997). The Arten-profile index was calculated using the basal area of tree species in individual stand layers. Diameter and height differentiations are related to the ratio between the larger and the smaller diameter/height of all nearest neighboring trees. Finally, the stand diversity index was calculated in connection with complex biodiversity (Jaehne, Dohrenbusch 1997). Total diversity is composed of the following components: tree species diversity, diversity of vertical structure, diversity of tree spatial distribution, and diversity of crown differentiation. The input variables are the number of tree species, maximum and minimum tree species proportion, maximum and minimum tree height, maximum and minimum tree spacing, minimum height to crown base, and minimum and maximum crown diameter (Table 1). Detailed information about the calculation of the used indices can be found in Vorčák et al. (2006) and Vacek et al. (2020).

Tree-ring increment series were individually crossdated (to remove errors caused by missing tree rings) using statistical tests in the PAST application (Version 4.5, 2008) (Knibbe 2007) and subsequently subjected to a visual inspection according to Yamaguchi (1991). If a missing tree ring was revealed,

Table 1. Overview of indices describing the stand diversity and their common interpretation

| Criterion                 | Quantifiers              | Label       | Reference                  | Evaluation                                                                                      |
|---------------------------|--------------------------|-------------|----------------------------|-------------------------------------------------------------------------------------------------|
| Horizontal structure      | aggregation index        | $R$ (C&Ei)  | Clark, Evans (1954)        | mean value $R = 1$ , aggregation $R < 1$ , regularity $R > 1$                                   |
| Vertical structure        | Arten-profile index      | $A$ (Pri)   | Pretzsch (2006)            | range 0–1, balanced vertical structure $A < 0.3$ , selection forest $A > 0.9$                   |
|                           | vertical diversity       | $S$ (J&Di)  | Jaehne, Dohrenbusch (1997) | low $S < 0.3$ , medium $S = 0.3–0.5$ , high $S = 0.5–0.7$ , very high diversity $S > 0.7$       |
| Structure differentiation | diameter differentiation | $TM_d$ (Fi) | Füldner (1995)             | range 0–1, low $TM < 0.3$ , very high differentiation $TM > 0.7$                                |
|                           | height differentiation   | $TM_h$ (Fi) |                            |                                                                                                 |
|                           | crown differentiation    | $K$ (J&Di)  | Jaehne, Dohrenbusch (1997) | low $K < 1.0$ , medium $K = 1.0–1.5$ , high $K = 1.5–2.0$ , very high differentiation $K > 2.0$ |
| Complex diversity         | stand diversity          | $B$ (J&Di)  | Jaehne, Dohrenbusch (1997) | monotonous structure $B < 4$ , uneven structure $B = 6–8$ , very diverse structure $B > 9$      |

C&Ei – Clark and Evans index; Fi – Füldner index; J&Di – Jaehne and Dohrenbusch index; Pri – Pretzsch index



a tree ring of 0.01 mm in width was inserted in its place. Residual chronologies and detrended average tree ring series were calculated in the ARSTAN program (Version 49v1a, 2017) (Cook, Holmes 1984). Firstly, negative exponential spline and subsequently, 0.67n spline were used for age detrending (Grissino-Mayer et al. 1992). The analysis of negative pointer years was carried out, as shown in Schweingruber (1996) and Desplanque et al. (1999). For each tree, the pointer year was tested as an extremely narrow tree ring that does not reach 40% of the increment average from the four preceding years. The occurrence of the negative year was proved if such a strong reduction in increment occurred in at least 20% of trees on the plot. To express the relationship between climate characteristics (monthly average temperatures and the sum of precipitation in particular years) and radial growth, the DendroClim software (Version 1.0, 2002) was used (Biondi, Waikul 2004).

The dendrochronological indicators were calculated in R software (Version 4.2.1, 2022) with the dplR package instructions (Bunn, Mikko 2018). The expressed population signal (*EPS*) was calculated to indicate the reliability of the chronology (Fritts 1976). The *EPS* dendrochronological data set results for every research plot were  $EPS > 0.85$  to preserve a strong climatic signal in the used chronology. The signal-to-noise ratio (*SNR*) indicator was calculated, representing the strength of the chronology. Finally, the *R-bar* (inter-series correlations) and *ar1* (first-order autocorrelation) was computed (Fritts 1976) for pine and spruce. The differences between individual tree species in terms of radial growth were tested in STATISTICA 13 (Version 13.4.0, 2018) using analysis of variance (ANOVA) and Tukey's HSD (honestly significant difference)

test. The variability of radial growth was indicated by the standard deviation.

## RESULTS

**Production potential.** Production characteristics of forest stands on permanent research plots differentiated by the species composition are shown in Table 2. The number of trees ranged from 256 trees·ha<sup>-1</sup> in spruce monoculture to 512 trees·ha<sup>-1</sup> in a stand with an equal proportion of spruce and pine (in this variant, the highest basal area was also reached – 39.0 m<sup>2</sup>·ha<sup>-1</sup>). Similarly, the stand density index of monospecific stands reached values 0.44–0.54 compared to higher numbers (0.60–0.71) in the case of mixed forests. Stand volume was in the range of 351–479 m<sup>3</sup>·ha<sup>-1</sup>, while mixed stands reached up to 29.8% higher production compared to monocultures. The mean annual increment ranged from 3.35 to 5.04 m<sup>3</sup>·ha<sup>-1</sup>·y<sup>-1</sup>. Likewise, tree biomass and carbon sequestration were more advantageous in mixed stands.

**Structure and diversity.** No differences were found in the horizontal structure between the individual plots, while the spatial pattern was random in all cases (Table 3). All other variants show considerable differences in structural indices favoring mixed stands over monocultures. The highest rich vertical structure was observed in the case of variant spruce 75:25 pine compared to the lowest for pure spruce stands. Height, diameter, and crown structural differentiation were low in monocultures and moderate in mixed forest stands, especially in variants with a 50% representation of spruce and pine. Regarding overall diversity, monocultures reached a complex *B* index in the range of 2.573–3.329 and mixed forests 4.661–5.960.

Table 2. Production characteristics of the stand on permanent research plots differentiated by the species composition (variants) in 2022

| Variant     | <i>DBH</i><br>(cm) | <i>h</i><br>(m) | <i>v</i><br>(m <sup>3</sup> ) | <i>N</i><br>(trees·ha <sup>-1</sup> ) | <i>G</i><br>(m <sup>2</sup> ·ha <sup>-1</sup> ) | <i>V</i><br>(m <sup>3</sup> ·ha <sup>-1</sup> ) | <i>HDR</i><br>– | <i>SDI</i><br>– | <i>CC</i><br>(%) | <i>MAI</i><br>(m <sup>3</sup> ·ha <sup>-1</sup> ·y <sup>-1</sup> ) | <i>BIO</i><br>(t·ha <sup>-1</sup> ) | <i>C<sub>BIO</sub></i><br>(t·ha <sup>-1</sup> ) |
|-------------|--------------------|-----------------|-------------------------------|---------------------------------------|-------------------------------------------------|-------------------------------------------------|-----------------|-----------------|------------------|--------------------------------------------------------------------|-------------------------------------|-------------------------------------------------|
| Pine 100%   | 38.7               | 25.09           | 1.369                         | 256                                   | 30.0                                            | 351                                             | 64.8            | 0.54            | 74.9             | 3.73                                                               | 262                                 | 137                                             |
| Pine 75%    | 34.6               | 24.82           | 1.150                         | 416                                   | 38.9                                            | 479                                             | 71.7            | 0.71            | 81.6             | 5.04                                                               | 356                                 | 187                                             |
| Pine 50%    | 31.2               | 21.87           | 0.859                         | 512                                   | 39.0                                            | 440                                             | 70.1            | 0.68            | 67.6             | 4.58                                                               | 315                                 | 165                                             |
| Pine 25%    | 34.5               | 22.10           | 1.002                         | 400                                   | 37.1                                            | 401                                             | 64.1            | 0.60            | 61.7             | 4.18                                                               | 276                                 | 144                                             |
| Spruce 100% | 34.1               | 28.48           | 1.077                         | 304                                   | 27.7                                            | 328                                             | 83.5            | 0.44            | 75.7             | 3.35                                                               | 211                                 | 110                                             |

*BIO* – tree biomass; *C<sub>BIO</sub>* – carbon sequestration in tree biomass; *CC* – canopy closure; *DBH* – mean quadratic diameter at breast height; *G* – basal area; *h* – mean height; *HDR* – slenderness coefficient; *MAI* – mean annual increment; *N* – number of trees per hectare; *SDI* – relative stand density index (stocking); *v* – mean tree volume; *V* – stand volume

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Table 3. Indicators of stand biodiversity on permanent research plots by species composition (variants) in 2022

| Variant     | <i>R</i> (C&Ei) | <i>A</i> (Pri) | <i>S</i> (J&Di) | <i>TM<sub>d</sub></i> (Fi) | <i>TM<sub>h</sub></i> (Fi) | <i>K</i> (J&Di) | <i>B</i> (J&Di) |
|-------------|-----------------|----------------|-----------------|----------------------------|----------------------------|-----------------|-----------------|
| Pine 100%   | 0.907           | 0.537          | 0.364           | 0.256                      | 0.125                      | 0.744           | 3.329           |
| Pine 75%    | 0.948           | 0.404          | 0.732           | 0.280                      | 0.287                      | 1.358           | 5.631           |
| Pine 50%    | 0.964           | 0.682          | 0.676           | 0.417                      | 0.322                      | 1.387           | 5.960           |
| Pine 25%    | 0.989           | 0.706          | 0.749           | 0.393                      | 0.308                      | 1.051           | 4.661           |
| Spruce 100% | 1.021           | 0.244          | 0.266           | 0.270                      | 0.103                      | 0.495           | 2.573           |

*A* (Pri) – Arten-profile index (Pretzsch); *B* (J&Di) – stand diversity index (Jaehne and Dohrenbusch); *K* (J&Di) – crown differentiation (Jaehne and Dohrenbusch); *R* (C&Ei) – aggregation index (Clark and Evans); *S* (J&Di) – vertical diversity (Jaehne and Dohrenbusch); *TM<sub>d</sub>* (Fi) – index of diameter differentiation (Földner); *TM<sub>h</sub>* (Fi) – index of height differentiation (Földner)

Table 4. Characteristics of tree-ring chronologies for Scots pine and Norway spruce

| Tree species  | No. trees | Mean <i>RW</i> (mm) | Mean min–max (mm) | Age min–max | <i>ar1</i> | <i>R-bar</i> | <i>EPS</i> | <i>SNR</i> |
|---------------|-----------|---------------------|-------------------|-------------|------------|--------------|------------|------------|
| Scots pine    | 30        | 2.06 ± 1.08         | 1.09–3.32         | 77–92       | 0.69       | 0.83         | 0.90       | 9.38       |
| Norway spruce | 30        | 3.34 ± 1.45         | 1.36–4.08         | 73–104      | 0.63       | 0.85         | 0.92       | 11.02      |

Age min–max – age range of youngest and oldest sample tree; *ar1* – first-order autocorrelation; *EPS* – expressed population signal; mean min–max – mean ring-width range in mm from smallest to biggest tree; mean *RW* – mean ring width in mm; No. trees – number of trees; *R-bar* – inter-series correlation; *SNR* – signal-to-noise ratio

**Radial growth and climate.** Characteristics of tree-ring chronologies for Scots pine and Norway spruce in Table 4 showed that spruce revealed a significantly ( $P < 0.05$ ) higher radial increment compared to pine (by 38.3%). Scores of *EPS* and

*SNR* were also higher for spruce in both cases. On the other hand, pine showed lower radial growth variability. Higher variability of growth, including its dynamics in spruce is shown in Figure 1. This figure also demonstrates that the only negative

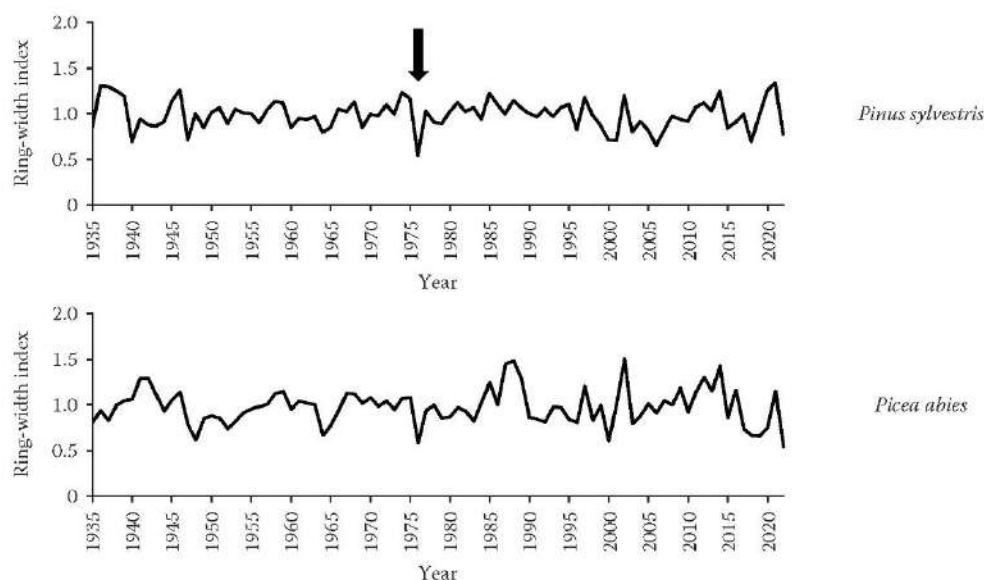


Figure 1. Standardised mean chronology of Scots pine and Norway spruce in 1935–2022 after removing the age trend expressed by the tree-ring index

Negative pointer years are highlighted with a black arrow.

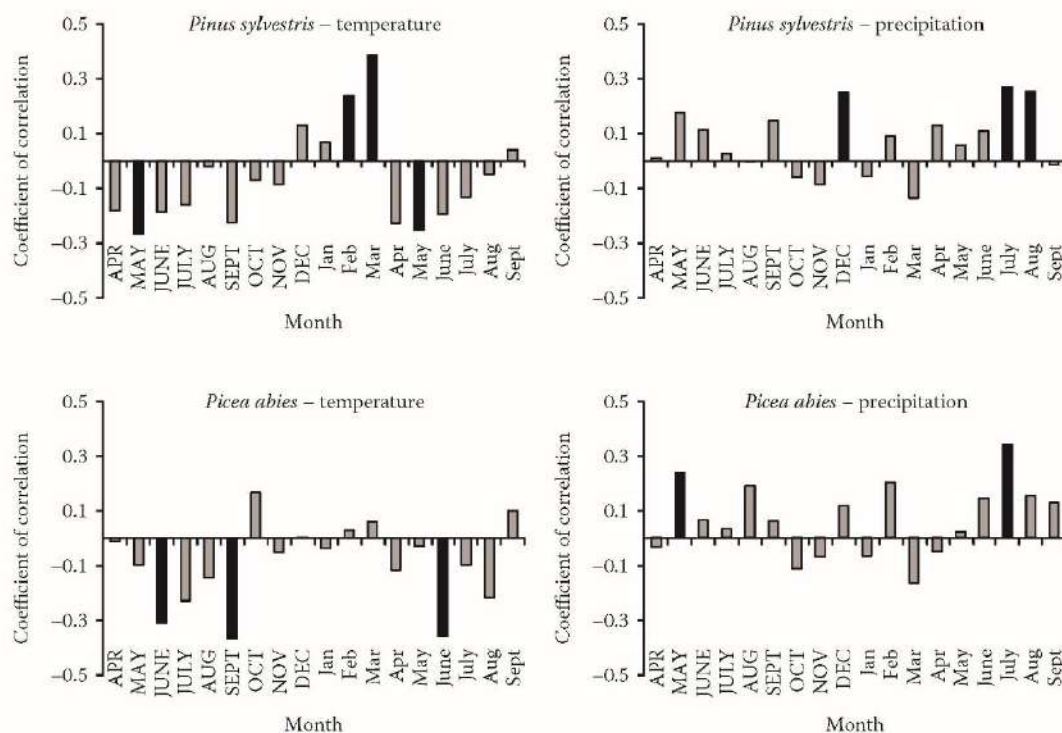


Figure 2. Coefficients of correlation of the regional residual index tree-ring width chronologies of Scots pine and Norway spruce with monthly average air temperature and monthly precipitation differentiated according to tree species

The period from April of the preceding year (capital letters) to September of the current year (lower-case letters) between 1962 and 2021 was used for all correlation analyses presented. Correlation values are highlighted only if a significance level corresponding to  $P < 0.05$  was reached.

pointer year characterised by extremely low growth was detected in pine for the year 1976. In that year, the extremely low temperature in March ( $-0.7^{\circ}\text{C}$ , historical mean  $2.6^{\circ}\text{C}$ ) and long-term drought in June (20 mm, mean 84 mm) was measured. The negative pointer year (NPY) was not found in the case of spruce.

Figure 2 illustrates the effect of climate factors on radial growth by coefficients of correlation of the regional residual index tree-ring width chronologies of Scots pine and Norway spruce with monthly average air temperature and monthly precipitation. Generally, pine was more sensitive to climatic factors compared to spruce. Compared to precipitation, temperatures had a greater influence on the radial growth of both tree species, especially in the growing season. The principal month affecting the radial growth was July of the current year for both tree species.

## DISCUSSION

Currently, forests are exposed to various disturbances, which are profoundly influenced by climate (Abdullah et al. 2019). Consequently, small- and large-scale natural forest disturbances or, at the least, a significant decline in tree growth is occurring, both at high elevations (Albrich et al. 2020) and at lower elevations (D'Andrea et al. 2019), where, moreover, a recent retreat or gradual mortality of once stable tree species is evident (Tangwa et al. 2022). Climate change is expected to affect the susceptibility of forests to calamities and also to affect the frequency, intensity, duration, and timing of various disturbances, particularly at lower elevations (Stanturf et al. 2014). Lack of precipitation and, as a consequence, more frequent and longer-lasting droughts will be an increasing risk to the growth, ecological stability, and vitality of forest

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ecosystems under global climate change (Seidl et al. 2011; Dyderski et al. 2018). This may often include the bare forest existence due to a significant increase in disturbances, especially in spruce and pine monocultures (Vacek et al. 2023). According to data from the Forest Protection Service [Lesní ochranná služba (Lubojacký, Knížek 2021)], the total infestation of Norway spruce by bark beetle in the Czech Republic in 2020 was at least 25 million m<sup>3</sup>. Hundreds of thousands of cubic meters more are represented by their infestation of Scots pine. In general, coniferous forests in Czech lowlands appear not to be very promising in the context of climate change, precisely due to the extreme damage caused by abiotic and biotic factors, especially in the last decade (Hlásny et al. 2021; Liška et al. 2021). Some sources, however, point to the high adaptability of pine, specifically to climate change, e.g. in relation to the afforestation of agricultural or logging areas (Vacek et al. 2021a). Of course, both of the most economically exploited coniferous tree species in the Czech Republic are demonstrably subject to negative environmental factors, but in order to meet the requirements of the industry, it is necessary to also grow their stands in the lowlands, using pine with spruce for normal forest establishment. One of the ways to maintain pine and spruce in the lowlands is to mix them, with the potential benefit of increased production (Remeš, Kozel 2006; Bielak et al. 2014; Švec et al. 2015; Ruiz-Peinado et al. 2021).

**Production potential.** The production potential of forest stands is influenced by several factors, whether abiotic, biotic, or internal – genetic dispositions (Schweingruber 1996). The structure, growth, and production and very existence of the forest depends on these factors (Vacek et al. 2023). Specific habitat and stand conditions and management practices play a crucial role (Poleno et al. 2007). In general, stands under 50 years of age grow faster, and stands of higher age grow more slowly. Faster growth of forest tree species has been attributed to a range of factors such as increased nitrogen deposition (De Vries et al. 2014), increased CO<sub>2</sub> concentration (Soulé, Knapp 2006), the effect of climate change (Nemani et al. 2003; Čermák et al. 2019), or the influence of management measures (Poleno et al. 2009; Lindner et al. 2010).

On the site of interest described in this study, research has already been conducted by Remeš and Kozel (2006), who report a stock of broad-

ly comparable production characteristics from spruce and pine stands in conversion with interspersed fir, oak, and beech. The range of stock was set at 366–378 m<sup>3</sup>·ha<sup>-1</sup>, i.e. the upper range of stock was 101 m<sup>3</sup> lower than in our study (which is 351–479 m<sup>3</sup>·ha<sup>-1</sup>). The production of mixed stands of pine and spruce is also described in studies by Pretzsch and Schütze (2016) or Ruiz-Peinado et al. (2021) in their research across Europe, where they concluded that it is such mixed stands that achieve a statistically significant increase in production compared to monocultures. Pretzsch and Biber (2016) have found up to a 35.9% increase in the production of mixed stands of pine and spruce with beech compared to monocultures. Their conclusions are confirmed by our work, in which we found that the variants from mixing 75% pine and 50% Scots pine are the most favorable in terms of stand stock and basal area. The production characteristics for Scots pine under given habitat and stand conditions in the Czech Republic are comparable to Vacek et al. (2016) and Čihák and Vejpusťková (2021). Similar production characteristics of Scots pine and Norway spruce from the Říčany Forest District are reported by Bílek et al. (2013), depending on the nature-friendly management methods and the conversion process. While the number of trees in our case ranged from 256 trees·ha<sup>-1</sup> in a spruce monoculture to 512 trees·ha<sup>-1</sup> in a stand with an equal proportion of spruce and pine, Bílek et al. (2013) set the range at 288–476 trees·ha<sup>-1</sup>. The same was true for stock (273–346 m<sup>3</sup>·ha<sup>-1</sup>) and basal area (24.2–27.6 m<sup>2</sup>·ha<sup>-1</sup>). For stands under conversion to a selection forest, Saniga and Szanyi (1998) reported a range of 270–725 trees·ha<sup>-1</sup>, and Réh (1978) reported a similar range of 348–985 trees·ha<sup>-1</sup>. The aforementioned differences in the production characteristics of the conversion stands can be justified by how conversion to a selective forest was initiated. In our case, it was introduced after a partial disruption of the forest stands (Remeš, Kozel 2006), while in the works of Saniga and Szanyi (1998) and Réh (1878), for example, the models are based on the assumption of a homogeneous closed stand.

**Structure and diversity.** Similar to our case, a predominantly random horizontal structure and only slightly clustered structure was found in other stands at Klokočná (Vacek et al. 2007). This also applied to a height and diameter structural differentiation, which was low in monocultures and



medium in mixed forest stands. In terms of overall diversity, in our case, monocultures achieved a complex *B* index of structural variability ranging from 2.573–3.329 (monotonous structure) and mixed forests from 4.661–5.960 (uniform structure). In other stands at Klokočná, the monocultures showed uniform to irregular structure, and the mixed stands showed heterogeneous structure (Vacek et al. 2007). Similar results were also found at School Forestry Enterprise Kostelec nad Černými lesy during the conversion of spruce stands to selective forest (Remeš 2006). Here, the horizontal structure of the stands was random to slightly regular. Also, the height and diameter structural differentiation was low, and the structural variability was also monotonous.

Gallo et al. (2020) attribute differences in the structure and diversity of pine stands in Spain and the Czech Republic to different forest management practices. On the other hand, Bílek et al. (2016), comparing different pine stands in the Czech Republic and Poland, document relatively little difference in the structure of stands managed with close-to-nature principles and unmanaged stands. Vacek et al. (2017, 2020), contrastingly, note a pronouncedly irregular to rich structure of relict mixed pine stands, which in this context, is due to two main factors of heterogeneous stand structure – natural gap formation and the existence of natural regeneration. Therefore, these findings confirm that the management method also has a substantial influence on stand diversity, so in our case, management according to selection principles positively influences the heterogeneity of the environment.

**Radial growth and climate.** A negative year was found for pine at Klokočná, with minimal growth in 1976 due to low precipitation during the growing season (especially in June). In comparable habitat and stand conditions in the Týniště region, this was the case in 1975 and 1980 (Vacek 2016). At our study site, a positive effect of average monthly temperature on radial growth was found in February and March of the current year and a negative effect in May of both the current and previous year. In the Týniště region, under similar habitat and stand conditions, the relationship between temperature and radial growth was statistically positive in March of the current year and positive for precipitation in November and December of the previous year, and in February to April and June of the current year (Vacek et al. 2016).

In contrast to the Klokočná site we monitored, a significant negative year with minimum growth was found for spruce in a nearby stand in comparable habitat and stand conditions at Kostelec nad Černými lesy in 1977, i.e. the year after the minimum increment of Scots pine. The average tree ring width in spruce at this site was 2.31 mm (Brabec et al. 2023), while at the Klokočná site, we monitored it at 3.34 mm. At Klokočná, temperature had a greater effect on the radial growth of both tree species compared to precipitation, especially during the growing season. One of the crucial months influencing radial growth for both species was July of the current year, which is consistent with several conclusions from various studies, with diverse habitat conditions in different forest stands (Rybníček et al. 2010; Remeš et al. 2015; Sidor et al. 2015). In contrast, in a nearby spruce stand near Kostelec nad Černými lesy, there was no statistically significant correlation of mean diameter increment with monthly temperatures. For monthly precipitation in relation to radial growth, a statistically conclusive positive correlation was found in June and July of the previous year and a negative correlation in August of the current year (Brabec et al. 2023).

Drought, in particular, has thus emerged as a determinant of radial growth and vigor of Scots pine and Norway spruce under conditions of advancing climate change (Augustaitis et al. 2007; Bogino et al. 2009; Putalová et al. 2019; Lubojacký, Knížek 2021; Brichta et al. 2023). Moreover, trees damaged by browsing and bark stripping, which is very common in spruce compared to pine, suffer more from lack of precipitation and reduced growth (Cukor et al. 2019a, b; 2022). Especially in response to drought, perhaps it is the use of selection principles that will ultimately allow for greater plasticity and mitigation of negative impacts related to climate change in this context (Vacek et al. 2016).

## CONCLUSION

In the context of the climatic fluctuations of the last decades and the increasing adaptability of forest stands under Central European conditions, it is increasingly necessary to reflect on silvicultural options for the essential commercial tree species. In many places, Scots pine and Norway spruce are beginning to fail when managed traditionally, but this does not mean that these two now semi-fragile species cannot be combined into mixed stands.

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Based on our results, we conclude that mixed stands of Scots pine and Norway spruce are not only significantly more resilient to various environmental factors, have a diverse structure and biodiversity, and offer opportunities for mixing with other tree species but are also significantly more productive and have higher carbon sequestration compared to monocultures. This is, of course, also linked to the economic benefits of mixed forests in terms of higher profits, long-term sustainability, and reduced production uncertainty. These benefits can also be enhanced by interspersing other tree species due to the higher heterogeneity of such stands. However, given the wide range of both species, it is necessary to continue research into these forms of mixing, with as large a sample of study sites as possible, evenly across the range of pine and spruce. In conclusion, however, it should be stressed that within the framework of the different ecological requirements of the species present, mixed forests must not be managed as monocultures.

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### 5.3.4 3. publikace: *Borovice lesní (Pinus sylvestris L.) vykazuje vysokou odolnost proti škodám loupáním zvěří*

**Originální název:** Scots pine (*Pinus sylvestris* L.) demonstrates a high resistance against bark stripping damage.

**Časopis:** Forest Ecology and Management (časopis zařazen do databáze SCOPUS a WOS, aktuálně IF – 3.7, Q1)

**Autorský kolektiv:** Jan Cukor, Zdeněk Vacek, Rostislav Linda, Václav Šimůnek, Zdeněk Macháček, **Jakub Brichta**, Anna Prokůpková

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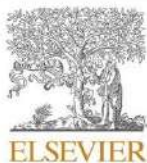
#### **Souhrn:**

Cílem předložené studie bylo předpovědět vliv různě silného poškození kůry stromu loupáním a následnou hnilobou na růstové parametry borovice lesní. Dalším cílem bylo také stanovit vliv klimatických faktorů na různě poškozené stromy.

Výzkum byl proveden v celkem 15 probírkových porostech borovice lesní, v západních Čechách, kde se zároveň objevuje početná populace jelena siky (*Cervus nippon nippon*). Poškození stromů bylo klasifikováno do 3 kategorií: zdravé stromy (poškozený obvod  $\leq 1/8$  obvodu kmene), menší poškození způsobené zvěří (poškozený obvod  $> 1/8$  a  $\leq 1/3$  obvodu kmene) a rozsáhlé poškození způsobené zvěří (poškozený obvod  $> 1/3$  obvodu kmene). Inventarizace byla dále doplněna o zajištění celkem 60 dendrochronologických vzorků. Pro potřeby analýzy rozsahu následné hniloby bylo také pokáceno 40 stromů, které byly následně rozděleny na 20 cm výřezy.

Dendrochronologická analýza stanovila signifikantní rozdíly v tloušťce a objemu zdravých a silně poškozených stromů. Obvodové poškození stromu nemělo signifikantní vliv na objem stromu, na rozdíl od výsledků obdobného výzkumu na smrku ztepilém. K prvnímu poškození stromu došlo průměrně v 18,5 letech života stromu. Bylo zjištěno, že hniloba, vzniklá poraněním kůry, od místa původního zranění nedosáhla délky  $> 50$  cm. Průměrná rychlost vertikálního šíření hniloby byla 0,9 cm/rok. Nebyl zjištěn významný rozdíl působení klimatických faktorů na poškozené a nepoškozené stromy (60 vzorků). Zdravé stromy však reagovaly více na vlivy teploty, poškozené stromy byly citlivější k množství srážek. Závěry výzkumu prokázaly vysokou rezistenci borovice lesní vůči loupání lesní zvěří.





## Scots pine (*Pinus sylvestris* L.) demonstrates a high resistance against bark stripping damage

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### ABSTRACT

Bark stripping damage reduces timber quality due to fungal infection and structural defects. Weakened stems may break and induce the death of trees, which strongly affects forest stability. Some tree species, such as Norway spruce (*Picea abies* [L.] Karst.), are highly susceptible to bark stripping, but Scots pine (*Pinus sylvestris* L.) has been studied to a lesser extent. The objective of this study was to predict the effect of the degree of bark stripping damage and rot on the production parameters of Scots pine and to determine the influence of climatic factors on various damaged trees. The research was conducted on 15 pine forest stands aged 40–42 years with a numerous sika deer (*Cervus nippon nippon*) population in the western part of the Czech Republic (425–492 m a.s.l.). The results showed significant differences in tree diameter and volume (but not height) between healthy and extensively damaged trees according to 417 pines measured. However, no differences were found between lightly damaged trees. Similarly, circumference damage did not significantly affect mean tree stem volume, in contrast to previously reported results for Norway spruce. The trees were first damaged by deer at the age of 18.5 years on average. According to the prediction model based on 40 felled and sampled trees, rot did not reach a distance > 50 cm from the site of the bark stripping on the stem, with a mean speed of vertical spreading of 0.9 cm yr<sup>-1</sup>. Concerning the effect of climatic factors on radial growth (60 core samples taken), the difference between healthy and minor to extensively damaged trees was negligible. However, healthy trees responded more to the effects of temperature, and damaged trees were more sensitive to the precipitation amounts. Scots pine appears to be a suitable tree species for afforestation in areas with high game pressure during continuing climate change.

### 1. Introduction

In recent decades, the European continent has not only seen an increase in the abundance of cloven-hoofed game populations but also an increase in the geographical range of their distribution (Baltzinger et al., 2016; Carpio et al., 2021; Heurich et al., 2015; Thulin et al., 2015; Valente et al., 2020). Thus, wild ungulate populations in some areas of Europe have reached levels that can be defined as overpopulated (Carpio et al., 2021; Valente et al., 2020). Cloven-hoofed game overpopulation can be characterized by several factors, including biological criteria such as the physical condition of the species, ecological criteria, e.g., negative impacts on different components of the ecosystem, and socio-economic criteria, which include, in particular, wildlife conflicts with humans and human management (Carpio et al., 2021; Marada et al., 2019; Warren, 2011).

This increase is not only due to environmental changes but also to

other factors, including the low numbers of large predators (Kuijper et al., 2013; Martin et al., 2020) which have also become diminished due to illegal hunting (Červený et al., 2019; Heurich et al., 2018). Hunting and its management have gradually become a tool to reduce game numbers (Bischof et al., 2012; Heurich et al., 2015; Hothorn and Müller, 2010). However, the effectiveness of hunting strongly depends on the hunting effort expended, local laws, and especially basic hunting philosophy (Williams et al., 2002, 2013).

Significant game damage to forest stands caused by high population density is not only affected by native wildlife species but also by introduced ones (Barrios-Garcia et al., 2012; Z. Vacek et al., 2020). One of the most successfully introduced species, in the context of the European continent, has been sika deer (*Cervus nippon nippon*) (Bartoš, 2009; Biedrzycka et al., 2012; McDevitt et al., 2009; Pérez-España et al., 2009). With their gradual increase in abundance, sika deer have been ranked among the 10 invasive species with the greatest negative impact

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on the European landscape (Gallardo, 2014), including the Czech lands, where they were introduced in 1891 (Kokes, 1970).

Therefore, the current increase in ungulate population density is reflected by an increase in negative impacts on forest ecosystems (Carpio et al., 2021; Gerhardt et al., 2013; Hothorn and Müller, 2010; Vacek et al., 2014; Valente et al., 2020). The effect of deer on woodland vegetation has resulted in significant changes in forest stand structure, composition, and stability (Gill and Beardall, 2001). One well-described impact of game damage is leader browsing on young trees (forest regeneration), which alters the stand structure and species composition and may retard woodland successional development (D'Aprile et al., 2020; Holík et al., 2021; Stokely and Betts, 2020; Vacek et al., 2014). Bark stripping is another serious type of damage caused to forest stands (Candaele et al., 2021; Gill and Beardall, 2001; Krisans et al., 2020; Nagaike, 2020; Verheyden et al., 2006).

Bark stripping has a direct effect on reducing radial growth and the production capacity of damaged trees (Cukor et al., 2019a; Månsson and Jarnemo, 2013). Moreover, damaged trees are generally more sensitive to drought, especially in drought-sensitive areas (Mäkinen et al., 2001). Bark-stripped trees by ungulates indicate a greater sensitivity to a lack of precipitation, especially in June, compared to healthy trees (Cukor et al., 2019b; Z. Vacek et al., 2020). Extreme climatic fluctuations and long-term drought periods are becoming more frequent in recent years due to ongoing climate change (Vicente-Serrano et al., 2020).

The most vulnerable trees to bark stripping are in young forest stands under 40 years of age (Gill, 1992; Welch et al., 1988), and the most vulnerable section of the trunk to bark damage was found to be between 30 and 210 cm above ground level; however, the potential height of damage can be significantly limited by low growing branches (Pach, 2002). Moreover, the bark stripping damage causes secondary rot infections of the wood mass by fungal pathogens (Arhipova et al., 2015; Burneviča et al., 2016; Z. Vacek et al., 2020). In particular, the subsequent spread of the stem rot negatively affects the stability of damaged stands (Krisans et al., 2020; Z. Vacek et al., 2020). This destructive effect has so far been described in Norway spruce (*Picea abies* [L.] Karst.) where the rot can affect a few meters of the stem according to the range of previous damage of the bark (Candaele et al., 2021; Cukor et al., 2019b; Krisans et al., 2020). Another tree species, which is affected by rot infection after bark stripping, is silver fir (*Abies alba* Mill.) (Pach, 2008, 2005, 2003). Scots pine (*Pinus sylvestris* L.), one of the most important commercial coniferous tree species in Europe (Mitschel et al., 2011; S. Vacek et al., 2020), is another tree species threatened by damage caused by ungulates. The Scots pine share in the European Union's commercial forests is approximately 20% (Marčiulynas et al., 2019; Mason and Alfa, 2000). The impact of bark stripping on the production characteristics of Scots pine has so far only been assessed on a limited scale in the Baltic States and Fennoscandia (Faber, 1996; Metelaid et al., 2013). However, detailed evidence of the impact of this type of damage is absent.

This paper aims to evaluate the effects of bark stripping by the introduced sika deer on the production characteristics of Scots pine in the common acid and poor-nutrient pine stands. The particular objectives of this study are to evaluate (i) production differences in terms of diameter, height, and stem volume of trees according to circumference damage, (ii) stem rot development in relation to different bark stripping parameters, and (iii) the effects of climatic factors (precipitation, temperature) on the radial growth according to the extent of the damage.

## 2. Material and methods

### 2.1. Area of interest

The impact of sika deer on pine stands was assessed in the south-western Czech Republic in the Úněšov hunting district (2,142 ha), Líšany-Hunčice hunting district (2,100 ha), Čeminy-Kumberk hunting district (1,502 ha), and Luhov hunting district (909 ha). Research was

conducted in five separate forest units (Fig. 1). Three stands were evaluated in each forest unit/hunting district (15 altogether). The age of the stands ranged between 40 and 42 years according to the forest management plan. In 2019, a game census was conducted in the area using thermal imaging devices, which determined the abundance of sika deer to be 18.2 individuals per 100 ha. The number of hunted individuals in 2004 to 2018 fluctuated between 13.9 ind. to 18.5 ind. with a long-term average of 14.7 sika deer individuals per 100 ha in the hunting district Líšany-Hunčice (center of the area) where the tree samplers were cut (see below). The number of hunted individuals in the surrounding hunting districts is comparable. Therefore, the area shows a well-established sika deer population in western Bohemia (Barančková et al., 2012).

The area of interest consists of secondary pine forests on *Fagetum acidophilum* sites at an altitude of 425–492 m a.s.l. The forest stands were artificially established as even-aged monocultures with 10,000 pine seedlings per hectare (in accordance with Regulation No. 13/1978). The stands are formed by predominant Scots pine (>90%) with interspersed Norway spruce, European larch (*Larix decidua* Mill.), and common oak (*Quercus robur* L.). All measured Scots pine stands are owned by the Czech state (Czech State Forests) and therefore their management is identical. The first thinning intervention was performed at 13–22 years of age, with a stocking reduction by a maximum of 20% (focusing on the removal of predominant and dying/dead trees according to standard silviculture practices of pine). According to the forest management plan, the average stand volume of studied pine forests is in the range of 115–160 m<sup>3</sup> ha<sup>-1</sup>. The slope ranges from 0 to 4°. The predominant soil type is modal oligotrophic Cambisol, and the parent rock is phyllitic shale.

The average annual temperature is 8.4 °C with a maximum (18.0 °C) in July, and annual precipitation is 488 mm with a maximum (67 mm) in June (data from the Kralovice meteorological station in 1961–2020). The study territory has typically warm, dry summers and cool, dry winters with a narrow annual temperature range (Cfb) according to Köppen climate classification (Köppen, 1936). The growing season ( $T_{max} > 10$  °C) lasts 155 days, with a mean precipitation of 325 mm and a mean temperature of 14.3 °C. The number of tropical days ( $T_{max} > 30$  °C) is 6, the number of frost days ( $T_{max} < 0$  °C) is 34, and the number of days with snow cover is 48.

### 2.2. Data collection

Growth characteristics (diameter at breast height and tree height) were measured on a total of 417 Scots pine specimens. The studied stands were measured after the first thinning. The predominant and dominant pine trees – according to the classification by Kraft (Kraft, 1884), were chosen as the significant growth response (Remeš et al., 2015). In each of the 15 forest stands, 24–32 trees were randomly selected using the RANDBETWEEN function (Excel). The diameter at breast height (DBH  $\geq 4$  cm) was measured with a standard forestry caliper (Haglöf, Sweden) to the nearest 0.1 mm. The height of individual trees was measured with a Laser Vertex hypsometer (Haglöf, Sweden) to the nearest 0.1 m. For each tree, the circumference damage, length of the damage, and distance of the center of the damage from the ground were recorded. Peripheral bark damage (old and new) was measured with a standard circumferential tape at the widest point of the wound with an accuracy of 1 mm. In the case of multiple lesions (located one above the other), the sum was recorded at the widest damage site. Furthermore, the length and mean height (widest damaged area on the stem) of bark stripping was documented to the nearest 1 cm.

Bark stripping was evaluated and classified using the methodology of the Institute of Forest Ecosystem Research, Ltd. (IFER, Jílové u Prahy, Czech Republic) and the Forest Management Institute (ÚHÚL, Brandýs nad Labem, Czech Republic), applying national inventory measurements. Game damage was measured along the girth of the tree stem utilizing a tape (to the nearest 1 mm) at DBH and was subsequently



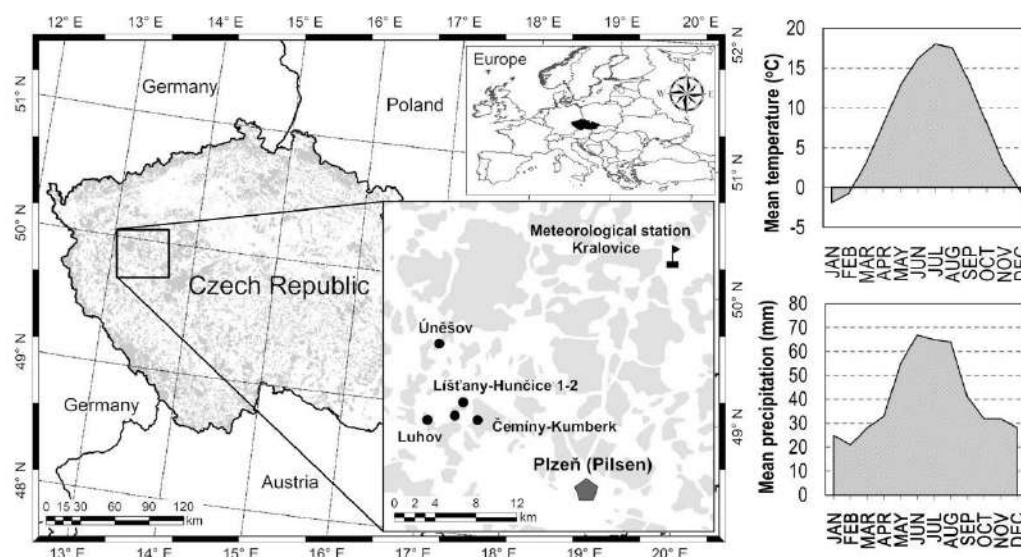


Fig. 1. Location of five separate studied forest units, and the Meteorological station Kralovice – the source of data used for dendrochronology analyses and the mean monthly climatic values (1961–2020); forest stands are marked in gray; the map was created in ArcGIS 10 software (Esri).

divided into three categories: healthy trees (damaged circumference  $\leq 1/8$  of the stem girth), minor game-induced damage (damaged circumference  $> 1/8$  and  $\leq 1/3$  of the stem girth), and extensive game-induced damage (damaged circumference  $> 1/3$  of the stem girth) (Cukor et al., 2019a; Kosmala et al., 2008; Z. Vacek et al., 2020). Repeated damage was very rare in the damaged trees. However, if there was more damage of the tree stem, these bark damages were added together around the circumference for analysis (does not apply if the damage was below each other - the maximum damage can reach max 100% of the stem circumference).

To assess the vertical spread of stem rot in damaged trees and the age of the first damage, a total of 40 sample trees of Scots pine (DBH range 10.1–24.6 cm) with varying degrees of circumference damage (10 × trees each with the following damage ranges:  $\leq 10\%$ , 10–20%, 20–30%, and  $> 30\%$ ) were felled between January and April 2020. Trunks were then sampled in sections (the section length was 20 cm) from the point of the widest circumference damage, both toward the top and the base of the trunk (stem). In the case of rot occurrence, the boundary between the wood infected by fungal pathogens and healthy wood was marked on

each crosscut (see Fig. 2). Each mark was documented on every crosscut using a Canon camera (Canon, Ōta, Japan) with a focal length of 50 mm. The photos of the rot-damaged areas were measured in the ImageJ processing program (Schindelin et al., 2015). The age at the first occurrence of bark stripping damage was determined from photos of the crosscuts of the stem at the widest point of damage. The age of the damage was deducted from the annual rings and subsequently, 4 years were added to the total age of the first damage due to the growth of the tree to the mean height damage – 0.9 m (increase calculated from the surrounding, newly established pine stands by artificial regeneration).

The selected stands were bore-holed for subsequent analyses of radial increment in relation to climatic factors. In each of the 6 stands in the Lištany-Hunčice hunting district, 5 bores were taken from healthy trees and 5 from extensively damaged individuals from randomly selected (RANDBETWEEN, Excel) predominant and dominant trees. A total of 60 Scots pine boreholes were collected for dendrochronology (30 samples of healthy trees and 29 samples of damaged trees were analyzed). The bores were taken with a Pressler auger (Haglöf, Sweden) perpendicular to the trunk axis at a height of 1.3 m in a north-south



Fig. 2. Scots pine trunk crosscuts and highlighting the rot-damaged area.



direction. Individual tree rings were then measured with an accuracy of 0.01 mm using an Olympus microscope on a LINTAB measuring table (RINNTECH) and recorded in TSAP-Win software (RESISTOGRAPH).

### 2.3. Data analysis

For each tree ( $\text{DBH} \geq 4$  cm), volume was calculated based on measured dendrometric characteristics (Petráš and Pajtók, 1991). Relationships between production parameters (average DBH, average height, and mean stem volume) were tested according to different degrees of game damage using analysis of variance (ANOVA). The demonstrable differences between variants were further evaluated using the Tukey post-hoc test. In the case of failure to meet the data normality condition (tested by the Shapiro-Wilk test), the Kruskal-Wallis test was used with subsequent multiple comparisons (Siegel and Castellan Jr., 1988). The aforementioned analyses were performed using Statistica 12 software (StatSoft, Tulsa).

A linear model was constructed for predicting the trunk volume ( $\text{m}^3$ ) based on DBH (cm) and stem circumference damage (in percentage). The mean tree height volume was considered in the model, i.e., the model intercept was corrected for the mean tree height. The results of the model are presented in the respective table (Table 1) and graphically depicted in the respective plot.

Linear and multiple linear regression were used (R Core Team, 2020) to examine the relationship between rot-damaged areas and damaged trunk girth, and between the vertical spread of rot (or the percentage of the area affected by rot) and the distance from the location of the damage on the trunk.

The tree-ring series were individually cross-dated (removing errors associated with the occurrence of possible missing tree rings) using statistical tests in the PAST software (Knibbe, 2007) and then visually inspected according to Yamaguchi (Yamaguchi, 1991). If a missing tree ring was found, a 0.01 mm wide ring was inserted in its place. Individual curves for specific variants were then standardly detrended by a 16-year spline for removing short-term fluctuations. Based on the detrending, an average tree-ring series was generated in the ARSTAN software. The expressed population signal (EPS) was calculated for the detrended data. EPS represents the reliability of the chronology as a fraction of the joint variance of an infinite perfect population. The limit for using the data for comparison against climate data was a significant EPS threshold, such that  $\text{EPS} > 0.85$  (Bunn, 2008). Also, the signal to noise ratio (SNR), which represents the signal strength of the chronology, and R-bar (inter-series correlation) were calculated (Fritts, 1976). First-order autocorrelation (Ar1) and signal-to-noise ratio were also performed. The EPS, SNR, R-bar, Ar1 values were calculated according to the “dplr” guidelines (Bunn, 2010) based on common dendrochronological theories (Fritts, 1976; Speer, 2010).

The analysis of negative pointer years was carried out as shown in Schweingruber (1990) and Desplanque et al. (1999). For each tree, the negative pointer year was tested as an extremely narrow tree ring that does not reach 40% of the average increment calculated from the previous four years. The occurrence of a negative pointer year was evident if this severe reduction in increment occurred in at least 20% of the trees from a given variant. The DendroClim software was used for the investigation of radial growth response to climate (Biondi and Waikul,

2004). The regional tree-ring index of healthy and extensively damaged pine trees was correlated with monthly air temperature and monthly sum of precipitation from April of the previous year to September of the current year in the period 1984–2019. Monthly climatic data were taken from the Kralovice meteorological station (468 m a.s.l.; WGS84 49°58'51"N, 13°29'06"E), which is on average 30 km away from the site of interest. The period 1984–2019 was chosen depending on the value of EPS, and whether it was substantial enough for dendrochronological analyses.

## 3. Results

### 3.1. Extent of the damage and the production of damaged trees

Out of 417 examined trees for estimation of production parameters, 258 (62%) were classified as healthy trees (the bark-stripping damage did not reach 1/8 of the stem circumference). Minor damage was observed on 122 trees (29%), and extensive damage (the bark-stripping damage reached over 1/3 of the stem circumference) was observed on the rest (37 trees; 9%). The mean damage of the stem circumference in the category of trees with minor damage reached 19.0%, or 41.8% in the case of extensively damaged trees. On average, the center of bark stripping damage was found at the height of 89.8 cm  $\pm$  1.7 SE above ground. The average length of the damage (along the stem) was observed to be 43.3 cm  $\pm$  2.1 SE.

Significant differences between the variants studied (healthy trees, trees with minor damage, and trees with extensive damage) were found in the DBH (K-W test,  $H = 6.61$ ,  $p < 0.034$ ) and the volume of the mean stem of the pines (K-W test,  $H = 7.62$ ,  $p = 0.022$ ; Fig. 3). In these cases, there were significantly ( $p < 0.05$ ) higher stem diameter and volume in healthy trees compared to extensively damaged. In contrast, no difference in overall height between the variants was found (K-W test,  $H = 1.49$ ,  $p = 0.481$ ).

The highest mean diameter was found in undamaged trees (18.9 cm  $\pm$  0.2 SE), compared to lightly damaged (18.3 cm  $\pm$  0.3 SE) and extensively damaged individuals (17.4 cm  $\pm$  0.5 SE). The height ranged from 18.8 m  $\pm$  0.3 SE for extensively damaged individuals to 19.2 m  $\pm$  0.1 SE for undamaged individuals, but their means were not significantly different. The highest percentage of difference was found in the mean-stem volume, with lightly damaged individuals showing a volume loss of 11.1% (0.238  $\text{m}^3 \pm$  0.009 SE) and extensively damaged individuals up to 16.9% (0.222  $\text{m}^3 \pm$  0.014 SE) compared to healthy trees (0.267  $\text{m}^3 \pm$  0.008 SE).

The results of the linear model for prediction of the mean tree height stem volume based on the DBH and stem circumference damage are shown below (Table 1). The constructed model has the form of  $y = -0.246 + 0.027 \cdot \text{DBH [cm]} - 0.00009 \cdot \text{CD [\%]}$ , where  $y$  denotes the stem volume in  $\text{m}^3$ , the DBH and circumference damage (CD) in %. The stem volume was significantly affected by DBH ( $p < 0.001$ ), but no statistical significance was found for circumference damage ( $p = 0.23$ ). The model is valid for the DBH range present in the dataset used (9.9–31.1 cm), and the  $R^2$  value reached 0.96. The following form of a linear model was used to fit the data (R software notation; R Core Team, 2020: Mean tree height stem volume  $\sim$  DBH + Relative circumference damage).

### 3.2. Effect of damage on the spread of rot in the trunk

Based on the crosscuts, the relationship between the crosscut area of the rot-damaged trunk at the widest point of trunk damage – in relation to the extent of circumference game damage – was determined using linear regression (Fig. 4). The results indicate a relatively good ability to predict the area of the rot-infested crosscut at the point of the largest circumference damage by measuring the damaged circumference of the trunk. The coefficient of determination ( $R^2 = 0.48$ ) reaches a lower value, primarily because of the two outliers with a greater extent of rot

**Table 1**

The results of the linear model for predicting mean tree height stem volume based on the DBH and stem circumference damage. Significant results are marked in bold.

| Variables                         | R squared = 0.96 |               |                   |
|-----------------------------------|------------------|---------------|-------------------|
|                                   | Estimate         | t value       | p value           |
| Intercept                         | -0.246           |               |                   |
| <b>DBH (cm)</b>                   | <b>+0.027</b>    | <b>71.629</b> | <b>&lt; 0.001</b> |
| Relative circumference damage (%) | -0.00009         | -1.199        | 0.231             |



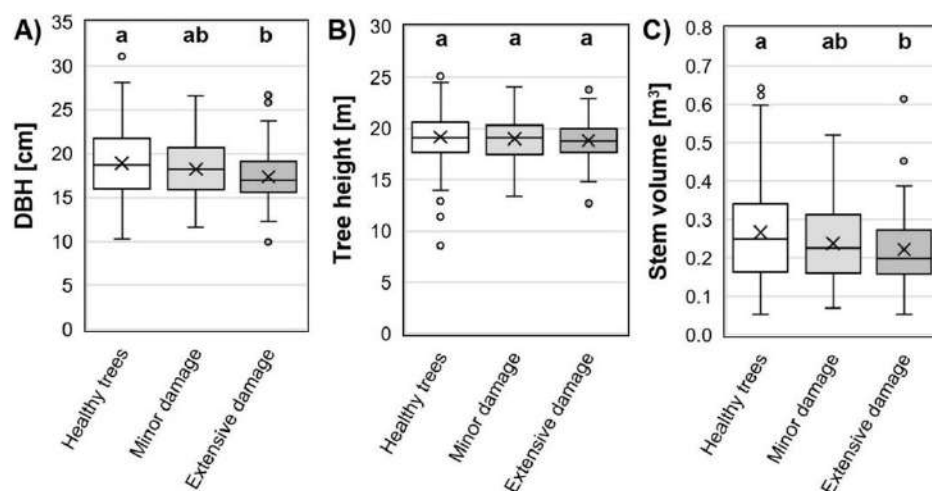


Fig. 3. The mean DBH (plot A), mean height (plot B), and volume of the mean stem (plot C) differentiated according to damage variants (healthy – no damage; minor damage – circumference damage < 1/3 of the trunk girth; extensive damage – circumference damage > 1/3 of the trunk girth); significant differences between variants at the 0.05 significance level are indicated by different letters.

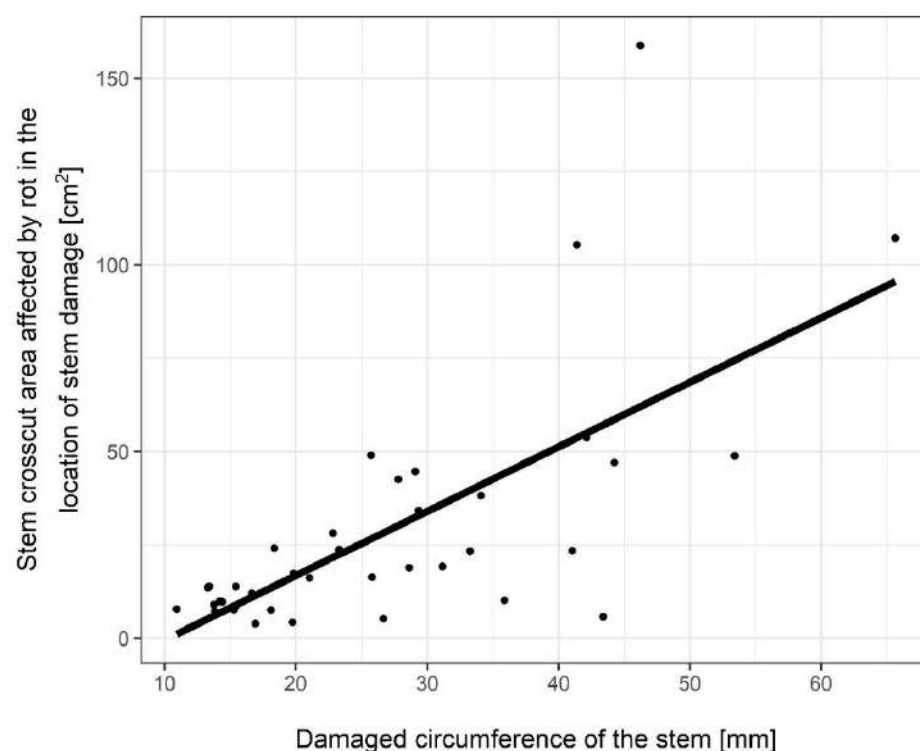


Fig. 4. Dependence of rot-damaged crosscut area at the damaged location on the damaged stem circumference.

damage. Tests of statistical significance show a decidedly significant relationship ( $p < 0.001$ ). The minimum value of the rot-damaged crosscut area at the stem damage was  $0.71 \text{ cm}^2$  (with a damaged stem circumference of  $3.2 \text{ cm}$ ), while the maximum value observed was  $158.67 \text{ cm}^2$  (with a damaged circumference of  $46.2 \text{ cm}$ ). The predicted value of the rot-damaged area on the crosscut at the damaged location increased by  $1.73 \text{ cm}^2$  ( $\text{SE} = 0.295$ ) with each millimeter of damaged stem circumference.

A quadratic function regression was used to model the vertical spread of rot through the stem (Fig. 5). The crosscut area damaged by rot at the bark-stripped spot was used as a reference (rot-damaged area at the damaged spot = 100%). According to the visualization of the regression with a quadratic function, the vertical spread in the trunk can be predicted as fairly good (coefficient of determination reaches  $R^2 = 0.58$ ). The model shows that the rot-affected crosscut area decreases rapidly with increasing distance from the damage location. Half of the

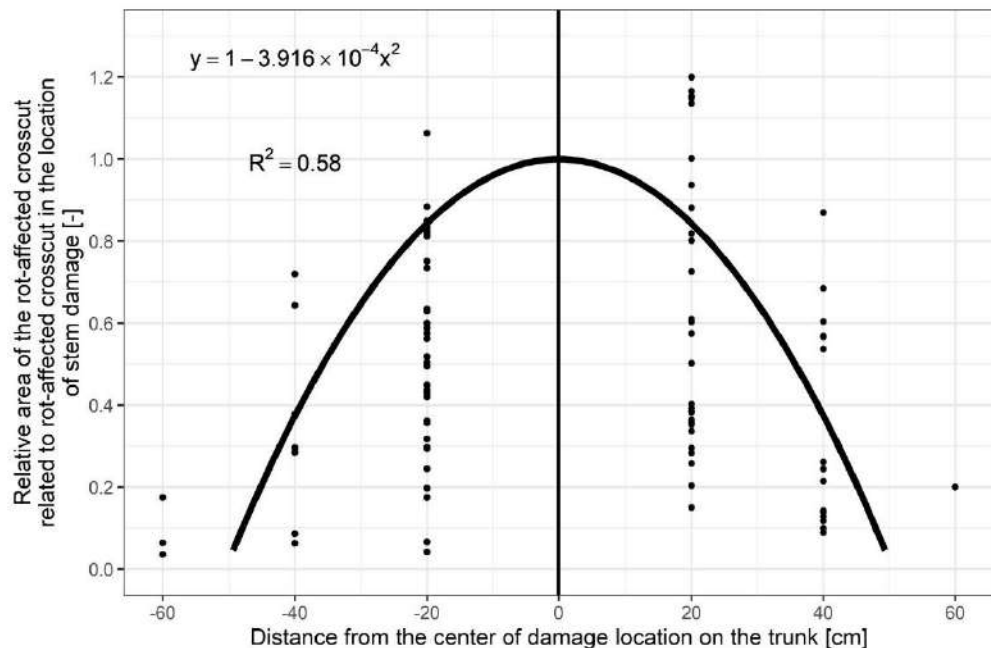


Fig. 5. Dependence of the relative area of the rot-affected crosscut through the trunk on the distance of the crosscut from the location of the stem damage.

extent of rot in relation to the damage location (crosscut, point 0 on the X-axis) can be expected as early as about 35 cm toward the tip and base of the tree. The model assumes that rot no longer occurs more than 50 cm from the damage location. The average rate of vertical spread of rot is 0.86 cm/year, with the average first bark stripping damage to the trunk occurring at  $18.5 \pm 1.5$  SE (8–35 years; Fig. 6). The most frequent period of the first damage was found in pine trees aged 8–11 years (37.5% of trees), when the average DBH of debarked trees was in the range of 3.3–6.4 cm.

The dependence between the area on the crosscut affected by rot, the age when the damage was caused, and the relative circumference damage (%) was assessed by a linear model. The results are given in the following table (Table 2). The area of the crosscut affected by rot damage was significantly ( $p < 0.01$ ) affected by the range of damaged circumference, but no statistical significance was found for the age at the first damage occurrence ( $p = 0.82$ ).

### 3.3. Effect of damage on radial increment and climate sensitivity

The mean tree-ring width of undamaged individuals during the study

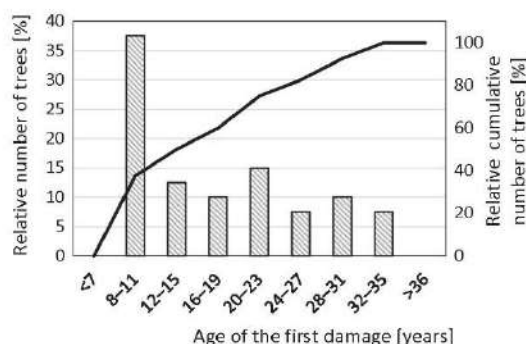


Fig. 6. Age distribution of the first bark stripping damage of Scots pine trees.

Table 2

The results of a linear model for predicting relative crosscut damage by rot based on relative circumference damage and tree age when the first damage occurred. Significant results are marked in bold.

| Variables                                | R squared = 0.19 |             |               |
|------------------------------------------|------------------|-------------|---------------|
|                                          | Estimate         | t value     | p value       |
| Intercept                                | 7.45             |             |               |
| Age at the first damage occurrence (y)   | -0.05            | -0.23       | 0.8206        |
| <b>Relative circumference damage (-)</b> | <b>27.89</b>     | <b>2.76</b> | <b>0.0091</b> |

period (1984–2019) was  $2.54 \text{ mm} \pm 0.32 \text{ SE}$ , whereas the width of extensively damaged pine individuals was 18% lower ( $2.08 \text{ mm} \pm 0.24 \text{ SE}$ ; Table 3). Extensively damaged pines ( $1.25\text{--}3.37 \text{ mm}$ ) had lower values of minimum and maximum radial growth than healthy pines ( $1.53\text{--}5.15 \text{ mm}$ ). Fig. 7 shows that a pronounced decline of radial growth in damaged trees began in 1991 (about 2–5 years after the most frequent debarking damage), and this decline lasted until 2002. In this period, the ring width of healthy trees ( $3.51 \text{ mm} \pm 0.10 \text{ SE}$ ) reached higher values by 51% compared to extensively damaged trees ( $2.33 \text{ mm} \pm 0.06 \text{ SE}$ ). Then, again, the radial growth of both variants (undamaged and extensively damaged trees) is balanced. In terms of EPS, both variants studied are reliable enough for comparison with climatic data, with damaged pines having  $\text{EPS} = 0.85$  and healthy ones  $\text{EPS} = 0.88$ . The other parameters, i.e.,  $\bar{R}$ ,  $\text{EPS}$ , and  $\text{SNR}$ , did not show significant differences; however, damaged pine trees have slightly lower values compared to the healthy ones.

Fig. 8 also shows a difference in the radial growth dynamics of Scots pine on the detrended tree-ring curve (removal of the age trend), primarily in the first half of the study period. Overall, greater variability in growth was found in extensively damaged individuals ( $\text{SE } 0.03$ ) compared to undamaged trees ( $\text{SE } 0.01$ ). No significant year with extremely low radial increment was found in either variant.

The effect of monthly precipitation and average temperature on the radial growth (regional tree-ring width index) of healthy and extensively damaged trees was tested in relation to climatic factors in the period

**Table 3**  
Dendrochronological characteristics of the pine radial growth in 1984–2019.

|                  | Number of samples | Mean RW (mm)        | RW<br>min–max (mm) | Sample age<br>min–max | Ar1  | R-bar | EPS  | SNR  |
|------------------|-------------------|---------------------|--------------------|-----------------------|------|-------|------|------|
| Extensive damage | 24                | 2.08 ( $\pm 1.30$ ) | 1.25–3.37          | 17–39                 | 0.70 | 0.23  | 0.85 | 5.82 |
| Healthy          | 25                | 2.54 ( $\pm 1.77$ ) | 1.53–5.15          | 21–36                 | 0.76 | 0.26  | 0.88 | 7.11 |

Note: RW – tree-ring width; Ar1 – first-order autocorrelation; R-bar – inter-series correlation; EPS – expressed population signal; SNR – signal-to-noise ratio.

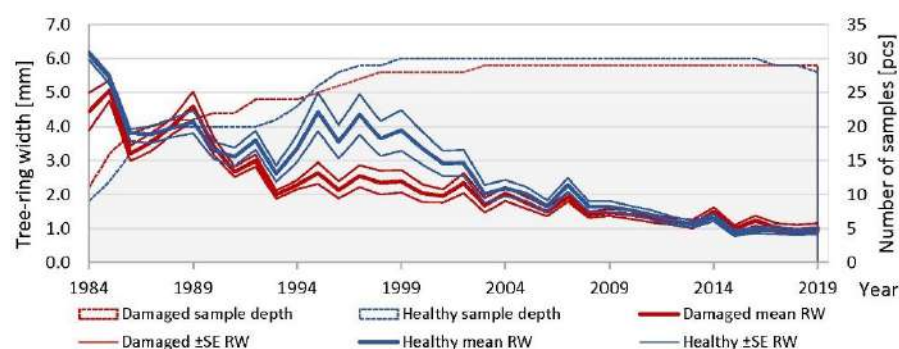


Fig. 7. Dynamics of mean tree-ring width (RW) of Scots pine with standard error ( $\pm$ SE) and sample depth (number of core samples) according to variants of circumference damage (healthy trees, extensively damaged trees) in 1984–2019.

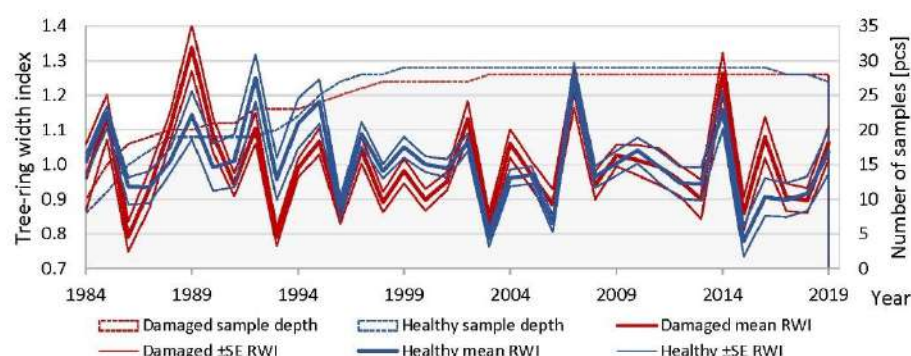


Fig. 8. Dynamics of mean tree-ring width index (RWI) of Scots pine with standard error ( $\pm$ SE) and sample depth (number of core samples) by variants of circumference damage (healthy trees, extensively damaged trees) in 1984–2019.

1984–2019. Fig. 9 shows the significant effect of average precipitation and temperature on the radial growth of Scots pine in different months. A difference was found in the case of precipitation. Extensively damaged trees were more affected by precipitation (5 significant months)

compared to healthy trees (3 significant months).

In the case of temperature, no demonstrably different effect on the radial growth was found between healthy and damaged trees. Healthy trees were more correlated with temperature, while precipitation had a

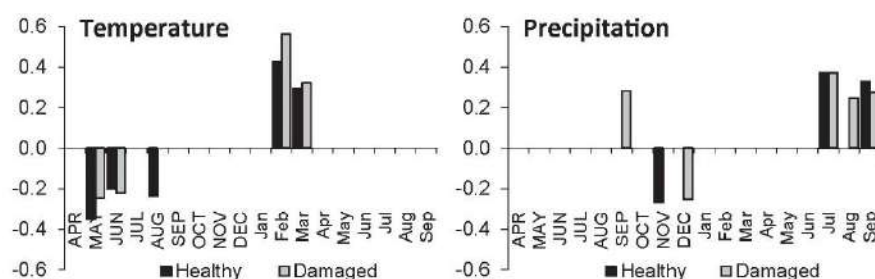


Fig. 9. Correlation coefficients of the regional tree-ring index of Scots pine with mean monthly temperatures from April of the previous year to September of the current year, in 1984–2019, differentiated by circumference damage; statistically significant ( $p < 0.05$ ) values are highlighted in black (for healthy trees) and grey (for extensively damaged trees); capital letters indicate months of the previous year, while small letters represent months of the current year.



greater effect on the radial growth of damaged trees. Temperatures in the previous year's growing season had a negative effect on pine growth and positive ones in February and March of the current year. Precipitation had a predominantly negative effect in winter and a positive effect in the growing season of the current year. Overall, February was identified as the most important month that influences the radial growth in regard to temperature ( $r = 0.42\text{--}0.56$ ) and July for precipitation ( $r = 0.37$  for both variants).

#### 4. Discussion

##### 4.1. Production potential in relation to damage

The research confirmed demonstrable differences between the growth parameter sizes of extensively damaged and undamaged Scots pines. Significant differences in diameter and standing volume of trees with minor damage compared to undamaged ones were not found. Moreover, the effect of circumference damage on height growth was not confirmed. Based on our findings, it is possible to state that the Scots pine indicated a high resistance to circumference damage in relation to growth parameter sizes. In the case of Norway spruce stands, under comparable conditions, a significant effect on the diameter and mean stem volume was already demonstrated for minor damage (damaged circumference  $> 1/8$  and  $\leq 1/3$  of the stem girth; (Cukor et al., 2019a,b; Z. Vacek et al., 2020). However, height increment was also less affected in the case of Norway spruce, with only a strong effect confirmed under comparable conditions in southwestern Bohemia (Cukor et al., 2019b).

Generally, it is possible to state a lower effect of game damage on the height and diameter increment of Scots pine stands compared to spruce stands. The sensitivity of Norway spruce to game-induced damage has been emphasized in the past (Gill, 1992; Vospernik, 2006). Pine has also been significantly less studied to date compared to spruce. Only one relevant study from Estonia simulated damage by artificial bark removal (Metslaid et al., 2013). However, no demonstrable differences between height increment of damaged and control individuals were found in young pine stands in the 5-year period after damage (Metslaid et al., 2013), similar to our results in older stands.

##### 4.2. Bark stripping and stem rot

The occurrence of the first damage was found at the range of 8 to 11 years. A comparable age was described by Gill (1992), who reports that the most vulnerable age for Scots pine is between 5 and 16 years. This time period is significantly shorter compared to Norway spruce (5 to 50 years) which could be explained by different bark thickness. At the age of 8 to 11 years, the DBH of Scots pine was between 3.3 and 6.4 cm. The wider diameter range of debarked trees was also described from the natural environment of sika deer in Japan (mostly 5 to 15 cm; Akashi and Nakashizuka 1999), which was also confirmed by Nagaike (2020) who reported that most trees subjected to bark stripping were small ( $< 10$  cm at DBH). Of the total of 417 trees examined for circumference damage, 62% of pines were classified as healthy, 29% as lightly damaged, and 9% as extensively damaged. However, not only is the circumferential extent of the damage important, but other parameters such as the length of the damage also play a significant role (Gill, 1992). In our case, the average length of the bark stripping was 43.3 cm at an average height of 89.8 cm above ground. Similarly, the values of both length (39.0 cm) and height (87.9 cm) of damage were documented by (Z. Vacek et al., 2020) from spruce stands damaged by sika deer.

Scots pine has shown considerable resilience to the spread of stem rot in damaged trees compared to Norway spruce. Thanks to the presence of chemical compounds in their heartwood, pine species are often more resistant to stem rot even after damage to the stem (Baudet et al., 2020; Marciulynas et al., 2019; Rennerfelt and Nacht, 1955) when compared to other coniferous species, especially to Norway spruce (Swedjemark et al., 1999). This fact was also confirmed in our study. In the case of

pine damage, the rot protruded vertically within a maximum of 60 cm of the trunk crosscut at the point of the widest circumference damage, with an average rate of spread of  $0.9 \text{ cm yr}^{-1}$ . In contrast, in a previously conducted study on Norway spruce in comparable conditions (the same locality with comparable soil conditions, sika deer density, and age of the trees analyzed), stem rot progressed vertically up to 4.5–6.0 m with a spread rate of  $5.7\text{--}9.6 \text{ cm yr}^{-1}$  in middle-aged stands between 40 and 50 years (Z. Vacek et al., 2020). The rot spread was confirmed also in silver fir, where the stem rot spread maximally up to 3 m above the ground level in middle-aged stands with a spread rate of 4.7 cm per year (Pach, 2005). Moreover, silver fir showed considerable regenerative potential. The average rate of wound closure in the first five years after the injury was  $3.29 \text{ mm yr}^{-1}$  and a more rapid closure was observed in smaller wounds (Pach, 2008).

The rot infection of Scots pine is affected by several factors, including different origins – provenances, or soil types when e.g., the vulnerability to *Heterobasidion annosum* infection was confirmed on afforested agricultural land (Lygis et al., 2004; Marciulynas et al., 2019). Similarly, the low vertical spread of rot was found in lodgepole pine (*Pinus contorta*) damaged by bark stripping in Estonia, where the spread of rot did not exceed 10 cm above and 20 cm below the margins of the wound (Arhipova et al., 2015).

##### 4.3. Radial growth in response to climate

Our results further reveal that overall, greater variability in radial growth was found in damaged individuals compared to undamaged trees, yet no significant negative years, i.e., significant years with extremely low radial growth, were confirmed. This is mainly due to the better soil, and thus moisture conditions at a given site in the studied secondary pine stands compared to natural pine stands in rocky and exposed sites with a shallow soil profile (S. Vacek et al., 2020). In this study of relict pine stands in the Kostecké bory Nature Reserve in the Czech Republic, three significant negative pointer years (1922, 1976, and 2017) with significantly low radial growth were reported due to a lack of precipitation in the growing season. However, the effect of climatic conditions varies according to microhabitat characteristics in the given location. In comparison with the same area, several negative pointer years (2003 and 2015) were found for Norway spruce due to drought and high temperatures (Z. Vacek et al., 2020), which was not observed in our study for pine. In addition to habitat conditions, the growth of Scots pine is greatly influenced by silvicultural practices (Břenek et al., 2016; Mäkinen and Isomäki, 2004; Saarinen et al., 2020).

Our study proves that a demonstrable difference was found in the relationship between precipitation and radial growth. For precipitation, the negative effect was predominant in winter and positive in the growing season (July) of the current year. Temperatures in the growing season of the previous year had a negative effect on the radial growth of Scots pine, while the effect was positive in February and March of the current year. Similarly, Vacek S. et al. (S. Vacek et al., 2020) reported a positive correlation of radial growth with temperature in April and precipitation in May and July in natural pine forests. In lowland pine forests in eastern Bohemia, radial growth was also positively correlated with temperature in March, and especially with precipitation in the growing season of the current year (Vacek et al., 2016). Also, other studies from the Mediterranean and Alpine environments (Augustaitis et al., 2007; Bogino et al., 2009; Vacek et al., 2017) indicate that precipitation or drought are critical factors for radial growth of Scots pine in Central Europe. Similarly, according to Insinna et al. (2007), temperature has less influence on growth processes of pine than precipitation.

Concerning bark stripping and rot, extensively damaged pine trees were more affected by precipitation, while healthy trees responded more to the effects of temperature. The higher sensitivity of damaged trees to a lack of precipitation and drought stress was also confirmed by other studies on coniferous tree species in the Czech Republic (Cukor et al., 2019b; Z. Vacek et al., 2020) and Finland (Mäkinen et al., 2001). This is



related to bark stripping and extensive damage of the phloem, which is essential for distributing water-soluble nutrients and organic matter throughout the tree, crucial for radial growth (Ryan et al., 2014).

#### 4.4. Recommendations and study limitations

An increase in damage to forest ecosystems could be expected in the future, with increasing population densities of wild ungulates leading to an overabundance on a local scale (Cukor et al., 2017; D'Aprile et al., 2020) but also in wider areas or on the territory of particular European countries (Carpio et al., 2021; Valente et al., 2020; Warren, 2011). This relationship between ungulate population density and game damage has been demonstrated not only for sika deer (Völkl, 1999) but also for native European deer (*Cervus elaphus*) (Ueckermann, 1956; Verheyden et al., 2006) or for browsing intensity on pines by moose, where the damage was positively related to moose pellet group counts (Edenius et al., 2015). However, the bark stripping intensity is not only influenced by local and regional wild ungulate abundance, but also by other factors like winter food shortages and stand properties like thermal and visual cover and scarcity of a herbaceous layer (Candaele et al., 2021). Another factor is the direct effect of human disruption on wildlife populations (Ando et al., 2004; Cukor et al., 2021), which significantly increased the browsing pressure by ungulates (Möst et al., 2015; Szwaigrzyk et al., 2020). The deer disruption could be affected not only by anthropogenic activities but also by natural predators. For instance, the browsing intensity by moose was higher in the high-wolf utilization areas compared to areas with low-wolf utilization (van Beeck Calkoen et al., 2018). It was confirmed that the control of red deer populations is a key measure for bark stripping reduction (Candaele et al., 2021).

Based on the findings, the possibility of the increased use of Scots pine in places with locally elevated deer populations can be assumed, in light of the advancing global climate change (Hanewinkel et al., 2012; Hlásny et al., 2017). Scots pine, in particular, is one of the tree species relatively tolerant to the negative effects of climate change, such as warming, prolonged periods of drought, or extreme weather fluctuations (Kellomäki et al., 2018). Also, the first forest inventory in the Czech Republic shows that only 6% of Scots pine individuals in the second age class (21–40 years) is damaged by game, while the damage in Norway spruce is about 5.5 times higher in the same age class (Vašíček et al., 2007). The relevance of the issue of the negative impact of wild game on forest stands has been highlighted in recent years by the current situation in forest management with the devastating bark beetle calamity of Norway spruce and advancing climate change (Černý et al., 2020; Riedl et al., 2019; Sommerfeld et al., 2021). These salvage clearings will need to be restored with resilient tree species, such as Scots pine, planted to increase stability, maintain production potential, and enhance the adaptation to climate change (Pretsch et al., 2020; Steckel et al., 2020).

A limitation of this study is that bark stripping damage was evaluated at only one broad location (15 forest stands; 5 separate forest units). Scots pine is the tree species with a wide extension area (Kowalska et al., 2017; Marčiulynas et al., 2019). However, the acidic and nutrient-poor sites where the bark stripping was studied are one of the most typical sites with Scots pine stands (Kowalska et al., 2017; Matuszkiewicz et al., 2013; Sharma et al., 2017). Moreover, the experiment was conducted with even-aged stands between 40 and 42 years of age. This age range was chosen deliberately because of high thinning intensity in forest stands between 30 and 45 years of age (Aun et al., 2021; Niemistö et al., 2018; Saarinen et al., 2020) when e.g., in the 45-year-old (middle-aged) stands, the thinning intensity could be up to 24% (Aun et al., 2021). Therefore, our findings have significant application potential, especially in forest management practice, because the thinning intensity may not reflect the range of bark stripping damage on Scots pine stands compared to Norway spruce, where the influence of bark stripping has a significant impact on wood production and stand stability (Cukor et al., 2019b; Krisans et al., 2020; Z. Vacek et al., 2020).

## 5. Conclusion

Analyses of Scots pine exhibited a relatively low impact of bark stripping damage on the production characteristics of stands. Circumference damage had no significant effect on wood production potential, with the lowest effect on tree height. In addition, the secondary rot was minimally spread in the stem. In relation to climatic factors, extensively damaged trees were more sensitive to drought stress, but again, only negligibly when compared to healthy trees. On the other hand, healthy trees responded more to the effects of temperature. In this context, when the climate change is more pronounced (mean temperature rise, long-term droughts, climatic extremes), these findings can be important for forest management regarding the stability of damaged pine stands. However, the limited area of interest at lower altitudes, where there is a relative lack of precipitation, must be taken into account when interpreting these results.

The results thus highlight the potential utilization of Scots pine in the areas with more abundant deer populations, especially under conditions of global climate change, where Scots pine has a much greater chance for successful development when compared to Norway spruce, which suffers much more from precipitation deficit. However, in order for the young-growth pine stand to grow successfully, it is first necessary to ensure that the culture is well-established. This is difficult to achieve in areas with a local increase in game numbers. It should therefore be emphasized that the observed resistance of Scots pine was only assessed in terms of the stands at the small-pole stage. In addition to focusing on damaged pine stands at higher elevations, future research should not only focus on both young stands and tree diameter preferences for bark stripping, but also on old stands where the effect of stem rot may be more pronounced.

#### CRedit authorship contribution statement

**Jan Cukor:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – original draft. **Zdeněk Vacek:** Formal analysis, Conceptualization, Funding acquisition, Investigation, Writing – original draft. **Rostislav Linda:** Formal analysis, Visualization, Writing – original draft. **Stanislav Vacek:** Supervision, Validation, Writing – original draft. **Václav Šimůnek:** Writing – original draft. **Zdeněk Macháček:** Writing – original draft. **Jakub Brichta:** Writing – original draft. **Anna Prokšpíková:** Writing – original draft.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## 6. DISKUZE

### 6.1 Vliv strukturujících pěstebních zásahů na úspěšnost přirozené obnovy borovice lesní

S ohledem na klimatické výkyvy, potřebu snižovat náklady na obnovu porostů, udržovat lokální populace lesních dřevin, či také v kontextu mimoprodukčních funkcí zachovávat lesní prostředí, je potřeba zkoumat alternativní způsoby obnovy lesních porostů. V případě borovice lesní je výše zmíněné navíc velmi aktuální, neboť se jedná o jednu z nejvíce hospodářsky významných dřevin Evropy. Současná i historická odborná literatura v tomto kontextu zmiňuje možnosti podrovního hospodaření také se světlomilnou borovicí, kdy lze dosáhnout dobrých výsledků jak v rámci ekologie lesa, tak z hlediska ekonomických aspektů jeho obnovy.

Možnostem podrovního hospodaření s borovicí lesní se v rámci disertační práce věnovala studie BRICHTA et al. (2020). Ke zjištěným výsledkům je nejprve nutné dodat, že ačkoli byla prokázána nejvyšší hustota jedinců přirozené obnovy pod mateřským porostem zakmenění 0,4, samotnou hustotu mateřského porostu nelze taxativně považovat za faktor, který má na početnost jedinců obnovy jednoznačně pozitivní vliv. Mateřské stromy vytváří konkurenci o dostupné sluneční záření, živiny i vodu, a to jak mezi sebou, tak ve vztahu k nové generaci lesa (VALKONEN et al. 2002; SÁNCHEZ-SALGUERO et al. 2013). Negativní efekt konkurence nemusí být patrný bezprostředně po opadu semen či jejich počátečnímu vzejití, očekává se však s dalším odrůstáním jedinců obnovy (BELAND et al. 2000), a to jak v případě borovice lesní, tak borovice vejmutovky (*Pinus strobus* L.) (PITT et al. 2011). Nižší hustotu přirozené obnovy na holoseči lze odůvodnit zejména skutečností větší vzdálenosti semenných stromů, tedy řádově nižším počtem semen na ploše (KUULUVAINEN & PUKKALA 1989). Nižší počet semen na holoseči, v porovnání s počtem semen pod mateřským porostem výzkum BRICHTA et al. (2020) potvrdil. Podobný experiment stanovili také BELAND et al. (2000), a sice obdobně pro několik variant zakmenění mateřského porostu (200 mateřských stromů/ha; 160 mateřských stromů/ha; holoseč), s využitím přípravy půdy kombinovanou lesní frézou. Zatímco šetření BRICHTA et al. (2020) stanovilo nejvyšší počty jedinců přirozené obnovy (32 402 ks/ha) v porostu se zakmeněním 0,4 (cca 120 mateřských stromů/ha), ve studii BELAND et al. (2000) pro nízkou hustotu porostu (160 mateřských stromů/ha) bylo zaznamenáno až 53 000 ks/ha. Ještě vyšší hodnoty byly zjištěny v porostu s nejvyšším zakmeněním (200 mateřských stromů/ha; 90 000 ks jedinců přirozené obnovy/ha). HUTH et al. (2022) ve své studii, podobné



studiím BELAND et al. (2000) či BRICHTA et al. (2020) popsali hustotu jedinců přirozené obnovy pod porostem, s různými variantami přípravy půdy, v intervalu 5 900–199 000 ks/ha. Práce BELAND et al. (2000) rovněž zjistila velmi nízký počet jedinců obnovy v prostředí holoseče (3 700 ks/ha). BRICHTA et al. (2020) uvádí počet jedinců přirozené obnovy na holoseči v závislosti na konkrétní metodě skarifikace půdy od 11 500 ks/ha do 21 960 ks/ha, nicméně se vždy jednalo o hustotu obnovy nižší než pod mateřským porostem zakmenění 0,4 (32 402 ks/ha).

Dobré výsledky přirozené obnovy pod uvolněným mateřským porostem (zakmenění 0,4) lze odůvodnit také lepšími podmínkami mikroklima v částečném krytu mateřských stromů, které díky měření teploty půdy a vodního potenciálu půdy potvrdil také výzkum disertační práce (BRICHTA et al. 2020). Na základě měření vodního potenciálu půdy a teploty půdy lze tedy usuzovat, že ideální mikroklima zaručuje kryt silně rozvolněného mateřského porostu, nikoli prostředí holoseče nebo naopak hustého mateřského porostu. Zmíněnou myšlenku potvrzují také studie LIMOUSIN et al. (2008), DEL CAMPO et al. (2014), či GEBHARDT et al. (2014), kteří uvádí, že uvolnění mateřského porostu má pozitivní vliv na vodní potenciál půdy, zejména díky nižší interpci mateřského porostu (LIMOUSIN et al. 2008), stejně jako jeho snížené konkurenci a evapotranspiraci (KELLOMÄKI et al. 1998; GIUGGIOLIA et al. 2013). Silným snížením hustoty mateřského porostu je tak možné zvýšit množství vody v půdě o 20-40 % (DEL CAMPO 2014).

Zjištěná nízká hustota jedinců přirozené obnovy pod mateřským porostem je nicméně známá z Turecka (KARA & TOPAÇOĞLU 2018), kde 5 let po clonné seči v mateřském porostu o zakmenění 0,5 činil průměrný počet jedinců pouze 7 000 ks/ha, což je v podstatě srovnatelné s výzkumem ALEKSANDROWICZ-TRZCIŃSKA et al. (2014), kteří uvádí 9 190 ks/ha na holoseči. Výsledky disertační práce potvrzují pozitivní vliv přípravy půdy na iniciaci přirozené obnovy, jak pod mateřským porostem, tak na holoseči. Příkladem lze uvést rozdíl nejvyšší hustoty přirozené obnovy z kontrolních variant - bez přípravy půdy (5 902 ks/ha) a nejvyšší počet jedinců přirozené obnovy na ploše s přípravou půdy kombinovanou lesní frézou (32 402 ks/ha). Podobné závěry byly publikovány mnoha autory (ÖRLANDER et al. 1990; KARLSSON & ÖRLANDER 2000; HILLE & OUDEN 2004; BARBEITO et al. 2011). Kromě okamžitého vzejití semenáčků především hlubší příprava půdy významně snižuje také poměr

C/N, zvyšuje množství P, Mg a S (ÖRLANDER et al. 1996) a potlačuje konkurenci přizemní vegetace (HILLE & OUDEN 2004; NILSSON et al. 2002; GAUDIO et al. 2011; HYPPÖNEN et al. 2013).

Důležité je také porovnat, jak se počty jedinců přirozené obnovy pod mateřským porostem na úrovni zakmenění 0,4 (až 32 402 ks/ha; BRICHTA et al. 2020) liší od platných doporučení a aktuální legislativy. Platné normy pro minimální počty sazenic při obnově lesa v České republice činí 8 tis. ks/ha (VYHLÁŠKA MZE č. 456/2021 Sb), v Polsku 8–10 tis ks/ha (ZHL 2023), či 6–10 tis ks/ha v Německu (VERSUCHSANSTALT 2008). V tomto kontextu můžeme tvrdit splnění zákonné povinnosti a vyhovění doporučení, v našem případě prostřednictvím podrovního hospodaření. S ohledem na inventarizaci jedinců přirozené obnovy (BRICHTA et al. 2020) právě po 3 letech od provedení clonné seče, lze v podmínkách ČR zároveň porost považovat za zalesněný (ZÁKON č. 289/1995 Sb.). V současné době je pro potřeby zkoumání podrovního hospodaření s borovicí lesní založen nový projekt mezinárodního týmu CLIMAFORCEELIFE (LIFE). Výsledky části projektu inspirovaného designem výzkumu BRICHTA et al. (2020) by měly odpovědět na otázky jak ekonomické efektivnosti iniciace přirozené obnovy pod porostem, tak na tuto alternativu z hlediska klimatické změny.

Na základě výsledků publikace BRICHTA et al. (2020) můžeme potvrdit, že ačkoli přirozená obnova pod mateřským porostem ve srovnání s holosečí vykazuje větší hustotu, dimenze nově vzniklých jedinců (výška rostliny a šířka koruny) jsou zastíněním mateřských stromů ovlivněny spíše negativně. Se zmíněným závěrem je v souladu také další studie předložené disertační práce (ŠLEGLOVÁ et al. 2023), kde bylo měření jedinců ze stejné lokality provedeno s vysokou přesností, v laboratorních podmínkách. Obecně nejlepší výsledky dimenzí přirozené obnovy v práci BRICHTA et al. (2020) a ŠLEGLOVÁ et al. (2023) byly pozorovány na holoseči, ačkoli v porostu se zakmeněním 0,4 byly dimenze v některých případech zkoumaných variant srovnatelné. Vyšší hodnoty výšek jedinců obnovy v případě holoseče a porostu o zakmenění 0,4 pravděpodobně souvisí s lepší dostupností světla. Ačkoli VÍTÁMVÁS et al. (2018) uvádí, že u jednoletých jedinců borovice lesní má oslunění evidentní vliv ve větší míře na podzemní část rostliny, tak RIIKONEN et al. (2016) popisují velmi dobrou schopnost mladých borovic v reakci na uvolnění stromového patra zvětšením šířky koruny. Zmíněný fakt potvrzují nejen starší literární prameny (WIEDEMANN 1925), ale také další aktuální studie (ŠLEGLOVÁ et al. 2023). Výzkum zaměřený mimo jiné na stanovení vlivu zastínění mateřského porostu na

dimenze jedinců přirozené obnovy borovice lesní potvrdil, že přímé oslunění má pozitivní vliv na šířku koruny i na její rozvětvenost. Z dané studie tak vyplývá, že čím více světla má rostlina k dispozici, tím více větví různých řádů se na ní nachází. Výsledky práce FINNEY et al. (2013) zmíněný vztah posuzují z hlediska konkurence ostatních rostlin, tedy že borovice lesní v konkurenčním prostředí soustředí více energie v růstu do výšky rostliny než s ohledem na šířku její koruny. V tomto kontextu je známá informace také o fototropismu borovice lesní (RAUH 1939). K vlastnostem větvení jedinců přirozené obnovy lesních dřevin je však nutné také dodat, že příliš četné větve různých řádů nejsou pro praktické lesnictví žádoucí, neboť vytváří velké množství suků (STEVENS & PERKINS 1992; JELONEK et al. 2022). Také v tomto kontextu se tedy doporučuje pěstovat borovici lesní pod mateřským porostem, nicméně s dostatečným přísunem světla (ŠLEGLOVÁ et al. 2023).

Ve výzkumu BRICHTA et al. (2020) se nepodařilo prokázat pozitivní vliv přípravy půdy na dimenze jedinců přirozené obnovy. Vliv skarifikace půdy na výšku rostlin a šířku jejich korun nicméně prokázaly jiné studie (NILSSON et al. 2002; GAUDIO et al. 2011). Pozitivní vliv skarifikace na dimenze mladých borovic je obecně odůvodňován lepšími chemickými a mechanickými vlastnostmi půdy, stejně jako nižší konkurencí bylinné vegetace (KARLSSON & ÖRLANDER 2000; VARMOLA et al. 2004; SAURSAUNET & MATRISEN 2018).

## **6.2 Produkce a struktura diferencovaných a smíšených borových porostů, vliv vybraných abiotických a biotických faktorů na vitalitu borovice lesní**

### ***6.2.1 Produkce diferencovaných a smíšených borových porostů***

Šetření zásoby studovaných heterogenních borových porostů v různých státech Evropy (BRICHTA et al. 2024) dosáhlo velmi širokého rozpětí hodnot, a to od 91 do 510 m<sup>3</sup>/ha, s kruhovou základnou od 11 do 47,6 m<sup>2</sup>/ha. Souhrnné charakteristiky porostů se však v jednotlivých zemích výzkumu lišily. Vysoká variabilita produkčních parametrů borových porostů byla potvrzena i v dalších studiích, a to jak u přírodě blízkých borových porostů, tak u běžně obhospodařovaných porostů borovice lesní (VACEK et al. 2019). Nejnižší produkční parametry byly dle BRICHTA et al. (2024) pozorovány na výzkumných plochách, které se vyznačují přirozeným vývojem porostu již od 40. let 20. století (VACEK et al. 2023). Zásoba porostu s podobnou spodní hranicí intervalu byla pozorována také v další studii

předložené disertační práce (VACEK et al. 2019), v podmínkách přirozených borových porostů, a to 88–176 m<sup>3</sup>/ha. Některé další studie (BALVANERA et al. 2006; SZWAGRZYK & GAZDA 2007; ERCANLI & KAHRIMAN 2015) nicméně potvrzují, že existuje souvislost pozitivního vlivu strukturní diferenciace borových porostů na jejich produkci. Ve studii BRICHTA et al. (2024), prostřednictvím které byly studovány strukturně diferencované porosty borovice lesní napříč Evropou, byl zaznamenán nejvyšší radiální přírůst kodominantních a dominantních stromů na lokalitách ve Velké Británii (průměrná šířka letokruhu - 2,22 mm), nejnižší v České republice (0,95 mm), zatímco ve Španělsku (1,33 mm) a Polsku (1,25 mm) byl tento přírůst průměrný. Vysoké hodnoty šířky letokruhů v borových porostech Velké Británie lze vysvětlit zdejším mírným klimatem, zajištěným prouděním Golfského proudu (DAWSON 2009; PALTER 2015).

Také s ohledem na výrazné změny klimatických podmínek je důvodné zabývat se nejen adaptací čistého borového či čistého smrkového hospodářství na tyto změny, ale rovněž případnými možnostmi smíšení v kontextu zvyšování produkce (BRABEC et al. 2023). Smrkové a borové porosty zejména v posledním desetiletí vykazují slabou odolnost vůči abiotickým a biotickým faktorům prostředí (HLÁSNÝ et al. 2021; LIŠKA et al. 2021; HABERSTROH et al. 2022). Jsou však známy také studie, které borovici lesní považují za dřevinu adaptabilní na probíhající klimatické změny, a to v souvislosti se zalesňováním bývalých zemědělských ploch či s prostou obnovou lesa (VACEK et al. 2021b). Je nicméně dostupná celá řada publikací tvrdících opak, a to na základě zkušeností s chřadnutím borových porostů, v různých přírodních podmínkách (MASON & ALÍA 2000; OBERHUBER 2001; BIGLER et al. 2006; GAO et al. 2017; BURAS et al. 2018; HABERSTROH et al. 2022). Výzkumy z různých stanovištních podmínek však naznačují, že je možné borovici se smrkem pěstovat dohromady, formou strukturně diferencovaných smíšených porostů (REMEŠ & KOZEL 2006; BIELAK et al. 2014; ŠVEC et al. 2015; RUIZ-PEINADO et al. 2021). Zmínění autoři rovněž hovoří nejen o lepším plnění funkcí lesa, ale také o lepší produkci porostu borovice se smrkem. Tento fakt potvrzují také výsledky našeho výzkumu (BRABEC et al. 2023).

Na zájmové lokalitě (LÚ Klokočná) popsané v této studii, již proběhl výzkum REMEŠ & KOZEL (2006), kteří uvádějí zásobu zhruba srovnatelných produkčních charakteristik ze smrkových a borových porostů, pomístně doplněných jedlemi, duby a buky. Rozsah zásob porostů byl v tomto případě stanoven na 366–378 m<sup>3</sup>/ha. Horní hranice tohoto rozsahu byla o 101 m<sup>3</sup> nižší než v případě výzkumu BRICHTA et al. (2024), tedy 351–479 m<sup>3</sup>/ha. Ještě nižší



hodnoty zjistili také BÍLEK et al. (2013) ve studii ze stejné oblasti (až 346 m<sup>3</sup>/ha). Produkci smíšených porostů borovice a smrku popisují i studie PRETZSCH & SCHÜTZ (2016) nebo RUIZ-PEINADO et al. (2021), kteří ve svém výzkumu dospěli k závěru, že takové smíšené porosty dosahují statisticky významného nárůstu produkce oproti monokulturám. PRETZSCH & BIBER (2016) dále stanovili až 35,9 % nárůst produkce smíšených porostů borovice a smrku s příměsí buku ve srovnání s monokulturami. Jejich závěry potvrzují i výsledky šetření BRABEC et al. (2023) závěrem, tedy že varianty smíšení se 75 % či 50 % zastoupením borovice lesní v porostu jsou z hlediska celkové porostní zásoby porostu nejpříznivější. Známa je nicméně také studie NOVÁK et al. (2019) z lesních porostů Městských lesů Hradec Králové, kde byla naopak zjištěna vyšší produkce borovice po odstranění smrkové spodní etáže. Autoři tento výsledek argumentují odstraněním efektu korunové intercepce podúrovňových smrků, ve prospěch nadúrovňových borovic. Tato částečně protichůdná myšlenka by pak měla být námětem pro výzkum vlivu odstranění smrkové etáže také z porostů na LÚ Klokočná výzkumu BRABEC et al. (2023). Samostatná produkce borovice lesní na obdobných stanovištích v České republice je srovnatelná s prací VACEK et al. (2016) a ČIHÁK & VEJPUŠTKOVÁ (2021). Podobné produkční charakteristiky borovice lesní a smrku ztepilého ze stejné oblasti uvádí BÍLEK et al. (2017), a to v závislosti na přírodě blízkých metodách hospodaření a procesu přeměny na výběrné hospodářství. Na základě výsledků inventarizace práce BRABEC et al. (2023) lze tvrdit, že smíšené porosty borovice lesní a smrku ztepilého vykazují lepší produkční schopnosti, jak s ohledem na produkci, tak na počet jedinců. VALINGER (1992) tvrdí, že potenciál zvýšení přírůstu je ve směsi v případě borovice ve srovnání se smrkem výrazně nižší. Šetření disertační práce (BRABEC et al. 2023) je s vyšším přírůstovým potenciálem smrku ve směsi s borovicí v souladu, a to i s ohledem na fakt, že borovice lesní ve studovaných porostech často tvoří dominantní postavení z hlediska vertikální struktury porostu.

### ***6.2.2 Struktura diferencovaných a smíšených borových porostů***

V práci BRICHTA et al. (2024) byla horizontální struktura heterogenních porostů borovice lesní v různých státech Evropy ve většině případů náhodná či agregovaná. Toto tvrzení je v souladu se studií VACEK et al. (2016), kteří dále popisují, že v heterogenních porostech borovice lesní s omezenými pěstebními zásahy se zpravidla objevuje agregovaná až náhodná struktura porostu, na rozdíl od typických produkčních porostů, kde se setkáváme s pravidelným rozmístěním jedinců. Výzkum VACEK et al. (2019) či práce MASON et al. (2007) navíc

horizontální strukturu heterogenních borových porostů popisují tak, že skupinkovité rozmístění jedinců platí především pro mladší stromy, kdežto starší stromy jsou rozmístěny spíše pravidelně. Analýza vývoje porostu (SZMYT & TARASIUK 2018) následně odhaluje pravidlo změny struktury přirozených borových porostů s přibývajícím věkem, od náhodné struktury ke shlukovitému uspořádání porostu, avšak konkrétně v případě dubu se v daném porostu postupem času vytváří pravidelná struktura.

Studie BRICHTA et al. (2024) prokázala rozdíly vertikální struktury mezi zkoumanými heterogenními porosty, a sice nízkou vertikální diverzitu v případě lokalit ve Velké Británii, naopak vysoké hodnoty vertikální diverzity ve Španělsku. Vysoká vertikální diverzita, ale také tloušťková a výšková diferenciace, včetně korunové diferenciace na lokalitách Valsaín (Španělsko) může být způsobena typickým horským prostředím, významnými disturbancemi v této oblasti (PARDOS et al. 2017), ale především systémem hospodaření, zaměřujícím se na individuální výběr v porostu (MONTES et al. 2005; EDWARDS & MASON 2006). Ačkoli MALTAMO et al. (2000) konstatuje, že tloušťková diferenciace v heterogenních porostech je ve srovnání s homogenními porosty významně vyšší, tak v případě výsledků disertační práce (BRICHTA et al. 2024) byly hodnoty tohoto indexu (0,200–0,428) spíše nízké až střední. BARBEITO et al. (2009) také dodává, že rovněž výšková diferenciace je v heterogenních porostech s omezeným managementem vyšší než v porostech homogenních. Výzkum MALTAMO et al. (2000) se však v případě výškové diferenciace heterogenních borových porostů od studie BRICHTA et al. (2024) neodchyluje, oproti tomu zmiňuje podobné hodnoty výškové diferenciace. Naše výsledky obsahují také hodnoty indexu korunové diferenciace, která zde činila 1,101–2,642, což v intencích střední až velmi vysoké korunové diferenciace naznačuje také velmi vysokou variabilitu získaných dat. Hodnoty korunové diferenciace jsou nicméně srovnatelné s výsledky studie CASTAGNERI et al. (2015).

Výzkumem struktury smíšených lesních porostů na Klokočné se kromě studie předložené disertační práce (BRABEC et al. 2023) rovněž zabývala šetření REMEŠ & KOZEL (2006), VACEK et al. (2007) či BÍLEK et al. (2016). Autoři shodně potvrdili převážně náhodnou horizontální strukturu v porostech výběrného charakteru. Náš výzkum z hlediska celkové diverzity prokázal u monokultur homogenní strukturní diverzitu, pro porosty smíšené strukturní diverzitu bližší heterogennímu stavu. V ostatních porostech na Klokočné, v jiných studiích, monokultury vykazovaly jednotnou až nepravidelnou strukturu, smíšené porosty strukturu heterogenní

(VACEK et al. 2007). Obdobné výsledky byly zjištěny i na Školním lesním podniku Kostelec nad Černými lesy, které jsou shodně ve stádiu přeměny homogenních porostů na výběrný les (REMEŠ & KOZEL 2006). V práci REMEŠ & KOZEL (2006) byla nicméně popsána horizontální struktura porostu jako nahodilá až mírně pravidelná, zároveň zde byla nízká tloušťková i výšková diferenciaci, včetně celkové strukturní diferenciaci. Tento výsledek je pravděpodobně ovlivněn původním složením porostů ve formě smrkových monokultur na Školním lesním podniku v Kostelci nad Černými lesy, naopak v našem případě byla původně na lokalitě Klokočná ve velké míře přítomna také borovice lesní. VACEK et al. (2017, 2020) upozorňují na výrazně nepravidelnou až bohatou strukturu reliktních smíšených borových porostů, která je v tomto kontextu utvořena dvěma hlavními faktory heterogenní struktury porostů – přirozenou tvorbou mezer a existencí přirozené obnovy. Tato zjištění jsou také v souladu se studií GALLO et al. (2020), kteří potvrzují, že na diverzitu porostů má podstatný vliv také způsob hospodaření. V rámci naší studie (BRABEC et al. 2023) lze v tomto kontextu tvrdit, že individuální výběrné principy pozitivně ovlivnily heterogenitu lesního prostředí.

### ***6.2.3 Vliv vybraných abiotických faktorů na vitalitu borovice lesní***

I přes odlišné přírodní podmínky různých států Evropy změna klimatu stojí za častým chřadnutím borových porostů téměř na celém evropském území. Hlavními abiotickými faktory způsobujícími chřadnutí až odumírání borovic jsou nedostatek srážek a zvyšující se průměrná teplota (VITAS 2008; DAUŠKANE et al. 2011; MARTÍNEZ-VILALTA et al. 2012; SÁNCHEZ-SALGUERO 2012; CAMARERO et al. 2015; ŠRÁMEK & HELLEBRANDOVÁ 2016; GAO et al. 2017; BURAS et al. 2018; ETZOLD et al. 2019). Mnohé studie popisují změny klimatu jako příliš limitní pro borové hospodářství v současné podobě, známe však také práce, jejichž závěry jsou s negativním efektem změny klimatu na růst borovice lesní v rozporu. KÜSTERS (2002) z podmínek Bavorska uvádí schopnost borových porostů regenerovat na změny klimatu a udržet přijatelné tempo růstu, a to i navzdory zvyšujícím se průměrným teplotám, a naopak ubývání dostupných srážek. STÜBNER (2007) dokonce popisoval možné rozšíření růstového areálu borovice lesní. Jiné práce (BORCHERT & KÖLLING 2004; LASCH & SUCKOW 2007) sice klimatická rizika zmiňují, avšak s argumentem, že se borovice z hlediska zdravotního stavu s klimatickými extrémny vyrovná díky své velmi široké ekologické amplitudě. BORCHERT & KÖLLING (2004) však také dodávají, že v tomto kontextu u borovice dojde

ke snížení přírůstu, tedy i celkové produkce. Nutno dodat, že výše zmíněné studie, hovořící o nepříliš zásadním efektu klimatických změn na růst borovice lesní, již nejsou zcela aktuální.

Závěry jednotlivých výzkumů předložené disertační práce potvrzují aktuálně větší vliv klimatických extrémů, zejména na radiální růst borovice lesní. Výsledky studie BRICHTA et al. (2024), zabývající se heterogenními porosty borovice lesní v několika evropských zemích, naznačují, že hlavním klimatickým faktorem, ovlivňujícím radiální růst borovice je teplota. Nižší korelaci mezi radiálním přírůstem a srážkami uvádí také studie ze Švédska (MACIAS et al. 2004), která shodně se závěrem výzkumu BRICHTA et al. (2024) tvrdí, že je to teplota, která významněji ovlivňuje radiální růst borovice. Zmíněné závěry potvrzují také výsledky našeho dalšího výzkumu (BRABEC et al. 2023) na Klokočné, v podmínkách smíšených porostů borovice lesní a smrku ztepilého, a sice větší vliv teploty než srážek na radiální růst obou dřevin, zejména ve vegetačním období. Šetřením porostů předložené disertační práce, konkrétně v podmínkách přirozených borových porostů Kosteleckých borů (VACEK et al. 2019), či homogenních porostů borovice lesní na západě Čech (CUKOR et al. 2019) bylo naopak zjištěno, že korelace mezi srážkami a přírůstem byla silnější než v případě teplot. Výsledky jednotlivých výzkumů disertační práce se tedy v tomto kontextu liší, pravděpodobně zejména z důvodu různého charakteru porostů. Výzkum borových porostů v několika evropských zemích (BRICHTA et al. 2024) nicméně statisticky nepotvrdil vztah srážek ani teploty s radiálním růstem borovic na lokalitách ve Velké Británii. Toto překvapivé zjištění lze nicméně odůvodnit přítomností Golfského proudu, který zajišťuje výrazné oteplování západních břehů Evropy, zejména v zimě, čímž zde udržuje mírné klima (DAWSON 2009) a snižuje frekvenci extrémních klimatických výkyvů (PALTER 2015). Možnost ovlivnění růstu stromů Golfským proudem může být vyvrácena polohou výzkumných lokalit, tedy polohou vnitrozemí, s nadmořskou výškou 250–280 m n. m. Celkově lze u všech zkoumaných lokalit výzkumu BRICHTA et al. (2024) v případě měsíčních srážek zmínit méně významnou korelaci s radiálním růstem než s měsíčními teplotami, s výjimkou lokalit ve Velké Británii, kde byly naopak zjištěny významnější korelace se srážkami. Toto zjištění se odlišuje od výsledků GRACE & NORTON (1990), kteří v klimatických podmínkách Velké Británie naopak zjistili, že teplota má větší vliv na radiální přírůst než celkový úhrn srážek. Avšak GRACE A NORTON (1990) či ALDEA et al. (2021) připomíná, že také nedostatek srážek samozřejmě ovlivňuje radiální růst borovic. Výsledky práce BRICHTA et al. (2024) potvrzují, že teplota je hlavním faktorem



určujícím radiální růst borovice, což se projevuje vyššími korelacemi měsíčních teplot s radiálním růstem stromu.

Potřeba je také zmínit, že žádná ze studií disertační práce nehodnotila vliv klimatu na různě staré či různě dimenzované jedince. VEJPUŠKOVÁ et al. (2020) v tomto kontextu nicméně zmiňuje, že nejvíce jsou teplotními extrémy a nedostatkem srážek ovlivněny porosty střední až vyspělé kmenoviny. Další z publikací předložené disertační práce (ČUKOR et al. 2022) pak potvrzuje, že borovice poškozené loupáním kůry jsou více ovlivněny případnými negativními vlivy klimatu. Studie MARQUES et al. (2022) však signifikantně potvrdila, že suchá období snižují růst borovice bez ohledu na vitalitu stromu. Výsledky našich studií (VACEK et al. 2019; BRABEC et al. 2023; BRICHTA et al. 2024) sice souhrnně naznačují, že teplota, respektive srážky jsou hlavními faktory ovlivňujícími radiální růst borovice, nicméně je také faktem, že v minulém století byl radiální růst jistě ovlivněn také znečištěním ovzduší (LEBEDEV 1862; VACEK et al. 2019; KUKARSKIH et al. 2022; SENSULA et al. 2022). Na základě našeho šetření přirozených borových porostů v prostředí Kosteckých borů (VACEK et al. 2019) můžeme zmíněnou tezi o vlivu znečištění ovzduší na radiální růst borovic potvrdit. Také v souladu s dalšími studiemi (WILCZYŃSKI 2006; VACEK et al. 2017) potvrzujeme, že radiální růst borovic byl negativně korelován s koncentracemi  $\text{SO}_2$  a expozicí ozonu.

Pro jednotlivé výzkumy disertační práce, zabývající se vlivem klimatu na radiální růst borovice lesní (VACEK et al. 2019; BRABEC et al. 2023; BRICHTA et al. 2024) byl pro podmínky střední Evropy jako statisticky významný negativní rok shodně stanoven rok 1976. Zmíněný rok byl charakteristický extrémně nízkou březnovou teplotou, zároveň dlouhodobým suchem v červnu. Spektrální analýzy letokruhových sérií borovice lesní napříč Evropou (BRICHTA et al. 2024) potvrdily výrazný pokles kolísání indexu letokruhů a ztrátu přirozené růstové cykličnosti dospělých jedinců, projevující se již zhruba 30 let. Ztrátu přirozené cykličnosti růstu letokruhů přisuzujeme zejména dynamicky se měnícím klimatickým podmínkám (FÜSSEL 2016; SEIDL et al. 2017; IPCC 2019; VENÄLÄINEN et al. 2020; DE FRENNE et al. 2021; IPCC 2023). Výzkum BRICHTA et al. (2024) zjistil přítomnost 2 až 7letých cyklů radiálního růstu borovice lesní, spojených pravděpodobně s častými výkyvy teploty a srážek (TSONIS et al. 2007; MATVEEV & JUMP 2017). Bylo také prokázáno, že krátkodobé signály (cykly) radiálního růstu borovice lesní (2 až 7 let) jsou méně výrazné než dlouhodobé cykly. Dendrochronologická analýza dat z několika zemí Evropy navíc ukázala, že na většině studovaných lokalit byl evidentní růstový

cyklus 9 až 11 let. Zmíněný cyklus může mít spojitost také se slunečními cykly, popsanými pro srážky i teploty mimo jiné pro podmínky celé Evropy (LAURENZ et al. 2019; LÜDECKE 2020). Jedenáctiletý růstový cyklus byl pro buk lesní popsán jak pro podmínky České republiky a Itálie, tak pro Bulharsko (ŠIMŮNEK et al. 2020, 2021a, 2021b). Sluneční cykly jsou nicméně s ohledem na radiální růst stromů popsány také u borovice lesní, v tomto kontextu v prostředí západního Ruska (SHUMILOV 2011a; SHUMILOV 2011b; MATVEEV & JUMP 2017).

Borovice lesní je v celé střední Evropě velmi ohrožena suchými periodami a zvyšující se průměrnou teplotou. Na tento fakt lze reagovat různými způsoby. Máme již informace o tom, že v podmínkách přirozených borových stanovišť lze adaptovat současné borové porosty na měnící se podmínky klimatu změnou jejich managementu. Některé studie (PARDOS 2017; LUNDGVIST et al. 2019; BRICHTA et al. 2020) naznačují, že minimálně počáteční fáze pěstování strukturně diferencovaných borových porostů, prostřednictvím iniciace přirozené obnovy pod porostem, může být cestou k zachování borovice lesní do budoucna. Konkrétní benefity strukturně diferencovaných borových porostů lze najít také v obecně vyšší odolnosti proředených porostů vůči extrémnímu suchu (SPITTLEHOUSE & STEWART 2004; DEL RÍO GAZTELURRUTIA et al. 2017; AMEZTEGUI et al. 2017; NOVÁK et al. 2021). Ačkoli výše zmíněné výzkumy, hovořící o lepší odolnosti proředených porostů pojednávají především o výchovných zásadách, lze se domnívat, že v dospělých porostech bude tento efekt obdobný.

#### ***6.2.4 Vliv vybraných biotických faktorů na vitalitu borovice lesní***

Výzkum disertační práce hodnotil vliv loupání zvěří na zdravotní stav výchovných porostů borovice lesní, ale také atraktivitu jedinců přirozené obnovy borovice lesní v prostředí reliktních borů. Problematika vlivu loupání kůry na zdravotní stav borovice lesní byla popsána ve studii CUKOR et al. (2022). V rámci zmíněného výzkumu bylo zjištěno, že k prvním škodám loupáním zvěří dochází ve věku jedince 8 až 11 let, což je v souladu se studií GILL (1992), který uvádí, že borovice je v tomto ohledu nejzranitelnější ve věku 5 až 16 let. Pozitivním faktem je, že časový rozptyl popsáný pracemi CUKOR et al. (2022) i GILL (1992) je výrazně kratší než v případě smrku ztepilého (5 až 50 let) (WELCH A KOL. 1987) či douglasky tisolisté (12 až 44 let) (REIJNDERS & VAN DER VEEN 1974). Také s ohledem na to, že v inkriminovaném věku (8 až 11 let) poškozování jedinci borovice lesní dosahovaly výčetní tloušťky 3,3 a 6,4 cm, lze tvrdit, že je borovice poškozována v intencích dimenzí výčetní tloušťky <10 cm. Toto

zjištění potvrzuje také výzkum NAGAIKE (2020). Z prostředí přirozeného výskytu jelena siky v Japonsku AKASHI & NAKASHIZUKA (1999) uvádí poškození stromů s výčetní tloušťkou od 5 do 15 cm, nejčastěji však zmíněných <10 cm. Z celkového počtu (417 ks) inventarizovaných jedinců studie CUKOR et al. (2022) bylo 62 % borovic klasifikováno jako zdravé, 29 % jako lehce poškozené a 9 % jako rozsáhle poškozené. Zásadní jsou však dimenze a lokace daných poškození. V našem případě byla průměrná délka poškození loupáním stanovena na 43,3 cm, při průměrné výšce 89,8 cm nad zemí. Podobné hodnoty délky (39,0 cm) a výšky (87,9 cm) poškození dokládá obdobná studie VACEK et al. (2020), z prostředí smrkových porostů. Zásadní je nicméně především zjištění, že borovice lesní ve srovnání se smrkem ztepilým vykazuje výraznou odolnost vůči šíření následné hniloby z místa prvotního poškození stromu. Lepší odolnost vůči hnilobám lze přisuzovat chemickému složení jádrového dřeva borovice (MARČIULYNAS et al., 2019; BAUDET et al., 2020), zejména v porovnání se smrkem ztepilým (SWEDJEMARK et al. 1999). Dalším zkoumaným parametrem byla průměrná rychlost šíření hniloby, která v případě našeho výzkumu (CUKOR et al. 2022) dosahovala u borovice rychlosti 0,9 cm/rok, kdežto v případě smrku (VACEK et al. 2020) dosahovala rychlosti 5,7–9,6 cm/rok. Porovnat lze také s jedlí bělokorou, kde byla zjištěna průměrná rychlost šíření hniloby 4,7 cm/rok (PACH 2005).

Atraktivitu jedinců přirozené obnovy borovice lesní k okusu terminálního pupenu v předložené disertační práci hodnotí studie VACEK et al. (2019). Výzkum na lokalitách Kosteckých borů naznačil, že čím více je porost strukturně diferencovaný, tím méně jsou jedinci přirozené obnovy poškozováni zvěří. Výše zmíněné tvrzení lze argumentovat výrazně nižšími počty poškozených jedinců na lokalitách Kosteckých borů v rámci opakovaného měření v roce 2016, tedy oproti roku 2006, kdy zde proběhla základní inventarizace. V roce 2016 byl podíl jedinců s poškozením terminálního pupene velmi nízký (poškozených: borovice 1,6 %, smrk 8,7 %, bříza 0,2 %), pouze u buku byl vysoký (36,2 %). Nejvíce byli postiženi jedinci s výškou 20–80 cm. Rozdíl lze sledovat u hodnot na základě stejných parametrů, z roku 2006 (poškozených: borovice 12,2 %, smrk 19,4 %, bříza 2,3 %, buk 92,5 %). Konkrétně borovice lesní se v případě inventarizace škod okusem terminálního pupenu jevila jako nejméně atraktivní, podobný výsledek potvrzuje také rozsáhlá rešeršní studie BRABEC et al. (2024). Výše popsané závěry je však potřeba doplnit také o skutečnosti zastoupení jednotlivých dřevin na plochách, kdy jak v případě Výzkumu VACEK et al. (2019) z prostředí Kosteckých borů,

tak v případě rešeršní práce BRABEC et al. (2024), se jednalo o lokality, kde borovice lesní tvořila dominantní podíl dřevinné skladby. Na přímou úměru snižujících se škod zvíři se zvyšujícím se počtem jedinců přirozené obnovy upozorňuje také DOBROWOLSKA (2008). S ohledem na velmi málo informací o atraktivitě borovice lesní v kontextu okusu terminálních pupenů, či dokonce o vlivu strukturní diferenciacie porostu na výskyt takového poškození, však zatím nemůžeme potvrdit ani vyvrátit stupeň rezistence tohoto taxonu k okusu terminálu.



## 7. ZÁVĚR

Současný stav poznání o borovici lesní je založen na rozsáhlé škále různých literárních zdrojů a praktických zkušeností s jejím pěstováním. Přesto se ukazuje, že informace o daném taxonu jsou v současné době v mnoha ohledech nedostačující, zejména v kontextu probíhajících globálních změn klimatu. V rámci této disertační práce se podařilo detailně popsat aspekty morfologie, ekologie, rozšíření borovice lesní, včetně vlivu přírodních faktorů na vitalitu stromu, aktuálních rizik a možností obnovy borových porostů. Studie dále poukázala na skutečnost, že borovice lesní je navzdory dříve popsané rezistenci vůči suchým obdobím, velmi citelně ovlivněna klimatickými výkyvy. I přes často poškozené až labilní porosty suchem, se nicméně jedná o jednu z nejvýznamnějších hospodářských dřevin Evropy, a to především díky její široké ekologické amplitudě a schopnosti obsazovat taková stanoviště, na kterých ostatní dřeviny nemohou vytvářet souvislé lesní porosty.

S ohledem na potřebu snižovat náklady na obnovu porostů, zajistit jejich lepší stabilitu a adaptabilitu, ale také reagovat na zvýšenou poptávku po mimoprodukčních funkcích lesa, se jako perspektivní jeví na přirozených borových stanovištích využití podrostního způsobu hospodaření. Výsledky této práce naznačují, že alternativou k běžnému holosečnému hospodaření na přirozených borových stanovištích je právě clonná seč. Nejen, že díky vhodné zvolenému rozvolnění mateřského porostu s případnou skarifikací půdy připravíme dobré podmínky pro iniciaci přirozené obnovy, ale zároveň na dané lokalitě také udržíme lesní prostředí. Výsledky výzkumu rovněž ukazují, že při počátečním snížení zakmenění mateřského porostu na úroveň 0,4 a za využití skarifikace půdy, je iniciální hustota následné přirozené obnovy vyšší než na holoseči.

Výsledky výzkumů z již vyspělých borových porostů prokázaly, že borovice lesní je schopna přirozeně udržovat strukturně a druhově diferencované porosty v podmínkách přirozených borových stanovišť. Inventarizace porostů na LÚ Klokočná (LZ Konopiště, Lesy ČR, s.p.) také ukázala, že smíšené borovice lesní se smrkem ztepilým, při uplatnění výběrných principů hospodaření, může vést k vyšší produkční efektivitě než v případě porostů složených pouze z jedné dřeviny. Navíc smíšené porosty jsou oproti monokulturám také vhodnější v kontextu zvyšování ekosystémové rezistence vůči biotickým a abiotickým stresovým faktorům. Z těchto důvodů lze z praktického hlediska doporučit pěstování

smíšených borových porostů se smrkem, v podmínkách kyselých stanovišť nižších poloh. Z dlouhodobého hlediska je však nezbytné zvážit možnosti zavádění dalších druhů dřevin do borových porostů jako adaptivní strategie pro budoucí podmínky, například v souvislosti se změnou dostupnosti vody či změnami v sezónní dynamice růstu jednotlivých dřevin.

Výzkum dále prokázal vysokou rezistenci borovice vůči loupání lesní zvěří, naznačil také menší atraktivitu mladých borovic v rámci okusu terminálních pupenů. V oblastech se zvýšenou hustotou populací spárkaté zvěře se tedy borovice lesní jeví jako vhodná dřevina pro zakládání lesních porostů. Dendrochronologické analýzy však také potvrdily, že borovice je v současné době ve větší míře průkazně ovlivňována klimatickými extrémy, což postupně vede ke ztrátě přirozené cyklicity radiálního růstu stromu.

Předložená disertační práce neodpověděla na všechny otázky týkající se pěstování diferencovaných borových porostů, či s vlivu klimatických výkyvů na jejich růst, představuje však podklad pro další výzkum a tvorbu koncepce přírodě blízkého hospodaření borových lesů. Budoucí výzkum by se měl zaměřit nejen na podrobnější analýzu vlivu klimatických změn na růst a vitalitu borovice lesní, ale také na její genetickou variabilitu v kontextu adaptace na různé environmentální stresory, jako je dlouhodobé sucho, extrémní teploty či změny půdní vlhkosti. Významným směrem by mohlo být studium rozdílů mezi regionálními populacemi borovice, aby bylo možné lépe porozumět jejich odolnosti vůči specifickým lokálním podmínkám prostředí a identifikovat vhodné provenience pro výsadbu v oblastech nejvíce ohrožených změnami klimatu. Současně bude zásadní zohlednit i socio-ekonomické faktory, předně dostupnost dřeva pro průmysl, ochranu půdy a vody, nebo rostoucí požadavky na rekreační a ekologické funkce lesů.

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