

UNIVERZA V LJUBLJANI
BIOTEHNIŠKA FAKULTETA

Pia Caroline LIPUŽIČ

**RASTNI ODZIVI BELE JELKE (*ABIES ALBA*) IN
NAVADNE BUKVE (*FAGUS SYLVATICA*) NA
KLIMATSKE DEJAVNIKE VZDOLŽ KARPATOV**

DOKTORSKA DISERTACIJA

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**GROWTH RESPONSES OF SILVER FIR (*ABIES ALBA*) AND
EUROPEAN BEECH (*FAGUS SYLVATICA*) TO CLIMATIC FACTORS
ALONG THE CARPATHIANS**

DOCTORAL DISSERTATION

Ljubljana, 2025

Na podlagi Statuta Univerze v Ljubljani ter po sklepu Senata Biotehniške fakultete in sklepa Komisije za doktorski študij Univerze v Ljubljani z dne 27. 9. 2023 je bilo potrjeno, da kandidatka izpolnjuje pogoje za opravljanje doktorata znanosti na Interdisciplinarnem doktorskem študijskem programu Bioznanosti, znanstveno področje Upravljanje gozdnih ekosistemov. Za mentorja je bil imenovan doc. dr. Matjaž Čater.

Doktorska disertacija je rezultat raziskovalnega dela, ki je bilo opravljeno na Gozdarskem inštitutu Slovenije.

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AI Študija je sestavljena iz treh vsebinsko dopolnjujočih sklopov in daje vpogled v najnovejše odzive bele jelke in navadne bukke na okoljske dejavnike ter vključuje napovedi odziva na podnebne spremembe in prispeva pri oblikovanju gozdnogojitvenih usmeritev za gospodarjenje v prihodnje. Vzdolž gorskega masiva Karpatov od smo izbrali osem lokacij v odraslih, optimalno razvitih gospodarskih jelovo-bukovih sestojih in pragozdnih rezervatih nad 800 m nad morjem. Izmerili smo asimilacijski odziv mladja v treh zaporednih rastnih obdobjih in odvzeli izvrtke 15 dominantnih jelk in bukkev na izbranih lokacijah za dendrokronološko in lesno-anatomsko analizo. Največjo asimilacijsko učinkovitost jelke smo izmerili v svetlobnih razmerah pod zastorom matičnega sestoja, pri bukvi pa na odprtem. Tako bukkev kot jelka kažeta večjo debelinsko rast z več padavinami v juliju in manjšo rast z večjimi povprečnimi in največjimi temperaturami v juniju tekočega leta. Pri jelki smo potrdili statistično značilno pozitivno korelacijo med debelinsko rastjo in temperaturo pozimi, bukkev pa negativno korelacijo med debelinsko rastjo in temperaturo poleti. Severna rastišča postajajo za rast obeh vrst ugodnejša, zlasti za jelko. Pri jelki smo potrdili statistično negativno korelacijo med relativno prevodno površino in gostoto celic, povprečno površino celic in gostoto celic ter srednjo debelino tangencialnih celičnih sten in relativno prevodno površino. Izmerjene lastnosti trahej pri bukvi so v korelaciji s širino branik. Bukkev in jelka se odzivata na podnebne parametre na izbranih lokacijah različno, pri čemer je jelka bolj odporna na sušo kot bukkev.

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AB The study consisting of three complementary parts provides insights into the updated responses of silver fir and European beech, predicting the response to climate change with basis for silvicultural guidelines for future management. Along the Carpathian Mountains eight permanent plots were established in optimally developed, managed and old-growth beech and fir forests above 800m ASL. The assimilation responses of young trees were measured in three consecutive growing seasons; 15 dominant fir and 15 beech trees were double cored at every selected location for dendrochronological and wood-anatomical analysis. The maximum assimilation efficiency of fir was confirmed under the mature canopy light conditions and for beech in the open. Both beech and fir show better radial growth with higher precipitation in July and slower growth with higher average and maximum temperatures in June of the current year. Fir shows a positive correlation between radial growth and temperature in winter, while beech shows a negative correlation between radial growth and temperature in summer. Northern sites are becoming increasingly favourable for the growth of both species, especially fir. For fir, there is a negative correlation between the relative conductive surface and the cell density, the average cell surface area and the cell density, and the mean thickness of tangential cell walls and the relative conductive surface. Measured tracheal properties in beech show correlations with tree ring width. Beech and fir respond differently to climatic parameters at the selected sites, with fir being more drought tolerant than beech.

KAZALO VSEBINE

	KLJUČNA DOKUMENTACIJSKA INFORMACIJA	III
	KEY WORDS DOCUMENTATION	IV
	KAZALO VSEBINE	V
	KAZALO ZNANSTVENIH DEL	VI
	KAZALO SLIK	VII
	KAZALO PRILOG	VIII
1	UVOD	1
1.1	PREDSTAVITEV PROBLEMATIKE	1
1.1	HIPOTEZE	5
1.2	METODE RAZISKOVANJA	5
2	ZNANSTVENA DELA	8
2.1	ODZIV BUKVE IN JELKE NA RAZLIČNE INTENZITETE SVETLOBE VZDOLŽ KARPATOV IN DINARIDOV	8
2.2	VPLIV TEMPERATURE, RAZPOLOŽLJIVOSTI VODE IN LASTNOSTI TAL NA DIHANJE TAL V JELOVO-BUKOVIIH GOZDOVIH VZDOLŽ KOMPLEKSA KARPATOV	22
2.3	RASTNI ODZIV NAVADNE BUKVE (<i>FAGUS SYLVATICA</i> L.) IN BELE JELKE (<i>ABIES ALBA</i> MILL.) NA KLIMATSKE DEJAVNIKE VZDOLŽ KOMPLEKSA KARPATOV	33
2.4	PODNEBNE OMEJITVE RASTI NAVADNE BUKVE IN BELE JELKE VZDOLŽ KOMPLEKSA KARPATOV - NEDAVNO STANJE IN OBETI ZA PRIHODNOST	47
2.5	VPLIV PODNEBNIH SPREMENB NA LESNO-ANATOMSKE ZNAČILNOSTI JELKE IN BUKVE IZ TREH LOKACIJ V KARPATIH, ROMUNIJI	59
3	RAZPRAVA IN SKLEPI	85
3.1	RAZPRAVA	85
3.1.1	SMERNICE IN USMERITVE ZA GOSPODARJENJE Z JELOVO- BUKOVIMI GOZDOVI V SLOVENIJI	88
3.1.2	PRISPEVEK DISERTACIJE K RAZVOJU ZNANOSTI	91
3.2	SKLEPI	91
4	POVZETEK (SUMMARY)	93
4.1	POVZETEK	93
4.2	SUMMARY	95
5	VIRI	97
	ZAHVALA	1
	PRILOGE	2

KAZALO ZNANSTVENIH DEL

Čater M., Adamič P.C., Dařenova E. 2024. Response of beech and fir to different light intensities along the Carpathian and Dinaric Mountains. <i>Frontiers in Plant Science</i> , 15: 1380275.	8
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KAZALO SLIK

Slika 1: Raziskovalne lokacije vzdolž območja Karpatov (belo označene lokacije se nahajajo v gospodarskem gozdu, zeleno označene v pragozdu) 5

KAZALO PRILOG

Priloga A: Dovoljenje založnika za objavo članka »Effect of temperature, water availability, and soil properties on soil CO₂ efflux in beech-fir forests along the Carpathian Mts« v tiskani in elektronski verziji doktorske disertacije

Priloga B: Dovoljenje založnika za objavo članka »Climate growth limitations of European beech and silver fir along the Carpathian arc – the recent state and future prospects« v tiskani in elektronski verziji doktorske disertacije

1 UVOD

1.1 PREDSTAVITEV PROBLEMATIKE

Za napovedovanje odziva jelke in bukve na podnebne spremembe so potrebne celovite študije, ki omogočajo globlji vpogled v odziv in rast dreves na večjem geografskem prostoru ter zajemajo meritve odzivov sedanjega stanja in vključujejo napovedi prihodnjih podnebnih razmer.

Raziskava je osredotočena na bukev (*Fagus sylvatica* L.) in jelko (*Abies alba* Mill.), ključni drevesni vrsti sredo- in visokogorij večine evropskih držav (EEA, 2006; Dobrowolska in sod., 2017). Evropski gozdovi postajajo zaradi klimatskih sprememb in pogostejših sušnih razmer vse bolj izpostavljeni (IPCC, 2007; Brousseau in sod., 2016). Podnebni modeli napovedujejo za konec 21. stoletja v srednji Evropi povečanje letnih temperatur za 2,7 - 4 °C in zmanjšanje poletnih padavin za 21 - 28 mm (Weigel in Fischer, 2011; IPCC, 2012; Pflug in sod., 2018). Zmanjševanje debelinskega priraščanja po geografski širini potrjuje večanje vpliva sredozemskega podnebja proti severu (Gazol in sod., 2015). Povečevanje koncentracije atmosferskega CO₂ in vse večje temperature naj bi sicer v severni in zahodni Evropi delovale na priraščanje dreves ugodno (Lindner in sod., 2010), v južni in vzhodni Evropi pa večje število sušnih dogodkov in posledično tveganje presega napovedane pozitivne trende (Čater in Levanič, 2019). Odvisnost drevja od količine padavin se je v zadnjem stoletju povečala in sovпада z naraščajočim trendom sušnih dogodkov po letu 1951. Verjetni odziv vrst na podnebne spremembe bo različen, kar bo vplivalo na njihovo tekmovalno sposobnost, obstoj in posledično gozdnogojitvene odločitve in ukrepe (Brang in sod., 2014). Trenutne napovedi klimatskih sprememb slonijo na odnosih med trenutno geografsko razširjenostjo drevesnih vrst, klimatskimi razmerami in hipotetičnimi omejitvami zaradi ekstremnih temperatur in vlažnostnih razmer (Dillaway in Kruger, 2010). Dejanskega značaja omejitev v resnici ne poznamo zaradi pomanjkanja zanesljivih podatkov (Pearson in Dawson, 2003; Ibanez in sod., 2008).

Bukev je prevladujoča gozdna drevesna vrsta velikega gospodarskega in ekološkega pomena s širokim arealom, ki se razprostira od Skandinavije do Sredozemlja (Abstract, 2011). Kljub svoji funkcionalni prilagodljivosti in veliki ekološki plastičnosti jo prizadene suša, kar potrjujejo raziskave odziva v južni Evropi (Jump in sod., 2006). Modeli razširjenosti napovedujejo razširitev njenega areala na severu in zmanjševanje na južnem robu (Kramer in sod., 2010). Kombinacija toplotnega in sušnega stresa lahko povzroči zmanjšanje vitalnosti in njene konkurenčne sposobnosti (Gessler in sod., 2006; Kramer in sod., 2010; Hacket-Pain in sod., 2016). Kot najpogostejša drevesna vrsta v Evropi (Ellenberg, 1988) uspeva v čistih in mešanih sestojih z iglavci, posebno z jelko (Bošela in sod., 2018). Na območju vzhodnih Karpatov zaznavajo spremembe bukovih gozdov v zadnjih desetletjih (Durak, 2010), medtem ko veljajo bukovni pragozdovi severozahodnih Karpatov za stabilne ekosisteme (Kucbel in sod., 2011).

Po Evropi z bukovimi gozdovi večinoma gospodarijo tako, da oblikujejo in pospešujejo enomerne sestojne oblike (Roženberger in sod., 2008). Proizvodne dobe se razlikujejo po

regijah in so odvisne od rastišč in ciljnega premera (Hein, 2007). Ekonomsko uspešne primere prebiralno gospodarjenih bukovih gozdov najdemo v Franciji, Nemčiji in Švici, uporabljajo se tudi kombinacije različnih sistemov, npr. skupinsko-postopnega in zastornega sistema, še bolj pa kombinacijo različic skupinsko postopnega gospodarjenja, tako da so zaplate horizontalne zgradbe različno velike – od velikosti skupin, gnezd do velikosti sestojev (Bončina in Kadunc, 2012.). V slovenskih bukovih gozdovih gospodarimo skupinsko postopno z nekaterimi elementi zastornega gospodarjenja. Raznomerne bukove sestoje najdemo v zasebnih gozdovih, npr. v podgorskem pasu, kjer so bukvi primešane še druge drevesne vrste, predvsem iglavci (Roženberger in sod., 2008). V hrvaških čistih bukovih gozdovih prevladujejo enomerne in enodobne sestojne zgradbe, obhodnja traja okoli sto let, sestoje pa pomladijo z oplodno sečnjo v obdobju 10 let. Prebiralno gospodarjenje in druge zvrsti gojenja gozdov, ki oblikujejo malopovršinske raznomerne sestoje, so omejene predvsem na dinarske jelovo-bukove gozdove, v čistih bukovih gozdovih pa prebiranje opuščajo (Čavlović in Anić, 2008).

Jelka je zgodovinsko in gospodarsko eden pomembnejših iglavcev evropskih montanskih gozdov, ki prevladuje v hladnih območjih zmernega pasu (Ellenberg, 2009). Je ključna pri ohranjanju biotske raznovrstnosti zaradi sencozdržnosti, plastičnosti in sposobnosti sobivanja s številnimi drevesnimi vrstami. Tvori heterogene sestojne strukture. Ekotipi jelke kažejo velike razlike v odpornosti na zmrzal, sušo in senco. Naravna obnova jelke je vprašljiva, če s sestoji gospodarijo golosečno in s kratko pomladitveno dobo, v srednji Evropi se z njo gospodari na prebiralni način (Dobrowolska in sod., 2017). Vse večje zanimanje za jelko se pojavlja zaradi njene občutljivosti na podnebne spremembe (Cailleret in sod., 2014), ki bi lahko vplivala na njeno trajnostno rabo in gospodarsko vrednost (Vitali in sod., 2017). Med populacijami jelke so potrdili veliko diferenciacijo zaradi več ledenodobnih zatočišč - refugijev na južnoevropskih polotokih in migracijskih poti ter območij introgresije (Konnert in Bergmann, 1995).

Slovenski dinarski jelovo-bukovi gozdovi so se postopoma preoblikovali iz pragozdov in nikoli niso bili deležni golosečenj ali obsežnih umetnih obnov (Bončina, 2011; Bončina in sod., 2014). V njih so gospodarili na sonaraven način, predvsem s prebiralnim in skupinsko postopnim načinom ali kombinacijo obeh (Schädelin 1928, Leibundgut 1946, Mlinšek, 1972; Bončina, 2011). Ti načini gospodarjenja posnemajo nekatere procese, značilne za naravni režim motenj v mešanih pragozdovih v regiji, za katere je značilna dinamika majhnih do srednje velikih vrzeli (Motta in sod., 2011). Prebiralno gojenje ni primerno za vsa rastišča in vse drevesne vrste. Najuspešnejše je tam, kjer je naravno uspevanje sencozdržnih drevesnih vrst, trajno neovirano naravno pomlajevanje in spontan pojav raznomernih, stopničastih sestojnih zgradb. Najboljše primere negovalnega prebiralnega gojenja gozdov z dolgo tradicijo najdemo v Švici, Franciji, Sloveniji in na Hrvaškem. Iz Slovenije izvira sproščena tehnika gojenja gozdov (Mlinšek, 1968), ki združuje načela skupinsko postopnega in prebiralnega gojenja gozdov (Čater in Diaci, 2021) in jih celostno nadgrajuje, pri čemer posnema procese in sestojne zgradbe naravnih gozdov. Uporabljena je tudi v jelovo-bukovih gospodarskih gozdovih Dinaridov (Diaci, 2006).

Kljub visoki stopnji naravnih gozdov je upad jelke eden od glavnih problemov za celotno regijo. Opazili so ga že v 1930-ih in 1950-ih letih in ga pripisovali predvsem podnebnim ekstremom v povezavi z gradacijami podlubnikov (npr. Bambulović, 1930; Šafar, 1951). Pozneje je k upadu

prispeval onesnažen zrak (Elling in sod., 2009), njeno obnovo pa je v nekaterih delih regije ogrožalo preobjedanje (Mlinšek, 1969). Kot vzrok za nazadovanje jelke pogosto navajajo tudi način gospodarjenja, ki je povzročil spremembe gozdne klime zaradi močnih sečenj ali gradnje gozdne infrastrukture (Mlinšek, 1964), vendar so dokazi vprašljivi. Intenzivnost upada jelke se je zaradi različnih kombinacij vzrokov v regiji spreminjala (Diaci in sod., 2011), delež jelke v lesni zalogi pa se je v nekaterih gospodarjenih gozdovih celo povečal (Bončina, 2011). Trenutna debelinska struktura in značilnosti pomlajevanja kažejo na nadaljnjo nazadovanje jelke v prihodnjih desetletjih (Bončina in sod., 2009).

Podobno se je z jelko dogajalo tudi drugod po Evropi (npr. Schutt, 1978; Heuze in sod., 2005). Poleg onesnaženega zraka in preobjedanja mladja naj bi na uspešnost rasti avtohtonih populacij jelke v Evropi v zadnjih desetletjih negativno vplivale tudi podnebne spremembe: Macias in sod. (2006) so v drugi polovici 20. stoletja v Pirenejih ugotovili vse večji vpliv sušnega stresa na debelinsko rast jelke, v Sredozemlju pa so Battipaglia in sod. (2009) pokazali, da je jelka občutljiva na sušo in spremembe sezonske porazdelitve padavin kot tujerodna smreka. Ohranjanje jelke je ključnega pomena z ekološkega in gospodarskega vidika. Pomembno je za produktivnost rastišča, saj tvori številne habitate kot počasi razpadajoče odmrlo drevo. Je gospodarsko dragocena vrsta in najpomembnejši iglavec v dinarski regiji. Medtem ko je vzroke za propadanje jelke, kot so podnebne spremembe, onesnaženost zraka in preobjedanje, težko nadzorovati, postajajo za njeno ohranitev še pomembnejši dejavniki, na katere lahko učinkovito vplivamo z gozdnogojitvenimi ukrepi (npr. ustvarjanje primernih pogojev v sestoji, pospeševanje z nego in ohranjanje semenskega drevja) (Čater in sod. 2014, Čater in Diaci 2017).

Obe drevesni vrsti sta sencozdržni, pod zastorom lahko uspevata več desetletij. Predvsem jelka je kot pozno sukcesijska vrsta bolj občutljiva na vodni primanjkljaj na sušnih rastiščih (Rolland in sod., 1999) in v času ustvarjanja zaloga za naslednjo sezono (Macias in sod., 2006). Njena fotosintetska aktivnost ni omejena le na rastno obdobje kot bukev, saj asimilira preko celega leta (Brinar, 1964). Igllice so občutljive na temperaturna nihanja in hitre svetlobne spremembe, predvsem v začetku ravnega obdobja (Prpić in Seletković, 2001). Specifična asimilacijska kapaciteta jelke je manjša, manjši delež pigmentov potrjuje njeno sencozdržnost in sposobnost preživetja v veliko skromnejših svetlobnih razmerah od bukve. Ustvarjanje listnega aparata ni sezonsko pogojeno, kutikula iglic je debelejša in asimilacijske izgube so manjše (Aerts, 1995). Njena tekmovalna sposobnost je manjša, v vrzelih se prilagodi bukev na spremenjene svetlobne razmere hitreje in učinkoviteje od jelke (Čater in Diaci, 2017).

Geografski gradient lahko učinkovito služi pri napovedovanju vpliva klimatskih sprememb na bodoče odzive drevesnih vrst kot ustrezni prostorsko - časovni napovednik. Vpogled v spremembe daje možnost primerjave odziva drevesnih vrst med gospodarskimi gozdovi in pragozdovi. Kljub očitni povezanosti so študije odziva drevja na večjem geografskem prostoru razmeroma redke; opravljene so bile v borealnih gozdovih (Huang in sod., 2010; Lloyd in sod., 2011), na vzhodni strani Iberskega polotoka za črni bor (Martín-Benito in sod., 2010), na južni meji naravnega areala v Španiji, Italiji in Romuniji za jelko (Gazol in sod., 2015), na Balkanu za jelko in bukev (Čater in Levanič, 2019) ter za hrast, bukev in bor vzdolž krajšega transeкта

od vzhodne do zahodne Srbije (Stojanović in sod., 2018). V raziskavi Balkanskega polotoka (Čater in Levanič, 2019) so določili optimalna jelova in bukova rastišča glede na njihov fiziološki, morfološki in prirastni odziv.

Vzdolž geografske širine in dolžine se odražajo spremembe v temperaturah in padavinah, zato pričakujemo razlike v sezonski odzivnosti. Ekstremni vremenski dogodki in večanje povprečnih temperatur bodo vplivali na prihodnjo demografijo jelke. Pričakovana je verjetna sprememba razprostranjenosti v smeri večjih nadmorskih višin in proti severu (Tinner in sod., 2013; Klopčič in sod., 2017). Sočasno opažamo podobno odzivanje bukve na račun jelke in njeno splošno razširjanje v osrednji Evropi (Šamonil in Vrška, 2007; Vrška in sod., 2009; Janík in sod., 2016). Nedavne raziskave potrjujejo razlike v odzivu jelke na območju areala njene naravne razširjenosti (Diaci in sod., 2011; Bošela in sod., 2016). Njeno izginjanje na območju toplejših in sušnejših rastišč potrjujejo v fragmentiranih sestojih na robu njenega naravnega areala (Ficko in sod., 2011) in jugozahodnih predelih Evrope (Gazol in sod., 2015), kjer je njeno umiranje povezano s povečevanjem suše (Čavlović in sod., 2015); v jugozahodni Evropi poročajo o njeni večji odpornosti na klimatske ekstreme glede na ostale drevesne vrste (Bošela in sod., 2018). Sočasno so na območju Karpatov ločili dve populaciji jelke: vzhodno, ki je podobna balkanski in zahodno, ki je na poletne suše manj občutljiva (Bošela in sod., 2016). V raziskavi Bouriauda in Pope (2008) na južno izpostavljenih območjih vzhodnih Karpatov je bila jelka najmanj občutljiva drevesna vrsta. Za vse drevesne vrste so dejavnik minimuma padavine na suhih južnih pobočjih. Jelovo-bukovi pragozdovi južnih Karpatov kažejo veliko stabilnost in strukturno odpornost. Časovne spremembe vrstne sestave povzročajo manjša nihanja sestojnih parametrov, ki ne ogrožajo dolgoročnega sobivanja bukve in jelke (Petritan in sod., 2015).

Naša raziskava izhaja iz naslednjih izhodišč:

- Bukev je vse bolj razširjena vrsta, jelka nazaduje predvsem zaradi težav s pomlajevanjem.
- Znanost in stroka iščeta načine za ohranjanje konkurenčne sposobnosti jelke.
- Sedanje usmeritve slonijo na teoretičnih predpostavkah zahtev vrst po temperaturi in padavinah; dejansko stanje ni ovrednoteno in se odmika od dolgoročnih povprečij.

Doktorska naloga je sestavljena iz treh vsebinsko dopolnjujočih sklopov: ekofiziološko-ekološkega, dendrokronološkega in lesno-anatomskega. Multidisciplinarni pristop omogoča vpogled v realne odzive izbranih drevesnih vrst in oblikovanje gojitvenih usmeritev za gospodarjenje v prihodnje. Za napovedovanje odzivov na klimatske spremembe je potrebno ovrednotenje ekofizioloških omejitev v različnih intenzitetah svetlobe (Čater in Levanič, 2013) in primerjava z drugimi dejavniki (Meier in sod., 2011; Maiorano in sod., 2013). Dendrokronološke analize priraščanja sestojev omogočajo retrospektivni zgodovinski pregled odziva na klimatske dejavnike v različnih časovnih vrstah odraslih dreves (González in Eckstein, 2003). Kvantitativna lesna anatomija pojasnjuje vplive okolja na procese nastajanja lesa. Raziskave bukve na njenih optimalnih rastiščih so potrdile prilagajanje na sušo s številom celic (Hajek in sod., 2016) in ne s premeri (Prislan in sod., 2018), medtem ko lesno-anatomskih značilnosti jelke v povezavi z dejavniki okolja še niso proučevali.

1.1 HIPOTEZE

V doktorski nalogi smo oblikovali naslednje raziskovalne hipoteze:

H 1: Na spremembo asimilacijskega odziva jelovega in bukovega mladja na intenziteto svetlobe najbolj vpliva geografska širina.

H 2: Asimilacijski odzivi mladja na intenziteto svetlobe se med vrstama ne razlikujejo.

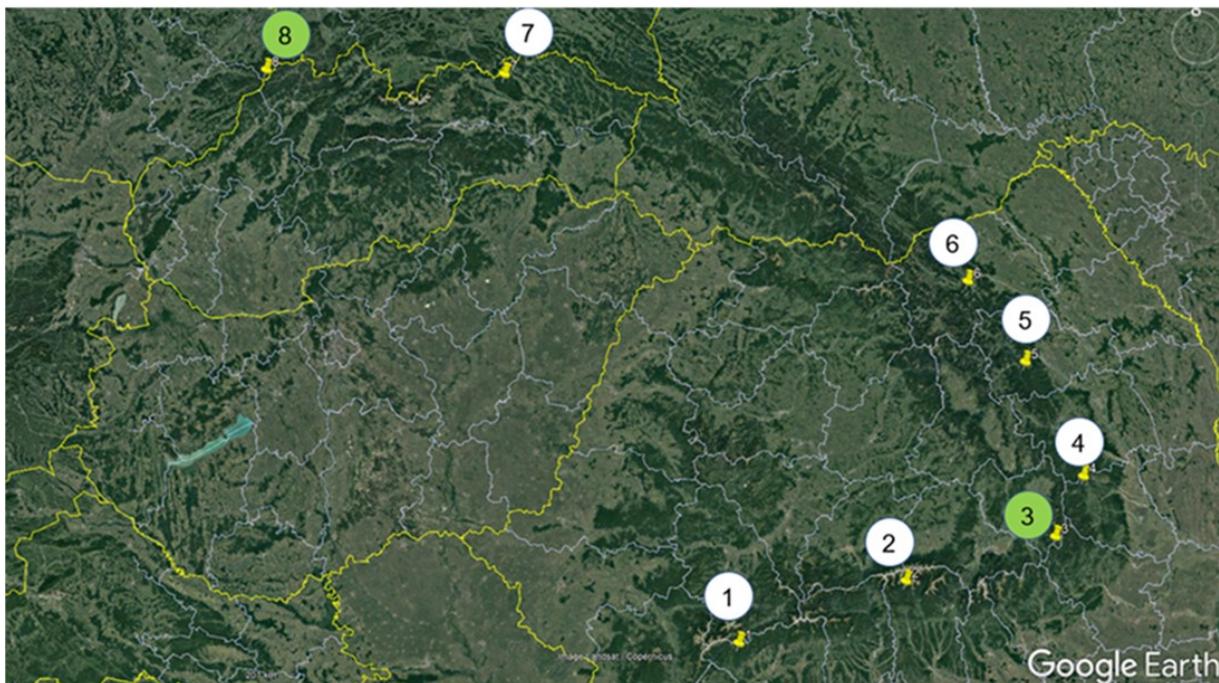
H 3: Gospodarjenje ne vpliva na rastne in asimilacijske odzive jelke in bukve; med gospodarskimi gozdovi in pragozdni rezervati ni razlik v odzivu.

H 4: Prirastni odzivi jelke in bukve na klimo so različni.

H 5: Lesno-anatomske značilnosti ne kažejo povezave z geografsko širino ali dolžino.

1.2 METODE RAZISKOVANJA

Po študiju literature smo določili raziskovalne lokacije na območju odraslih jelovo bukovich sestojev nad 800 m nadmorske višine vzdolž celotnega območja Karpatov od meje med Češko Republiko in Slovaško do Romunije s prisotnim naravnim pomladkom obeh drevesnih vrst in s podobnim - primerljivim načinom gospodarjenja (skupinsko postopno gospodarjenje). Raziskovalne lokacije se nahajajo v šestih gospodarskih gozdovih in v dveh pragozdnih rezervatih (Slika 1).



Slika 1: Raziskovalne lokacije vzdolž območja Karpatov (bele oznake predstavljajo gospodarske gozdove, zelene pragozdne rezervate)

Študij odziva jelke in bukve na območju Karpatov smo določili z meritvami na izbranih lokacijah v več zaporednih rastnih obdobjih. Na območjih vrzeli oz. presvetlitev smo z digitalnim DSLR in umerjenim objektivom »ribje oko« ter s programsko opremo WinScanopy izdelali hemisferne posnetke krošenj; na osnovi rezultatov smo določili tri potencialne

svetlobne kategorije (na odprtem, brez zastiranja, na gozdnem robu in pod zastorom odraslega sestoja) glede na deleže difuznega potencialnega sevanja (ISF %) (Čater in Levnič, 2019). Na istih mestih smo v več zaporednih sezonah opravili meritve asimilacijskega odziva mladja v kontroliranih okoljskih razmerah pri stalni temperaturi merilnega bloka, enaki vstopni koncentraciji CO₂, vode, pretoka) z IR prenosnim plinskim analizatorjem LI-6400 z lastnim svetlobnim virom in merilno komoro ter potrebnimi dodatki. V vsaki svetlobni kategoriji smo izmerili svetlobne saturacijske krivulje na najmanj 8 osebkih pri različnih svetlobnih intenzitetah (0, 50, 100, 250, 600, 1200 in 1800 $\mu\text{mol}/\text{m}^2\text{s}$). Na osnovi izdelanih svetlobnih krivulj za vsako vrsto in lokacijo smo pridobili podatke maksimalne svetlobne učinkovitosti (angl. quantum yield (Φ)) in jo v nadaljevanju primerjali vzdolž geografskega gradienta s svetlobnimi kategorijami in okoljskimi parametri (temperaturo in padavinami) zadnje dekade (Čater 2021, Čater in sod. 2024). Tovrstne meritve so se v dosedanjih raziskavah dinarskega visokega krasa (Čater in Levnič, 2013; Čater in sod., 2014; Čater in Kobler, 2017; Čater in Diaci, 2017) pokazale kot uspešne in reprezentančne. Meritve pigmentov ter količino foliarnega dušika v listju oz. iglicah smo določili na istih skupinah svetlobnih kategorij vsake od izbranih lokacij.

Na izbranih odraslih jelovih in bukovih dominantnih drevesih smo izvedli vzorčenje z izvrtki za določanje rastnega odziva v daljših časovnih obdobjih. Na vsaki lokaciji smo z obeh strani 15 odraslih, dominantnih jelk in bukev odvzeli dva izvrtka. Vsak izvrtek smo namestili na lesen nosilec in zbrusili postopno z uporabo vse bolj finega brusnega papirja. Izvrtke smo nato skenirali s sistemom ATRICS 45, letne debelinske prirastke pa izmerili do natančnosti 0,01 mm s programsko opremo Coorecorder in CDendro, ki je služila tudi kot nadzor kakovosti izmerjenih zaporedij širin branik. Zaporedja širin branik smo vizualno in statistično sinhronizirali z uporabo PAST-5. Posamezna zaporedja širine branik so bile standardizirane za odstranitev dolgoročnih trendov v zbirki dplR programa R. Po odstranitvi trenda smo kronologije širin branik primerjali s povprečnimi mesečnimi temperaturami, maksimalnimi temperaturami, mesečno vsoto padavin in dvema sušnim indeksoma z uporabo metode ponovnega vzorčenja in izračuna korelacijskega koeficienta v podatkovni zbirki treeclim programa R.

Analizo lesno-anatomskih parametrov smo opravili na šestih naključno izbranih vzorcih le treh lokacij zaradi dolgotrajnosti analiz. Vzorce smo pripravili v Laboratoriju za anatomijo lesa na Gozdarskem inštitutu Slovenije po protokolu, ki ga predlagajo von Arx in sod. (2016). Za pripravo vzorcev bukve smo uporabili drsni mikrotom z rezili OLFA-80 \times 9 mm (Gärtner in sod., 2015). Vzorci jelke smo vložili v parafin in narezali z rotacijskim mikrotomom LeicaRM 2245 (Leica Microsystems, Wetzlar, Nemčija) z uporabo rezil Leica 819 Low Profile Microtome (Leica Biosystems, Nussloch, Nemčija). Fotografije visoke ločljivosti vzorcev smo izdelali s svetlobnim mikroskopom Leica DM 4000 B (Leica Microsystems, Wetzlar, Nemčija) pri 50-kratni povečavi, digitalnim fotoaparatom Leica DFC 280 (Leica Microsystems, Wetzlar, Nemčija) in programsko opremo za analizo fotografij LAS (Leica Application Suite). Pobarvane in fiksirane mikroskopske preparate smo analizirali z uporabo programske opreme za analizo slik Image-Pro Plus 7.1 in programom ROXAS (v3.0.437; Prendin in sod., 2017; von Arx in sod., 2016).

Klimatske podatke smo dobili iz podatkovnih baz spletne strani »Climate Explorer« (<http://climexp.knmi.nl>), ki vključuje dnevne podatke od leta 1950 z 0.10° natančnostjo in mesečne podatke od leta 1900 z 0.25° natančnostjo. V novejših objavah smo uporabili dnevne klimatske podatke E-OBS verzije 30.0e na 0.1° mreži (Cornes in sod., 2018) in pridobili povprečne, najnižje in največje dnevne temperature ter vsoto dnevnih padavin iz najbližje merilne postaje. Primerjave odziva smo izdelali za obdobje po letu 1950 zaradi zanesljivejših klimatskih podatkov.

Asimilacijske odzive na različno svetlobno intenziteto obeh drevesnih vrst v vseh treh svetlobnih kategorijah, debelinsko priraščanje in lesno-anatomske parametre smo primerjali z dolgoročnimi padavinskimi in temperaturnimi nizi izbranih lokacij ter opredelili glavne dejavnike, ki omejujejo oz. vzpodbujajo njuno priraščanje. Izmerjene parametre smo primerjali tudi med odzivi vrst v gospodarskih sestojih in pragozdovih. Preverili smo kako se izbrani vsebinski sklopi med seboj dopolnjujejo in/ali razlikujejo. Odziv vsakega sklopa smo primerjali z obstoječimi meritvami vzdolž Balkana in določili morebitne vzporednice oz. razlike med obema. Vso potrebno raziskovalno opremo smo imeli na voljo na Gozdarskem inštitutu Slovenije.

Raziskovalno delo je bilo financiral program mladega raziskovalca v okviru programske skupine P4-0107 na Gozdarskem inštitutu Slovenije in projekt ARRS (J4-3086).

2 ZNANSTVENA DELA

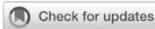
2.1 ODZIV BUKVE IN JELKE NA RAZLIČNE INTENZITETE SVETLOBE VZDOLŽ KARPATOV IN DINARIDOV

Čater M., Adamič P. C., Dařenova E. 2024. Response of beech and fir to different light intensities along the Carpathian and Dinaric Mountains. *Frontiers in Plant Science*, 15: 1380275, <https://doi.org/10.3389/fpls.2024.1380275>

Izveleček: Napovedovanje podnebnih sprememb na podlagi okoljskih spremenljivk, kot sta temperatura in razpoložljivost vode omogoča oblikovanje pomembnih hipotez, še vedno pa primanjkuje dejanskih okoljskih odzivov. Za določitev ekološke niše posamezne vrste je potrebna ocena fizioloških omejitev. Podrobne ekofiziološke študije o odzivu dreves vzdolž geografskega gradienta so redke in posredujejo ključno informacijo o odzivih vrste pri različnih intenzitetah svetlobe in drugih preučevanih parametrov. Gozdovi Dinaridov in Karpatov predstavljajo najboljše strnjene gozdne komplekse v jugovzhodni Evropi. V raznodobnih gozdovih vzdolž Karpatov (8 ploskev) in Dinarskega gorstva (11 ploskev) smo izmerili neto asimilacijo (A_{max}) in asimilacijsko učinkovitost (Φ) za bukev in jelko v treh vnaprej določenih svetlobnih kategorijah glede na deleže difuznega potencialnega sevanja (ISF %), pridobljene z analizo hemisfernih posnetkov krošenj v gospodarjenih gozdovih in pragozdovih, nad 800 m nadmorske višine. Meritve smo izvedli v kontroliranih okoljskih razmerah v vseh svetlobnih kategorijah na vsaki lokaciji v treh zaporednih letih. Za primerjavo neto asimilacije in asimilacijske učinkovitosti s klimatskimi parametri smo uporabili podatke podatkovnega niza CRU TS 4.01 zadnjih 50 let. Največja asimilacijska učinkovitost bukev smo izmerili v osrednjem delu Dinarskega gorstva ter v jugozahodni in severozahodni lokaciji Karpatov tako za bukev kot za jelko, medtem ko je bila za jelko največja v Dinarskem gorstvu na skrajni severozahodni lokaciji. Vrednost asimilacijske učinkovitosti za bukev se je v obeh kompleksih zmanjševala s povečevanjem povprečne letne temperature in je bila največja v svetlobni kategoriji na odprtem. Pri jelki v Karpatih se je asimilacijska učinkovitost s povečujočo povprečno letno temperaturo zmanjševala, medtem ko se je v Dinarskem gorstvu z večjo temperaturo povečevala in imela bolj razpršen odziv kot v Karpatih. Kratkoročni ekofiziološki odzivi bukev in jelke so bili skladni z dolgoročnimi opazovanji debelinske rasti na istih lokacijah. Rezultati so uporabni pri napovedovanju prihodnjega odziva dveh drevesnih vrst na podnebne spremembe z njihovo tekmovalno sposobnostjo, obstojem in posledično gozdnogojitvenimi odločitvami in ukrepi.



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Response of beech and fir to different light intensities along the Carpathian and Dinaric Mountains

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Predicting global change mitigations based on environmental variables, like temperature and water availability, although yielding insightful hypothesis still lacks the integration of environmental responses. Physiological limits should be assessed to obtain a complete representation of a species' fundamental niche. Detailed ecophysiological studies on the response of trees along the latitudinal gradient are rare. They could shed light on the behaviour under different light intensities and other studied traits. The forests of the Dinaric Mountains and the Carpathians represent the largest contiguous forest complexes in south-eastern Europe. In uneven-aged Carpathian (8 plots) and Dinaric Mountain (11 plots) forests, net assimilation (A_{Tmax}) and maximum quantum yield (Φ) were measured for beech and fir in three predefined light intensity categories according to the indirect site factor (ISF%) obtained by the analysis of hemispherical photographs in managed and old growth forests, all located above 800 m a.s.l. The measurements were carried out under fixed environmental conditions in each light category per plot for three consecutive years. Data from the last 50-year average period from the CRU TS 4.01 dataset were used for the comparison between A_{max} , Φ , and climate. The highest Φ for beech were observed in the central part of the Dinaric Mountains and in the south westernmost and northwesternmost part of the Carpathians for both beech and fir, while they were highest for fir in the Dinaric Mountains in the northwesternmost part of the study area. The Φ -value of beech decreased in both complexes with increasing mean annual temperature and was highest in the open landscape. For fir in the Carpathians, Φ decreased with increasing mean annual temperature, while in the Dinaric Mountains it increased with higher temperature and showed a more scattered response compared to the Carpathians. Short-term ecophysiological responses of beech and fir were consistent to long-term radial growth observations observed on same locations. The results may provide a basis and an indication of the future response of two tree species in their biogeographical range to climate change in terms of competitiveness, existence and consequently forest management decisions.

KEYWORDS

silver fir, beech, light response, Carpathian Mountains, Dinaric Mountains, temperature, precipitation

Introduction

Mixed fir-beech forests are an essential component of Central and South-Eastern European forest ecosystems and landscapes (Dobrowolska et al., 2017). Beech (*Fagus sylvatica* L.), the most common forest species in Europe (Ellenberg, 1988), grows in pure deciduous forests or in mixed forests with conifers, especially with silver fir (*Abies alba* Mill.) (hereafter fir), whose geographical distribution is comparable to that of beech, but is largely restricted to the Alpine and Carpathian arc (Bošela et al., 2018). Fir is the tallest tree in Europe and forms mixed forest stands in many regions (Aussenac, 2002; Dobrowolska et al., 2017). At its southern limit of distribution in the mountainous regions of the Iberian Peninsula and Italy, it forms mixed stands with Mediterranean tree species (Carrer et al., 2010). Species distribution modelling suggests that the current range of silver fir was determined by historical land use and which can mask the potential effects of climate change (Svenning and Skov, 2004; Tinner et al., 2013; Di Pasquale et al., 2014). However, there are several disagreements as to whether the recent increase in temperature alone or in combination with a reduction in precipitation will lead to a reduction in the species' range (Alba-Sánchez et al., 2010; Maiorano et al., 2013). Dendroecological studies have shown a decline in the growth of silver fir in the Iberian Peninsula (Linares and Camarero, 2012) and in the south-eastern European mountains (Diaci et al., 2011), which is probably due to the increase in summer water deficit in these areas (Giorgi and Lionello, 2008). The resilience of plant species or populations depends on their ability to acclimatise to the new environmental conditions. Beech, on the other hand, shows an increase in abundance and a successful ability to regenerate after large-scale disturbances such as windthrow or sleat (Čater and Diaci, 2017; Čater, 2021).

Recent research has shown that the vegetation in the Carpathian forests is changing in different intensities and directions, which can be attributed to various processes (Šamonil and Vrška, 2007), such as air pollution, soil acidification (Hédl et al., 2011), and the competitive influence of tree seedlings (Lysik, 2009). Of particular interest is the question of how ecologically and economically valuable species such as silver fir will cope with recent climate trends (Maiorano et al., 2013; Tinner et al., 2013). Adamič et al. (2023) already confirmed different stem radial growth in beech and fir since 1950s and their response to climate conditions along the Carpathians, while Darenova et al. (2024) related soil respiration spatial variability with soil water content, soil carbon and nitrogen content and no significant affect connected with canopy gaps.

Forest gaps are an integral part of forest ecosystems and play a crucial role in the regeneration of mixed beech-conifer forests and influence the future species admixture (Grassi and Bagnaresi, 2001; Čater et al., 2014). Harvests alter micrometeorological stand's conditions and ecological processes in the understorey. They result in higher soil temperature and precipitation throughfall, which temporarily increase soil respiration (Londo et al., 1999; Čater, 2021) and consequently increase the decomposition of soil organic matter. With reduced aboveground litter input, this leads to a loss of soil organic carbon (Hukić et al., 2021).

When predicting the effects of climate change on the future performance of tree species, a geographical, particularly a latitudinal gradient, can serve as a useful space-time proxy and might provide valuable reference to predict future limitations of these tree species (De Frenne et al., 2013; Čater and Levanič, 2019; Weithmann et al., 2022; Smith et al., 2023), also comparing responses in managed and old-growth forests. Many projections and predictions of global change impacts are based on theoretical specifications of temperature requirements and moisture/water availability for the life cycle of specific species (Dillaway and Kruger, 2010). Unfortunately, they do not take into account the actual response to conditions in the natural environment, which could provide a sufficient mechanistic basis for the exact nature of the constraints. Physiological limits should be assessed to obtain a complete representation of a species' fundamental niche and then constrain it with biotic interactions and effects of dispersal limitation (Meier et al., 2011).

In a study on the Balkan Peninsula along the Dinaric High Karst, where diverse and well-expressed ecological factors intertwine in a relatively short geographical distance (ca. 1000 km) (Bohn et al., 2000), the response of beech and fir from the southern, warmer and drier sites already successfully served as a highly probable future prediction for the same species response on currently less extreme sites in the north (Čater and Levanič, 2019). On the contrary are the Carpathian Mountains more complex and exhibit a sufficient latitudinal and longitudinal gradient associated with significant differences in temperature/precipitation as well as differences in seasonal patterns (Micu et al., 2016). Quantum yield (Φ) in various light microsites proved that beech is more efficient in exploiting direct radiation in sun exposed parts of the gap, compared to silver fir (Čater et al., 2014). Microsite position significantly influenced Φ (Lambers et al., 1998) of young beech and firs, which changed with gap size, explaining their difference in competitive ability (Čater et al., 2014). The abundance of microsite light categories along the elevation gradient in two silvicultural systems well indicated the forest structure and its fragmentation, and after large scale disturbances (Čater and Diaci, 2017; Čater, 2021), with quantum yield (Φ) as the resulting trait. Such division may also be associated with spatial distribution of other ecological factors: direct radiation may be related with an increased evapotranspiration and higher drought probability, while diffuse radiation with rainfall patterns within gaps (Kremer, 1967).

Our aim was to compare the physiological responses of beech and fir along the geographical gradient of the Carpathian and Dinaric Mountains (1), to assess differences in the same light categories of both species between managed and old forests (2) and to verify the relationship between climatic parameters and ecophysiological traits of both species along both geographical gradients (3).

Material and methods

Research area

The Carpathians extend over a 1500 km long arc, the width of which varies from 170 km in the eastern and western parts to less

than 80 km in the southern part of the mountain range (Warszyńska, 1995). The wide variety of favourable ecological conditions is reflected in the great diversity of plants and animals and the rich biodiversity (Mirek and Piekos-Mirkowa, 1992).

Situated on the edge of the Atlantic and continental climate regions, the western climate type with its anticyclonic weather pattern dominates over most of the Carpathians. A continental climate prevails on the eastern slopes of the Eastern Carpathians. In the foothills of the Western Carpathians the average air temperature in July is 19 °C and in the Southern Carpathians 22 °C. In the south-western part, the air temperature drops by 0.81 °C per 100 metres difference in altitude and by 0.5 °C in the south-eastern part of the Carpathians. Annual precipitation ranges from around 500 mm at the foothills of the Southern Carpathians to over 2000 mm on the peaks of the Tatra Mountains (Vološčuk, 1999) in the north. Flysch predominates in the eastern and outer Western Carpathians, crystalline and volcanic rocks in the inner band, while metamorphic rocks predominate in the Southern Carpathians (Rădulescu and Săndulescu, 1973; Golonka et al., 2018).

The Dinaric Mountain range stretches from the southern edge of the Eastern Alps in Slovenia to the mountain massif in North Macedonia; it is bordered by the Adriatic Sea to the west and the Pannonian Basin to the east (Gams, 1969). Most of the mountain range consists of Mesozoic rocks, mainly limestone and dolomite. The depth of the limestone and dolomite rocks is unique and is typically 1 to 3 kilometres, with considerable local variations (Gams, 1969). Westerly winds bring large amounts of moisture to the higher elevations along the western side of the mountain range. Precipitation at higher altitudes is relatively evenly distributed during the year, with snow cover often remaining for up to six months (Mihevc, 2010). The forest structure and composition in the region is strongly influenced by the interaction between the mountain relief, the karst area, the soils and the climatic gradient. The mountain forests above 800 metres include mainly beech-dominated forests and uneven-aged mixed forests, in which beech,

fir and occasionally spruce occur to varying degrees. Large, forested areas inland have remained intact to this day and have been managed with low-intensity silvicultural systems for more than a century (Boncina et al., 2013), with several protected old-growth forest remnants scattered across the area.

Selected permanent research plots were located above an altitude of 800 m a.s.l., where mature beech and fir trees predominate and where there is abundant natural regeneration of both tree species. Eight plots were established in the Carpathian Mountains, which extend from the Czech Republic from the far north-west through Slovakia and Romania to the southern part of the mountain range, and eleven permanent observation plots in the Dinaric Mountains, which extend from Slovenia from the far north-west through Croatia, Bosnia and Herzegovina and Montenegro along the mountainous region of the Balkan Peninsula to North Macedonia in the southern part of the mountain range. Two old stands were selected in the Carpathian Mountains (plots 3 and 8) and three in the Dinaric Mountains (plots 3, 7 and 8) (Figure 1; Table 1).

Potential light categories

In each plot, three categories of different light intensities were defined based on the analysis of hemispherical photographs, taken with the Canon EOS Rebel T3 DSLR and a calibrated fisheye lens with the Regent WinScanopy pro-d accessory. Young beech and fir are strongly influenced by indirect light, which has been confirmed by our former research (Čater et al. 2014); therefore, the Indirect Site Factor (ISF %) was used, describing relative share between potential indirect (diffuse) light at the point of measurement and in the open. At least eight hemispherical photographs per every plot were made before any response measurements (Čater and Levanič, 2013) in each of three potential categories: under a closed canopy with Indirect Site Factor (ISF) < 15%, at the forest edge (15% < ISF < 25%) and in the open (ISF > 25%). Colour digital hemispherical photographs were taken

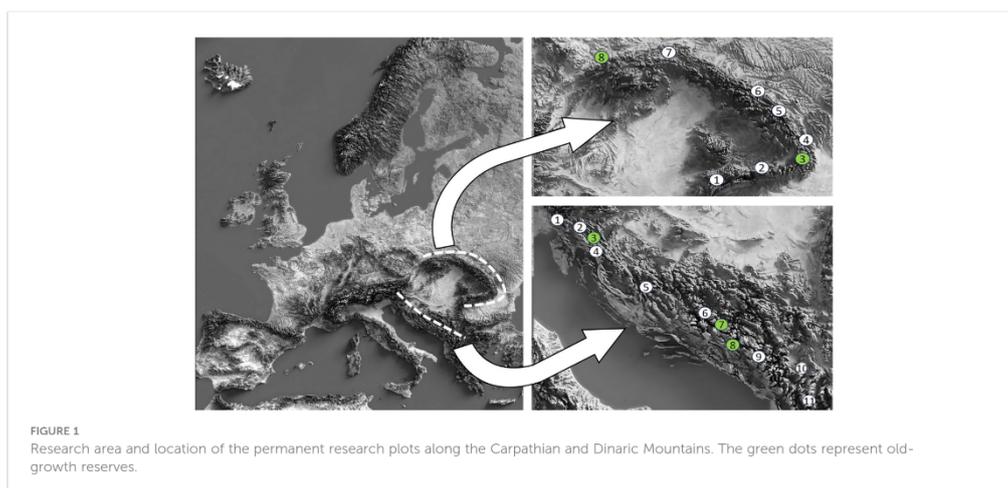


TABLE 1 Characteristics of the research plot; the meteorological data were obtained from the website "Climate Explorer" (<http://climexp.knmi.nl>) for the period 1985-2020, including the annual totals and the values for the April-September growing season.

Plot No/Region	Altitude ASL (m)	Long. Deg (°)	Latit. Deg (°)	Annual precipitation (mm)	Average annual air T (°C)	Apr.-Sept. precipit. (mm)	Average April-Sept. air T (°C)	
Carpathian Mts.	1	985	22.917°	45.169°	1073	4.7	695	10.7
	2	995	24.651°	45.460°	812	7.4	534	13.9
	3	1038	26.229°	45.614°	744	6.8	491	13.6
	4	830	26.604°	46.001°	603	8.3	412	15.6
	5	950	26.168°	46.854°	704	5.8	474	12.9
	6	850	25.683°	47.468°	738	5.4	501	12.0
	7	880	21.017°	49.255°	758	7.2	493	13.8
	8	820	18.417°	49.403°	744	7.1	491	13.4
Dinaric Mts.	1	814	13.757°	45.991°	1619	11.3	863	15.2
	2	807	14.464°	45.676°	1573	8.4	802	14.1
	3	871	15.004°	45.662°	1465	9.0	780	14.9
	4	1190	14.806°	45.271°	1108	9.3	616	14.9
	5	928	16.318°	44.307°	1349	8.6	645	14.5
	6	1204	18.269°	43.737°	1192	7.6	593	13.4
	7	1313	18.710°	43.320°	1229	7.7	607	13.4
	8	1408	18.646°	42.986°	1278	8.2	590	13.7
	9	1402	19.922°	42.553°	1163	6.6	548	13.1
	10	1410	20.885°	42.252°	850	8.6	418	14.6
	11	1315	20.741°	41.696°	836	8.4	357	14.0

during windless weather and standard overcast sky conditions 150 cm above the forest floor when the solar disk was completely obscured. Exposure fitting was done to above canopy conditions prior to shooting on every plot (Macfarlane et al., 2000; Zhang et al., 2005) without noteworthy blooming effects (Leblanc et al., 2005). In the process of hemispherical photograph analysis, a "standard overcast sky" (SOC) model was applied for diffuse light distribution. For the calculation within the vegetation period (30. April - 31. September), the sun's position was specified every 10 min. The solar constant was defined as 1,370 W/m²; 0.6 was set for atmospheric transmissivity and 0.15 for the proportion of diffuse radiation compared to calculated direct potential radiation. An automatic thresholding method based on the same colour scheme was applied for the discrimination between sky and canopy elements in all digital photographs, as the thresholding is crucial and may significantly affect the calculated parameters (Ishida, 2004; Nobis and Hunziker, 2005; Schwalbe et al., 2009).

Weather and climate

Monthly mean temperatures (°C) and monthly total precipitation data were interpolated for the 0.5° grids that include each selected plot and correspond to the CRU TS 4.01 dataset (Harris et al., 2014), obtained from the Royal Netherlands Meteorological Institute

'Climate Explorer' website (<http://cliexp.knmi.nl>). For the comparison between maximal net assimilation (A_{max}), quantum yield (Φ) and climate data (temperature and precipitation), data from the last 50-year average period (1981-2020) were used. For the long-term comparison between climate and tree response, we extracted gridded climate data for mean monthly temperature and sum of monthly precipitation using the CRU TS 4.01 dataset with a resolution of 0.5x 0.5-degrees from the KNMI website (Figure 2).

Nitrogen content and leaf mass per area

Leaves and needles were taken from the upper canopy position of at least 12 trees per light category and location and then stored in a cool, airtight place. Age of trees was similar in all three light categories. The same trees were also used to measure the maximum assimilation rate. Total leaf nitrogen concentration (N_{tot}) [mg/g] was determined (Laboratory of Soil Science, Faculty of Forestry and Wood technology, Mendel University, Brno) to compare macronutrient status (Leco CNS-2000 analyser) (Lambers et al., 1998; Larcher, 2003) for the open, forest edge and closed canopy categories under mature trees (Cater et al., 2014). Fresh leaves were weighed and scanned for leaf area. Leaves were dried to constant weight at 105°C for 24 hours and weighed in the laboratory to determine leaf mass per area open-, forest

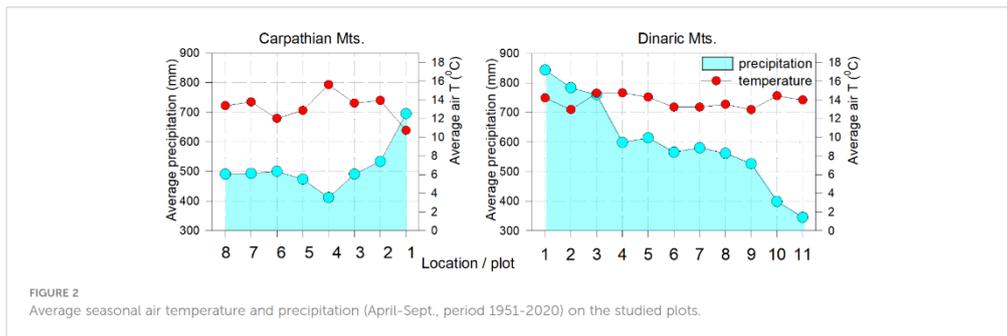


FIGURE 2
 Average seasonal air temperature and precipitation (April-Sept., period 1951-2020) on the studied plots.

edge- and closed canopy-category below mature trees (Čater et al., 2014). Leaves were dried to constant weight at 105°C for 24 hours and weighed in the laboratory to determine leaf mass per area (LMA) [g/m²].

Assimilation light response

For the light saturation measurements, which were carried out in June and July in three consecutive growing seasons, at least 8 young trees of the same height that were not obstructed by their neighbours were randomly selected (*sensu* Čater and Levanič (2019)). The age of the trees varied between 5-12 years. The light response was measured with a portable LI-6400 (Li-Cor, USA) system on at least four leaves/shoots per tree located in the upper third of the tree crowns. All assimilation values were recorded after they had held constant for 2 min or until the coefficient of variability (CV%) dropped below 5%.

- Light saturation curves were generated to compare net assimilation (A_{max}) in young beech and fir trees under the same light conditions. All assimilation measurements were performed in the field at a constant temperature of the measurement block (20°C), a CO₂ concentration of 420 μmol/l, an air flow of 500 μmol/s and different light intensities: 0, 50, 250, 600 and 1500 μmol/m²/s. The maximum assimilation rates (A_{max}) for the light saturation curves were used to compare the responses between different light categories and plots.

- The characteristic points of maximum quantum yield (Φ), defined as the maximum amount of fixed CO₂ per amount of absorbed light quanta (Lambers et al., 1998) measured as the initial slope of the light response curve of CO₂ fixation, were determined for each light category, species and plot, as described in Čater et al. (2014), using LiCOR software.

Statistical analysis

Differences between the same years for the LMA, N_{tot} , A_{max} and Φ were tested using two-way ANOVA with tree species (beech and fir) and light (open, edge, canopy) as dependent variables. Analyses of variance (ANOVA) and the HSD Tukey *post-hoc* test were performed after testing data to meet conditions of normality. Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant. Data analysis, correlation between the measured variables and multiple regression were performed using Statistica Data Analysis Software System (2011).

Results

Weather and climate

In both complexes, the long-term average temperatures show more homogeneous conditions over the longer Dinaric area and

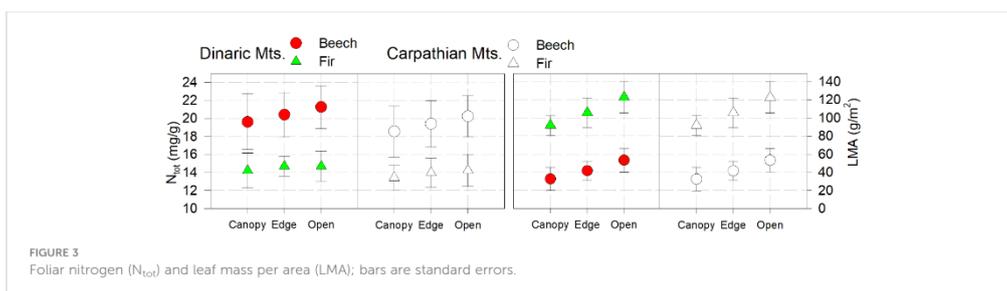


FIGURE 3
 Foliar nitrogen (N_{tot}) and leaf mass per area (LMA); bars are standard errors.

more variable conditions in Carpathians. The average annual precipitation in the Carpathian region is lower and corresponds to the conditions in the southern Dinaric mountains. (plot 9) (Figure 2).

Foliar nitrogen

In all plots, N_{tot} was highest for both beech and fir in the open and lowest in the closed canopy, without significant differences between light categories and years. On all studied plots N_{tot} was within the optimal thresholds 13-15mg/g for fir and 18-22mg/g for beech, as reported by Grassi and Bagnaresi (2001); Mellert and Göttlein (2012) or even above range reported by Yang et al. (2022) and Bachofen et al. (2020). The same trend was observed for LMA.

The values of N_{tot} and LMA were slightly and not significantly lower in all categories in the Carpathian Mountains than in the Dinaric Mountains (Figure 3, Table 2).

Maximum assimilation rate and quantum yield (Φ)

In the Carpathian and Dinaric Mountains, Φ followed the pattern of precipitation and temperature; in both complexes it was highest for beech in the open light and for fir under closed canopies. In old growth reserves of the Dinaric Mountains, Φ was shifted towards the response of open light category for both species, much more so than in the Carpathian Mountains. In all cases, the absolute values were higher in all light categories than in the neighbouring managed forest stands (Figure 4, Table 3).

The highest values (Φ) for beech were observed in the central part of the Dinaric Mountains region and in the south westernmost

and northwesternmost part of the Carpathian Arc for both beech and fir, while Φ for fir was highest in the Dinaric Mountains in the northwesternmost part of the studied area (Figure 4).

Post-hoc analyses revealed significant differences between all light categories for Φ in Dinaric Mountains, except in the old-growth reserves, where no significant differences between forest edge and open light were confirmed for either species. In Carpathian Mountains differences between light categories were not so pronounced (Table 4).

We confirmed positive correlation between Φ and annual precipitation, which increased with the light intensity for beech in all light categories and in both the Carpathian and Dinaric Mountains. The correlation was positive for fir, decreased with increasing light and was highest when the canopy was closed. Slope of the curve for fir was steepest for the closed canopies (Figure 5).

The quantum yield of beech in both complexes decreased with increasing mean annual temperature and was highest in the open. For fir in the Carpathian Mountains, Φ decreased with increasing mean annual temperature, while in the Dinaric Mountains it increased with higher temperature and showed a more scattered response compared to the Carpathian Mountains (Figure 5).

The relationship between Φ and five independent parameters (latitude, longitude, average annual air temperature, annual precipitation, and altitude) was tested in a linear multiple regression model for both species, both complexes and three potential light categories. As the number of variables increased, the regression coefficients for beech in the Carpathians and Dinaric Mountains became increasingly different; beech in Dinaric Mountains indicated strongest relation with annual temperatures and additional parameters did not increase correlations as much as for the beech in Carpathian Mountains. The regression coefficients for fir between Dinaric and Carpathian Mountains were at first different and highest in Carpathian Mountains and became with additional parameters increasingly similar (Figure 6).

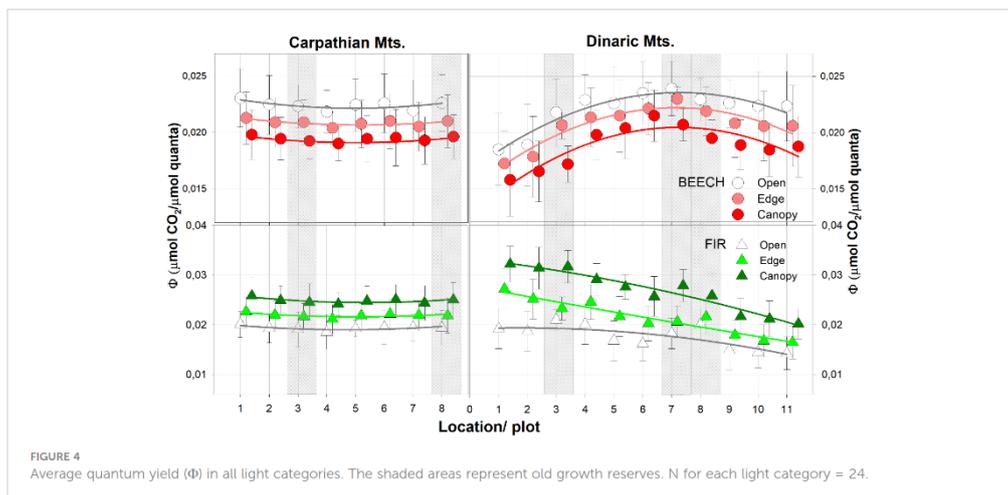


TABLE 2 ANOVA for leaf nitrogen (N_{tot}) and leaf mass per area (LMA) in both regions.

Region	Trait	Df 1;2	Species		Df 1;2	Light category		Df 1;2	Species X Light category	
			F	p		F	p		F	p
Carpathian Mts.	N_{tot}	1; 47	176.2	2e-17***	2; 43	4.2	0,0278*	2; 43	1.8	0,5731 ^{NS}
	LMA	1; 47	3215.4	2e-17***	2; 43	345.4	2e-17***	2; 43	28.2	2e-17***
Dinaric Mts.	N_{tot}	1; 65	193.2	2e-16***	2; 60	3.6	0,0336*	2; 60	0.7	0,5197 ^{NS}
	LMA	1; 65	5859.9	2e-16***	2; 60	415.1	2e-16***	2; 60	46.0	7.6e-13***

p<0.05 (*), p<0.001 (***), ns - non significant.

Discussion

Shifts in climate zones and changes in forest cover directly affect regional surface temperatures through the exchange of water and energy; as warming continues, the frequency, intensity, and duration of heat-related events, including heat waves, are expected to increase (Lee et al., 2023). Climate zones are projected to shift further poleward in the mid- and high-latitudes and forest disturbances such as drought, wildfires and pest infestations are projected to increase (Lee et al., 2023). Some spatial distribution models predict a reduction in the ranges of fir and beech forests by 2100 due to climate change in favour of more drought-tolerant species (Piedallu et al., 2013); however, several studies question the predominant effects of ecological rather than macroecological and phytogeographical gradients on vegetation (Willner, 2002; Marinšek et al., 2013).

The selected sites in both studied mountain complexes were above 800m a.s.l. to ensure comparable and similar climatic conditions. Altitude is the key factor controlling the microclimate in temperate mountain forest stands (Körner et al., 2016). The average annual temperatures at the selected Carpathian sites ranged between 12 and 14 °C with the exception of sites 4 and 1, while the average annual temperatures at the Dinaric sites showed more homogeneous conditions (13 to 14 °C). The average amount of precipitation in the Dinaric Mountains decreased evenly from the north-west to south-east, while the amount of precipitation in the Carpathians decreased from west to east.

Assimilation response

In the Dinaric Mountains, Φ was highest for beech in the central area (Bosnia and Herzegovina) and for fir in the north-western part of the

transect (Slovenia, Croatia), while in the Carpathians it was highest at the beginning and end of the studied transect, at the westernmost sites.

The responses (Φ) of the two species studied between the Carpathians and the Dinaric Mountains in the same light categories showed certain similarities: in both cases, Φ values were higher for beech in the open, and lowest under shaded canopies, and vice versa for fir - highest under shaded conditions and lowest in the open, confirming our previous studies (Čater and Levanič, 2013, 2019).

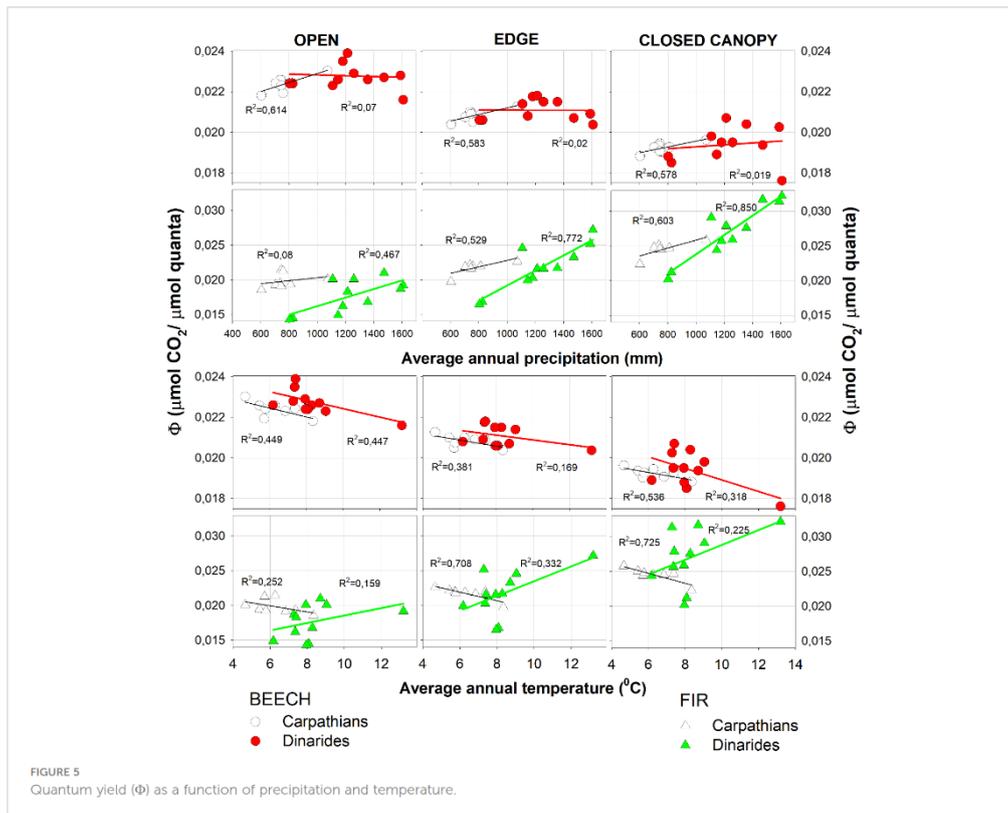
The differences between old-growth forest reserves and neighbouring managed forests in both mountain complexes showed the same, higher values in all light categories and species, although the response was less pronounced in the Carpathians than in the Dinaric Mountains (Figure 4). It is not clear what caused the shift of Φ in the edge light category in the old growth reserves towards the open category for both beech and fir, as leaf nitrogen values were comparable between sites and were in the optimal range on all plots. In old growth reserves Amax and Φ were significantly higher than in managed forests due to microclimate, relative air humidity (RH), higher water use-efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE) in old growth reserves (Čater and Levanič, 2013).

Despite the non-significantly lower amount of foliar nitrogen (N_{tot}) in the Carpathian categories, the variability of Φ and the differences between light categories were much higher for both beech and fir in the Dinaric Mountains (Table 3), possibly reflecting the more diverse growing conditions and more abundant water availability in the Dinaric Mountains than in the Carpathians (Micu et al., 2016). We assume that water is the most important limiting parameter, as the response of both species at all study sites in the Carpathians, except the first two, corresponded to the conditions in

TABLE 3 ANOVA for maximum assimilation rate (A_{max}) and quantum yield (Φ) for beech and fir in different light conditions and complexes.

Complex	Trait	Df 1;2	Species		Df 1;2	Light category		Df 1;2	Species X Light category	
			F	p		F	p		F	p
Carpathian Mts.	A_{max}	1; 1096	1783.5	2e-17***	2; 1096	1476.4	2e-17***	2; 1096	987.5	2e-17***
	Φ	1; 1096	622.2	2e-17***	2; 1096	214.9	2e-17***	2; 1096	2869.5	2e-17***
Dinaric Mts.	A_{max}	1; 1578	1454.3	2e-16***	2; 1578	1352.3	2e-16***	2; 1578	89.53	2e-15***
	Φ	1; 1578	73.0	2e-16***	2; 1578	231.0	2e-16***	2; 1578	775.4	2e-15***

p<0.001 (***).



the lower south-eastern part of the Dinaric Mountains, where the average annual precipitation was below 500 mm (Figures 2, 4).

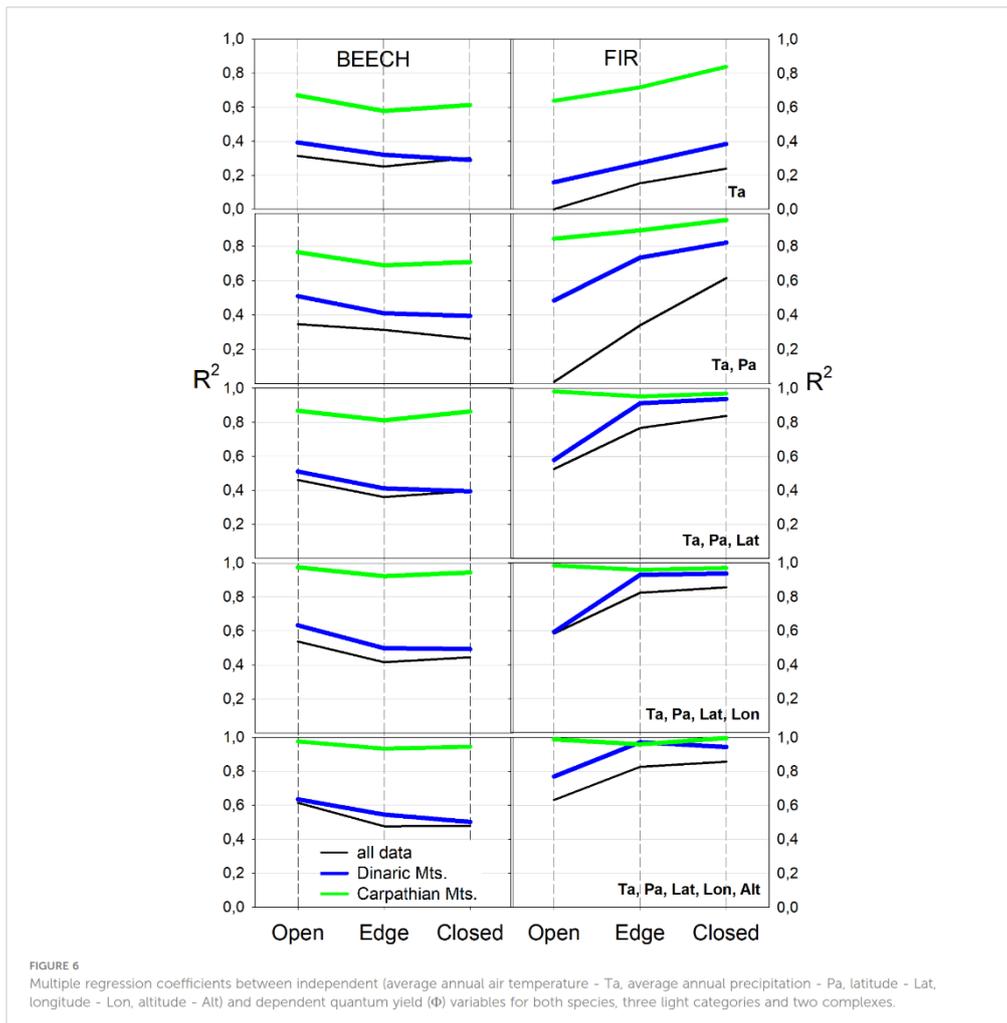
With increasing precipitation, Φ increased in both fir and beech in the Carpathian and Dinaric Mountains, especially in fir, where the slope and dependence on shading increased. The correlation between Φ and mean annual temperature was negative at all sites for beech and fir in the Carpathians, while in the Dinaric Mountains the correlation was reversed for fir (Figure 5). The main reason for the negative correlation between Φ and increasing mean temperature in all light categories for fir could be the lower precipitation in the Carpathians.

Precipitation may not be the only reason, as the Eastern Carpathians and the southern Dinaric Mountains represent the edge of the silver fir's natural range (Mauri et al., 2016; Caudullo et al., 2017). In south-eastern Europe, a higher resistance (compared to other tree species) to climate extremes was found (Bošela et al., 2018). At the same time, two populations of fir trees were distinguished in the Carpathians (Bošela et al., 2016): the eastern population reacts to drought similarly to the populations in the Balkan region, while the western population seems to be less affected by summer droughts. The fir of the western population might therefore be better adapted to the conditions of the Western Carpathians (Bošela et al., 2018) than the beech; although we observe a long-term expansion of beech and a decline of fir there

for other reasons - see Vrška et al. (2009) and might also be better adapted to climate change than the eastern fir population.

The value of the correlation coefficient of the multiple regression increased with increasing number of independent variables and Φ for the beech in the Carpathians, while it remained the same for the Dinaric Mountains, which could indicate that the independent variables influence the beech differently in both mountain complexes (Figure 6, left). Fir, on the other hand, showed a similar dependence on an increasing number of the same independent variables in both the Carpathians and the Dinaric Mountains.

Beech can tolerate a wide range of light conditions in the understorey and manages to grow under different light conditions at young growth stages (Collet et al., 2001; Stancioiu and O'Hara, 2006; Nicolini and Caraglio, 2011). Fir, on the other hand, is a late successional species that is more shade-tolerant and more sensitive to water deficits than beech (Rolland et al., 1999). Compared to beech, the competitive ability of fir is much greater under low and diffuse light conditions, but consequently lower under medium and extensive light conditions; in gaps, beech adapts better and faster to rapid changes in light intensity (Lichtenthaler et al., 2007; Wyka et al., 2007; Čater et al., 2014), while the acclimation of fir growth rate to light conditions occurs gradually over several years (Robakowski et al., 2004). Our study confirmed a better light utilisation of fir in the



shade and a different relationship with increased average temperatures in combination with lower precipitation. The lower Φ of fir utilisation of high-intensity solar radiation compared to beech could be a competitive disadvantage in large gaps in the canopy, which could limit the recruitment of species in the understorey or in small gaps, especially when mixed with beech.

Paralleling short term assimilation with the growth response

The dependence of tree growth on precipitation has increased over the last century, and there has been an upward trend in drought since the 1950s. The latitudinal progression of radial

growth decline and the proportion of positive trends indicate a rapid northward movement of the Mediterranean climate due to global changes and their impact on tree ecology (Gazol et al., 2015). The comparison of the assimilation response in young beech and fir trees was in good agreement with the growth response in adult trees (Čater and Levanič, 2019).

The study of Adamič et al. (2023) confirmed clear differences in the growth response to climate (temperature and precipitation) between southern, eastern and northern locations on the same study plots: a significant correlation between tree growth of both species and seasonal variables (temperature, precipitation) was observed on the eastern Carpathian sites (plots 4, 5 and 6), and a less or non-significant correlation in the southern sites (plots 1, 2 and 3). The fir in the north (plot 7) showed even less significant

TABLE 4 Post hoc (HSD) analysis for quantum yield (Φ) for beech and fir between C (canopy), E (edge) and O (open) light conditions.

Plot No/ Region	Beech			Fir			
	C-E	C-O	E-O	C-E	C-O	E-O	
Carpathian Mts.	1	*	***	*	*	***	*
	2	*	***	*	*	***	*
	3	*	***	ns	*	***	ns
	4	*	***	*	*	***	*
	5	*	***	*	*	***	*
	6	*	***	*	*	***	*
	7	*	***	*	*	***	*
	8	*	***	ns	*	***	ns
Dinaric Mts.	1	***	***	**	***	***	***
	2	***	***	*	***	***	***
	3	***	***	ns	***	***	ns
	4	***	***	**	***	***	***
	5	***	***	**	***	***	***
	6	ns	***	***	***	***	**
	7	***	***	ns	***	***	ns
	8	***	***	ns	***	***	ns
	9	***	***	***	***	***	*
	10	***	***	***	***	***	*
	11	***	***	***	***	***	*

Probability values: p<0.05 (*), p<0.01 (**), p<0.001 (***), ns - non significant.

correlations than those at the southern sites, while the beech in the north showed more significant correlations than at the southern sites, but less than at the eastern sites. Beech and fir showed the same significant correlations at the eastern sites, while fir showed slightly more significant correlations in the south (Adamič et al., 2023). Accordingly, the quantum yield of beech and fir showed the lowest values in the eastern part and the highest values in the west.

Our research in the Dinaric Mountains confirmed that the growth of fir responded more strongly to climate than that of beech in the same study plots, as shown in this study (Čater and Levanič, 2019). Both temperature and precipitation had a stronger influence on the growth of fir than on that of beech. The climate signal of fir became weaker from NW to SE, with only the drought indices remaining significant, while the response of beech to climate was weaker in all plots and decreased from NW to SE, similar to fir (Čater and Levanič, 2019). In the Dinaric Mountains, four different groups were formed according to similar growth responses: two northern regions - A (including plots 1-4) and B (plot 5), and two southern regions - C (plots 6-8) and D (plots 9-11). The average Φ corresponded well to the growth response of the same group (A, B, C, D) and was more pronounced for the longer latitudinal distance than for the Carpathian Arc, which is similar in distance but shorter in latitudinal scale.

In the future, above-average summer temperatures and the absence of summer precipitation (July) are expected to become more frequent (Adamič et al., 2023), which could influence the future demography of fir towards the north and higher altitudes (Tinner et al., 2013). Especially in the Carpathian Mountains, which already show a negative correlation between young fir trees and increasing temperatures (Figure 5), the increasing number of extreme weather events is likely to affect young fir regeneration. The reaction of beech at the expense of fir and its spread in Central Europe has already been reported (Šamonil et al., 2009; Vrška et al., 2009; Janík et al., 2014, 2016).

Recent studies describe different responses of fir along its range (Diaci et al., 2011), its disappearance from warmer and drier areas and at the limit of its range (Ficko et al., 2011) and in south-western Europe (Gazol et al., 2015), especially in the Mediterranean region, where the decline of fir is often related to increasing drought (Čavlovič et al., 2015). A higher resistance (compared to other tree species) to climate extremes was also found in south-east Europe (Bošela et al., 2018).

Studies also indicate a different response of the species along its distribution range. The radial growth of silver fir has increased significantly in Central Europe over the last 30 years, while it has

decreased in drought-prone Mediterranean regions (Büntgen et al., 2014). Furthermore, different growth patterns have been observed between northern and southern populations of silver fir in Italy (Carrer et al., 2010).

Understanding the light utilisation processes in the regeneration phase of uneven-aged forests, which represent the largest contiguous forest complexes in south-eastern Europe, and focusing on sites that already have lower resilience to increasing temperatures and lower precipitation could help to maintain and emphasise the necessary measures that would contribute to greater stability and ensure continuous forest cover in the long term (Schütz, 2002; Schütz et al., 2016). The future response of silver fir forests to climate warming is currently being debated by the ecological community, as millennia of human impact have greatly reduced the species' geographic distribution (Tinner et al., 2013; Di Pasquale et al., 2014). As the severity of disturbances is increasing and several Central European countries are facing unprecedented events (Nagel et al., 2017), the disadvantages of uneven-aged forest management include the dependence on shade-tolerant species that may be affected by the climatic conditions of the open areas created by disturbances. The most important silvicultural tool for the indirect promotion of silver fir is the creation of appropriately large gaps in the canopy and their temporal and spatial expansion. Most studies pointed to the predominance of fir under relatively closed canopies (Hohenadl, 1981; Stancioiu and O'Hara, 2006) and focused on different growth patterns without considering the ecophysiological processes involved.

In the present study, relatively short-term ecophysiological responses of beech and fir provided information on the behaviour at three different light intensity categories compared to long-term radial growth observations, which were consistent. The efficiency of beech increased with light intensity in all light categories and in both mountain complexes, while the response of fir was the opposite, decreasing with increasing light. The main difference between the two larger areas was the response of young fir to increasing temperatures, which correlated positively with increasing temperatures in the Dinarides and negatively in the Carpathians. In our opinion, this difference is related to the high precipitation in the Dinaric Mountains and the low precipitation in the Carpathians.

Our results may give an indication of how two important tree species in their biogeographical range will react to climate change in the future, which will affect their competitiveness, their existence and, consequently, forest management decisions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

No plants or animals (including human) were harmed during this study.

Author contributions

MC: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. PA: Investigation, Writing – review & editing. ED: Investigation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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2.2 VPLIV TEMPERATURE, RAZPOLOŽLJIVOSTI VODE IN LASTNOSTI TAL NA DIHANJE TAL V JELOVO-BUKOVIIH GOZDOVIH VZDOLŽ KOMPLEKSA KARPATOV

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Izveček: Jelovo-bukovi gozdovi v Karpatih so izpostavljeni izrazitim podnebnim spremembam. Spremembe dihanja tal, ki je glavni vir emisij CO₂ iz gozdnih ekosistemov v ozračje, bi lahko vplivale na prihodnje ravnovesje ogljika v gozdovih. Meritve dihanja iz gozdnih tal smo opravili na osmih izbranih lokacijah vzdolž Karpatov v letih 2022 in 2023. Primerjali smo dihanje tal z različnimi podnebnimi, mikrometeorološkimi in talnimi razmerami ter vpliv zastrtosti krošenj na vsaki lokaciji. Dihanje tal se je med letoma spreminjalo zaradi nihanja vsebnosti talne vode, medtem ko je na razlike med lokacijami najbolj vplivala vsebnost ogljika in dušika v tleh. Zastrtost krošenj ni vplivala na dihanje tal povsod enako; na nekaterih lokacijah je bilo dihanje na odprtem manjše kot pod zastorom, na drugih lokacijah pa je bilo ravno obratno. Zaključimo lahko, da je bilo dihanje gozdnih tal, izmerjeno na osmih lokacijah tesno povezano s talnimi lastnostmi in manj s podnebnimi ali mikrometeorološkimi razmerami. Morebiten vpliv podnebja na vnos nove organske snovi s produktivnostjo gozda in vrstno sestavo bo imel v prihodnosti pomembno vlogo pri razgradnji in shranjevanju organske snovi v tleh.



Effect of temperature, water availability, and soil properties on soil CO₂ efflux in beech-fir forests along the Carpathian Mts

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Soil water content

ABSTRACT

Carpathian Mountain beech-fir forests are exposed to severe pressures related to climate change. Alterations in soil respiration, the main source of CO₂ emissions from forest ecosystems into the atmosphere, could potentially impact the future carbon balance of these ecosystems. We performed soil CO₂ efflux measurements along the whole Carpathian arc on eight selected locations during two separate campaigns in 2022 and 2023. The correlations between soil CO₂ efflux and various climatic, micrometeorological, and soil conditions were evaluated as well as the impact of canopy gaps at each site.

Soil CO₂ efflux varied between the two campaigns primarily due to fluctuations in soil water content, while differences among the sites were more influenced by soil carbon and nitrogen content. The presence of a canopy gap did not consistently affect soil CO₂ efflux; in some sites, it was lower in the gap than under a closed canopy, while in others, the opposite trend was observed. In conclusion, soil CO₂ efflux measured at eight sites was closely associated with soil properties rather than with climate or micrometeorological parameters. Therefore, the potential influence of climate on the input of new organic matter through forest productivity and species composition will play a significant role in the decomposition and storage of soil organic matter.

1. Introduction

Carpathians are the largest mountain forest chain in Central Europe with Romania holding over 50 % of the Carpathians' surface (Murariu et al., 2021). Large area of the Carpathian slopes between 500 and 1450 m is covered with beech (*Fagus sylvatica* L.) and conifer (spruce and fir) mixed forests (Dinca et al., 2022; Knorn et al., 2013), which are highly influenced by human impact and climate change. Recent warming and frequent dry periods result in the decline of spruce, especially at warmer sites with lower amounts of precipitation (Kolár et al., 2017). Increased summer temperatures also negatively affect the stem radial increment of beech (Levanič et al., 2023). Silver fir (*Abies alba* Mill.), which contributes to the diversification of forests and increased resistance to climate change (Kerr et al., 2015), is very sensitive to air pollution and climatic extremes, especially those that proceed rapidly. Forest management influences successful fir regeneration in gaps, where beech is more efficient due to its higher tolerance under open light conditions (Cater and Levanič, 2019). The research on these forests along the large geographical range might provide valuable reference to predict future

limitations of these tree species. Such a geographical gradient is accompanied by a gradient in climatic conditions (Cater and Levanič, 2019; Huang et al., 2010; Kolár et al., 2017; Tei et al., 2021) where usually warmer and drier conditions represent the future environmental conditions (Fernández-Manjarrés et al., 2018).

To improve knowledge on this topic, a project including various ecophysiological measurements and satellite data analyses in beech-fir forests along the Carpathian Mountains was established. Adamič et al. (2023) already confirmed different stem radial growth in beech and fir since 1950s and their response to climate conditions along the Carpathians.

Soil respiration contributes substantially to ecosystem carbon flux and affects the forests' carbon storage due to its sensitivity to climate (Rodrigues et al., 2023). The impact of climate (especially temperature and precipitation) on soil respiration can be direct through enzymatic processes, or indirect through the effect on the tree community and their productivity (Macdonald et al., 2021). Soil respiration varies substantially on small spatial scales due to root distribution (Cater and Ogrinc, 2011), variability in soil organic matter and soil properties (Saiz et al.,

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2006), forest structure (Darenova and Čater, 2018) which affects soil respiration through soil microclimate (De Frenne et al., 2021), or new carbon supply by litter (Ishihara and Hiura, 2011).

Usually, forest soil respiration increases with mean annual temperature and mean annual precipitation (Wei et al., 2010). It is highest in tropical areas and decreases toward the poles (Hashimoto et al., 2015). The latitudinal trend was observed on a regional scale including pine (Maki et al., 2022) and spruce forests (Kim et al., 2013). The effect of climate and environmental gradients on different processes can also be studied along the altitudinal transects when a decrease in temperature and an increase in humidity are closely related to the elevation (Sundqvist et al., 2013).

Forest gaps are an integral part of forest ecosystems and play a crucial role in the regeneration of mixed beech-conifer forests (Cater et al., 2014; Grassi and Bagnaresi, 2001) and influence the future species admixture. Harvests alter micrometeorological stand's conditions and ecological processes in the understorey. They result in higher soil temperature and precipitation throughout, which temporarily increase soil respiration (Londo et al., 1999, Cater et al., 2021) and consequently increase the decomposition of soil organic matter. Together with reduced aboveground litter input, this leads to a loss of soil organic carbon (Hukić et al., 2021). Soil respiration in the gaps may vary with the gap age and site and that may complicate the estimations of the CO₂ emissions on the regional scale (Cater et al., 2021; Han et al., 2020).

We measured soil respiration as CO₂ efflux from the soil surface at eight beech-fir-dominant forest sites along Carpathians Mountain ridge characterised with different climatic conditions. Our aims were i) to determine potential topographical, biological or climatic factors driving soil CO₂ efflux variability along the Carpathian arc, which could be the potential drivers of changes in soil CO₂ efflux due to changing climate, and ii) to evaluate effect of gaps on soil CO₂ efflux and soil and micro-meteorological characteristics.

2. Methods

2.1. Experimental sites

Eight experimental sites were established along the Carpathian Mountains arc in Romania, Slovakia, and the Czech Republic (Adamić et al., 2023). The site characteristics are summarised in Fig. 1 and Table 1. All sites were located above 800 m on Cambisols in the optimally developed forests dominated by European beech and silver fir. All

Table 1

Location and environmental conditions of eight study sites along the Carpathian arc.

	Coordinates	Altitude (m a.s.l.)	MAT (°C)	MAP (mm)	Canopy gap fraction (%) ^a
Site 1	45°10'10.00"N22°55'1.00"E	985	4.8 (±0.9)	1074 (±163)	7.04
Site 2	45°27'37.00"N24°39'4.00"E	995	7.5 (±0.9)	817 (±121)	7.29
Site 3	45°36'51.00"N26°13'44.00"E	1038	7.0 (±0.9)	755 (±108)	7.82
Site 4	46°0'5.00"N26°36'14.00"E	830	8.5 (±0.9)	611 (±90)	8.75
Site 5	46°51'15.00"N26°10'6.00"E	950	5.9 (±0.9)	714 (±104)	9.04
Site 6	47°28'6.00"N25°40'60.00"E	850	7.0 (±0.9)	695 (±102)	7.18
Site 7	49°15'17.06"N21°0'59.62"E	880	7.4 (±0.8)	761 (±108)	6.54
Site 8	49°24'8.94"N18°25'0.50"E	820	7.3 (±0.8)	974 (±118)	6.89

MAT – mean annual temperature (1970–2020), MAP – mean annual precipitation (1970–2020).

^aCanopy gap fraction was estimated in 2023 from hemispherical photographs according to Darenova and Cater (2020).

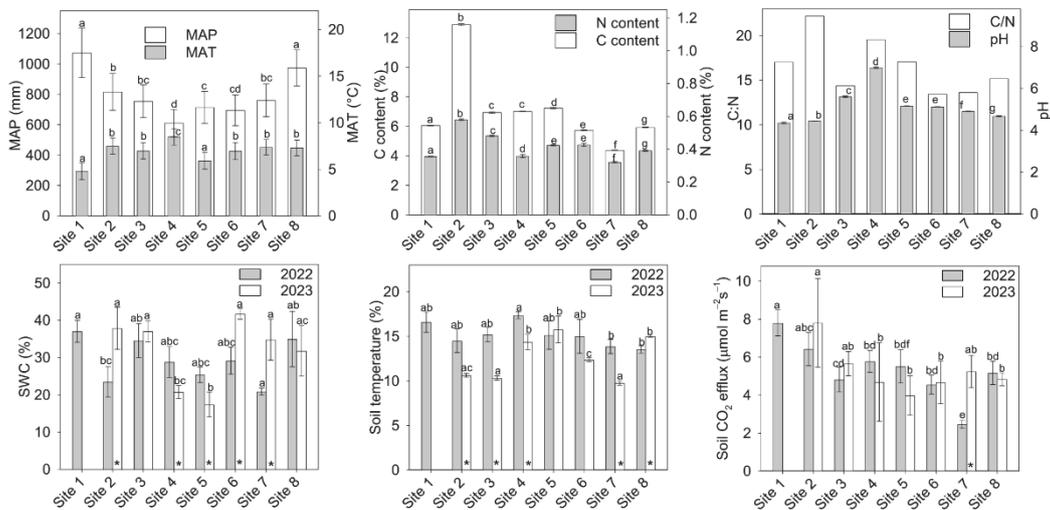


Fig. 1. Mean (±SD) meteorological and soil characteristics of the sites and measured parameters on the plots with closed canopy for eight study sites along the Carpathian arc: mean annual precipitation (MAP) and mean annual temperature (MAT) (1970–2020) from the database <http://climexp.knmi.nl>, soil carbon and nitrogen content, carbon–nitrogen ratio (C/N), pH, soil water content (SWC), soil temperature at a depth of 1.5 cm, and soil CO₂ efflux. The different letters indicate statistically significant differences between the sites (ANOVA). For SWC, soil temperature, and soil CO₂ efflux they indicate differences within one year, and the asterisks show statistically significant differences in the parameters in 2023 from those in 2022 (Two-Way ANOVA). Significant differences correspond to $p < 0.05$.

sites were representative in selected areas and had also convenient climate and soil conditions for abundant beech and fir natural regeneration. At each site, we randomly selected a medium gap size (100–200 m²) according to Han et al. (2020) or Lyu et al. (2022), where three plots were selected: forest with closed canopy cover (closed), forest adjacent to the gap (edge), and the gap without canopy (open).

2.2. Climate and micrometeorological data

Mean monthly temperature and total monthly precipitation interpolated for 0.5° grid were obtained for each site from the Royal Netherlands Meteorological Institute 'Climate Explorer' web page (<http://climexp.knmi.nl>) for the years 1901–2020 from which mean annual temperature (MAT) and mean annual precipitation (MAP) were calculated. The database interpolates meteorological data from the nearest meteorological stations and provides reliable information based on kriging with a resolution of 0.5-degree latitude-longitude grid.

During Rs measurements, soil temperature at a depth of 1.5 cm was measured in the middle of the plots during each measurement campaign using a TPD32 penetration thermometer (Omega, Stamford, CT, USA), and soil water content in the profile of 0–6 cm was measured next to each collar once per campaign using ThetaProbe ML2x (DeltaT Devices, Cambridge, UK).

2.3. Soil CO₂ efflux - Rs

For Rs measurements, three lines with three positions on each plot were established. On each position, a PVC collar (20 cm in diameter) was inserted 3 cm into the soil the day before the measurements. Rs was measured using a portable infrared gas analyser Li-8100 (LI-COR, USA) and 20 cm-survey chamber placed on the collars and working as the closed dynamic (nonsteady-state, through-flow) system.

Measurements were carried out in three rounds in two-hour intervals, 8 a.m., 10 a.m., and 12 a.m. during two campaigns, 2 June – 21 June 2022 and 5 June – 24 June 2023, keeping the period as short as possible. June was chosen for the stable temperatures without precipitation and fully developed mature canopy. Therefore, we assumed that our measurements were not affected by sudden weather changes and that the conditions characterised the whole campaign's period along the Carpathians. Soil respiration was not limited by seasonally changing environmental conditions.

2.4. Soil analyses

Soil sampling was performed for same measurement points during the 2022 campaign. Top 10 cm of soil (containing organic and mineral horizons) was sampled using a portable stainless steel soil core sampler of a diameter of 5 cm. Three samples were taken per each plot (one in each Rs-measurement line) and mixed. Samples were dried and sieved through a 2-mm sieve and analyzed for pH (H₂O), carbon and nitrogen content (%) for three replicates per sample. Total carbon and nitrogen content was measured using the macro elemental analyzer Vario Macro cube (Elementar, Germany). Sample's pH was measured in water using a ration 1:2.5 soil/water.

2.5. Data analyses

Differences between the sites were tested using ANOVA for climatic parameters (MAT and MAP) and soil properties (C and N content, C:N, and pH) and Two-Way ANOVA for Rs, soil temperature and SWC with the site and year as independent variables. Two-Way ANOVA with the site and plot as independent variables was used to test effect of canopy openness on measured parameters.

Pearson correlation tests were used to test the relationship between all variables. Principle Component Analysis was subsequently on Rs and the variables which showed correlation with Rs with $r > 0.5$ to visualise

the relationship of Rs with its main potential drivers and their interactions. To generalize what soil parameters affect Rs including canopy openness and differences in soil temperature and SWC during two campaigns, PCA was run when plots were given numbers as follows: closed canopy = 1, forest edge = 2, and open canopy = 3.

3. Results

3.1. Climate

Mean annual temperature (MAT) for the last fifty years ranged between 5.2 and 8.9 °C without any distinct pattern along the Carpathian arc (Fig. 1). There was no correlation between MAT and longitude or altitude of the sites (Fig. Supplementary 1). The warmest month was July when mean monthly air temperature was around 15 °C. After 1980 gradual increase in MAT was recorded at all sites (Fig. Supplementary 1). A decadal increase in air temperature was 0.54 °C for MAT, 0.71 °C for summer (July - August) and 0.53 °C for winter (January - March) temperatures. The increase declined with the latitude change towards north (Fig. Supplementary 3-A).

Mean annual precipitation (MAP) for the last fifty years ranged between 600 and 1100 mm. It was highest at Site 1, decreased to Site 4 and increased towards Site 8 (Fig. 1). Like MAT, MAP did not correlate with longitude or altitude of the sites (Fig. Supplementary 1). The rainiest months were June or July, when monthly precipitation usually exceeded 100 mm (150 mm at Site 1). Contrary to MAT, no visible trend in MAP was confirmed. At Sites 1–6, a substantial decrease in summer precipitation was evident (July - August) during the last decade (2011–2020) (Fig. Supplementary 3-B).

3.2. Micrometeorological conditions

Mean soil temperature at 1.5 cm (Ts) under the closed canopy ranged between 13.5 and 17.4 °C in 2022 (Fig. 1). The lowest temperatures were observed at two northernmost sites (sites 7 and 8). The site 4 had the highest Ts, which also corresponds with the highest MAT (Fig. 1). In 2023, the measured soil temperatures were lower than in 2022 (except for sites 5 and 8) and ranged between 9.8 and 15.8 °C. The lowest temperatures were observed at sites 2, 3 and 7.

Soil temperature tended to increase from closed canopy plots, through the gap edge to the open canopy conditions. Statistically significant differences were confirmed only for site 1 in 2022 and site 5 in 2023, but with the highest temperature on the edge. Soil temperatures had tendency to increase during the day from the first to the third measurement round (data not shown).

Soil water content under the closed canopy exceeded 20 % at all sites, except for site 5 in 2023 (Fig. 1). During 2023, we recorded significantly higher SWC at sites 2, 6, and 7 compared to the 2022, while lower SWC was observed at sites 4 and 5. In 2023, we confirmed significantly negative correlation between SWC and soil temperature (Fig. 2). The pattern among the plots was not uniform but mostly with the highest SWC under the open canopy (Fig. 3).

3.3. Soil analyses

Soil C content under closed-canopy conditions ranged between 4.4 and 12.9 % (Fig. 1). C content of 12.9 % was found at site 2 and highly exceeded C content at other sites. The second highest C content was found at site 6 and the lowest at site 7. Same trend was followed also by N content and C:N ratio (Fig. 1). N content ranged between 0.32 and 0.58 %, while C:N ranged between 13.6 and 22.2. The soil under the closed canopy was mostly strongly acid with pH below 5.5 (Fig. 1). Exceptions were site 3 with a pH of 5.6 (acid soil) and site 4 having neutral soil having a pH of 7.0. We found a negative correlation between pH and MAP. Moreover, N content and C:N significantly increased with C content (Fig. 2, Supplementary Figs. 4 and 5).

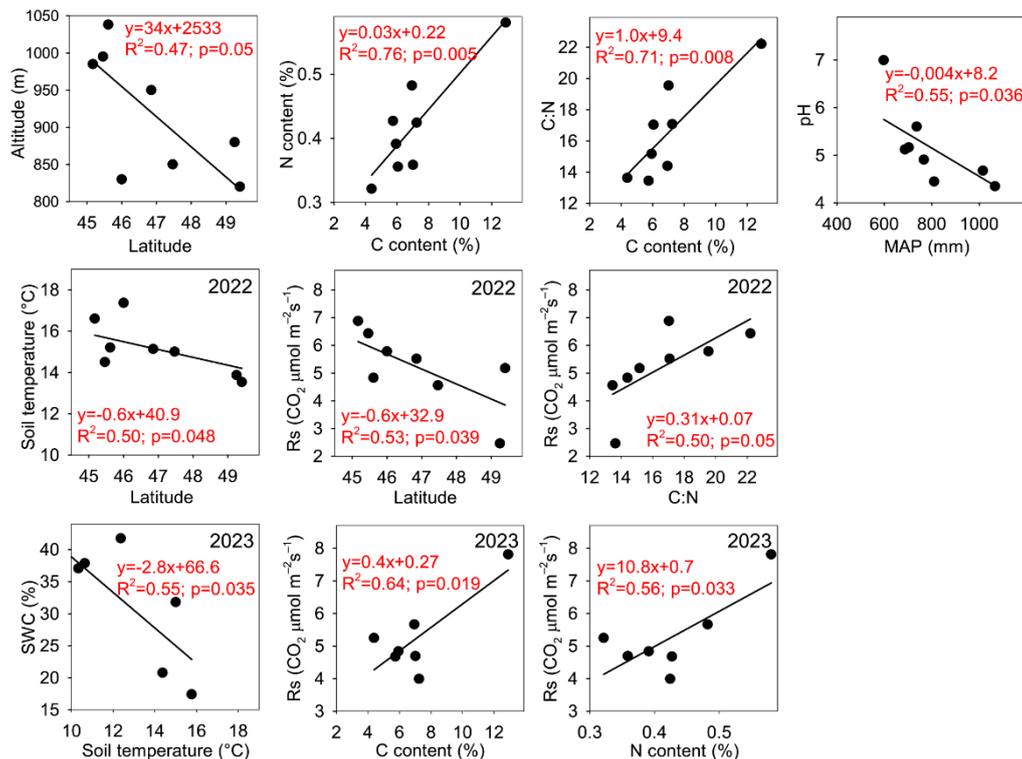


Fig. 2. Statistically significant linear regressions between different site characteristics and parameters measured on plots with the closed canopy during the campaigns in 2022 and 2023. All regressions are summarised in Supplementary Figs. 4 and 5.

Canopy openness did not have uniform effect on the studied soil properties. Carbon content at the gap edge was substantially higher than under closed canopy at site 1 (Fig. 4-A). On the contrary, lower carbon content at the edge was found at sites 2, 3, and 6. At the other sites, the difference was small or even insignificant. The similar pattern was observed for N content except for site 2 (Fig. 4-B). The difference in soil C and N content between open and closed canopy conditions indicated similar trends as for the edge but with a bigger magnitude.

The most abundant trend in C:N ratio at the sites 1–6 was closed > open > edge (Fig. 4-C). At sites 7 and 8, the lowest C:N ratio was found under closed canopy conditions.

3.4. Soil CO₂ efflux

Mean soil CO₂ efflux (Rs) under the closed canopy ranged between 2.5 and 7.8 μmol m⁻² s⁻¹ (Fig. 1). Despite the increase in soil temperature during the time of measurement, no increase was observed in Rs. The differences in Rs between 2023 and 2022 increased significantly with SWC changes (Fig. 5). A decrease in the Rs differences with soil temperature was also observed but was not significant ($p = 0.079$).

In 2022, Rs under closed canopy significantly decreased with latitude and increased with C:N (Fig. 2). In 2023, Rs significantly increased with both C and N content (Fig. 2). The relationships between Rs and parameters which correlated with Rs with correlation coefficient $r > 0.5$ and between these parameters are shown in Fig. 6-A and B using PCA.

The pattern in Rs among the plots was not uniform over the sites

(Fig. 3). While at sites 1, 2 and 7, Rs under the closed canopy was the highest in both years, at sites 5 and 6 was the lowest. While there was a tight linear relationship between differences in Rs in 2023 from 2022 and changes in SWC for closed canopy plots, a weaker but still significant relationship was confirmed for the edge conditions ($p = 0.046$). No relationship ($p = 0.17$) was confirmed for the open canopy (Fig. 5). The differences in Rs decreased with changes in soil temperature under closed canopy without significance ($p = 0.079$). For the edge and the open conditions, no effect of the soil temperature change was confirmed. The relationship between inter-annual differences in SWC and soil temperature had an expected decreasing trend which was statistically significant only for the edge ($r = -0.79$, $p = 0.019$).

We analysed if the pattern in Rs at each site depended on the variation in soil properties, especially in C and N content (Fig. 7). Correlations coefficients between Rs and C and N content were highly variable and ranged between -1.00 to 0.99 , therefore we cannot assume soil properties to clearly explain the Rs variability among the closed canopy, edge and open canopy conditions. Nevertheless, the soil C and N content had a substantial effect on the overall variability in Rs over the sites and plots, while soil temperature, SWC, and pH affected Rs variability negligibly (Fig. 6-C).

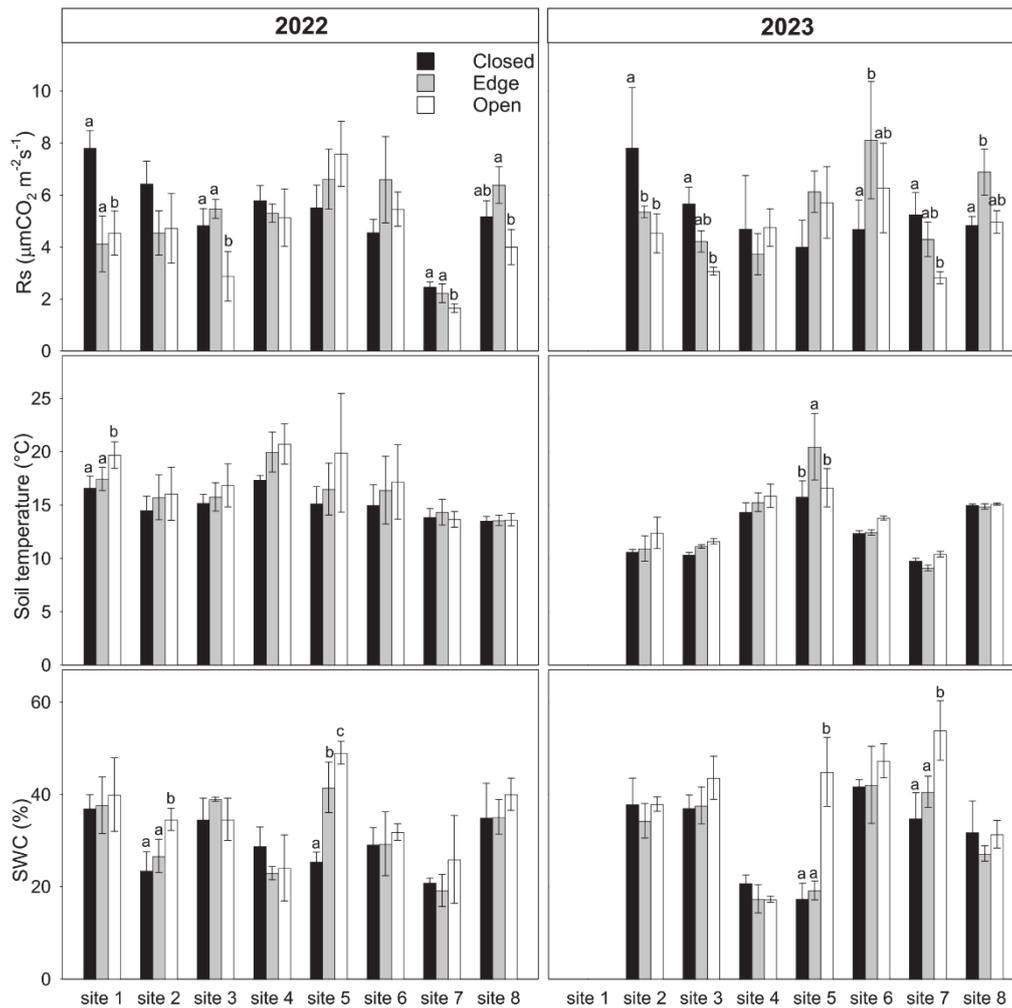


Fig. 3. Mean (\pm SD) soil CO₂ efflux (Rs), soil temperature at 1.5 cm (Ts), and soil water content (SWC) at eight study sites along the Carpathian arc in 2022 and 2023. At each site, plots under the closed canopy, at the forest edge, and under the open canopy (middle of a forest gap) were established. Different letters indicate statistically significant differences ($p < 0.05$) between the plots at one site (Two-way ANOVA).

4. Discussion

4.1. Soil CO₂ efflux along the Carpathian arc

Soil CO₂ efflux (Rs) varied substantially among the studied beech-fir-dominated forest stands along the Carpathian Mountains. As the future climate may affect forests due to increased temperature and changes in precipitation, we focused on the Rs response to temperature and water availability related factors and also response to soil carbon and nitrogen availability.

According to <http://climexp.knmi.nl>, decadal mean annual temperature (MAT) increased by 1.6–1.9 °C from 1971 to 80 to 2011–2020 at all experimental sites (Supplementary Fig. 2). Due to the canopy shading and lower soil temperature fluctuation under the canopy, we can assume

that a lower increase in soil temperature during this period and in the future may appear. Generally, Rs exponentially increases with soil temperature (Davidson et al., 2006). However, the effect of the long-term temperature increase on Rs can be weakened with its thermal acclimation (Bradford et al., 2008), which means that the temperature sensitivity of Rs decreases under warming (Luo et al., 2001). Carey et al. (2016), however, denied thermal acclimation in most of the ecosystems except deserts and boreal areas. In their meta-analysis on temperature manipulation studies, they quantified the Rs increase by 0.20–0.35 $\mu\text{molC m}^{-2} \text{s}^{-1}$ for temperate forests under SWC reaching 90–110 % of non-manipulated plots. This magnitude, however, decreased with a decreasing SWC which can likely accompany the soil warming (Fang et al., 2020). The Rs response to the warming can be gradually weakened due to a gradual substrate depletion (He et al., 2023). According to Dacal

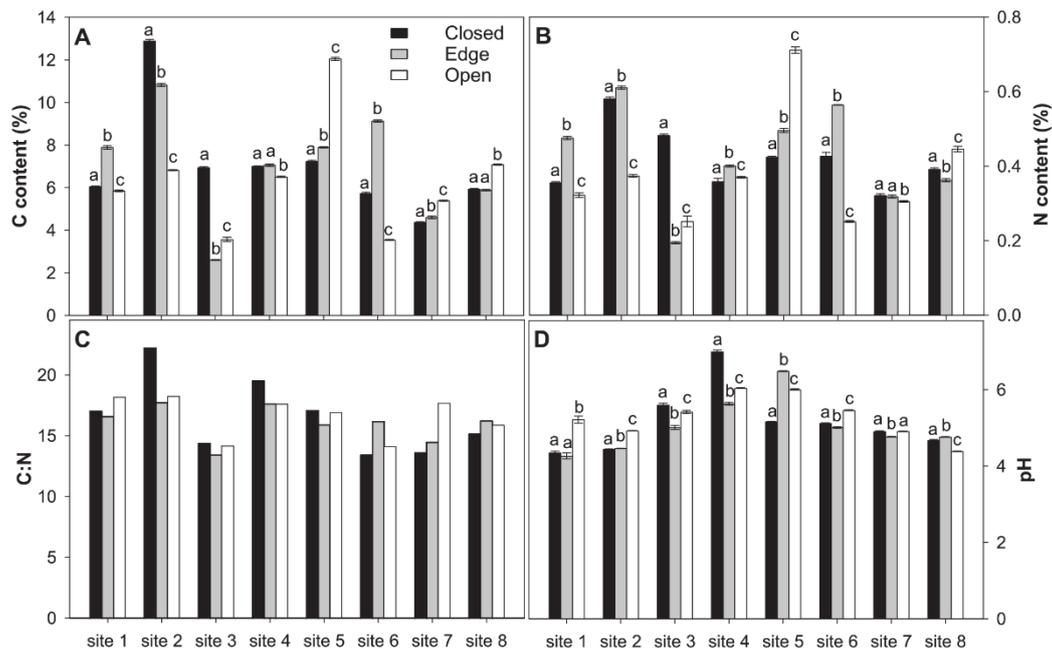


Fig. 4. Mean (\pm SD) soil carbon (C) and nitrogen (N) content, pH in H_2O , and C/N ratio for 10 cm topsoil at eight study sites along the Carpathian arc. At each site, plots under the closed canopy, at the forest edge, and under the open canopy (middle of a forest gap) were established. Different letters indicate statistically significant differences ($p < 0.05$) between the plots at one site (Two-way ANOVA).

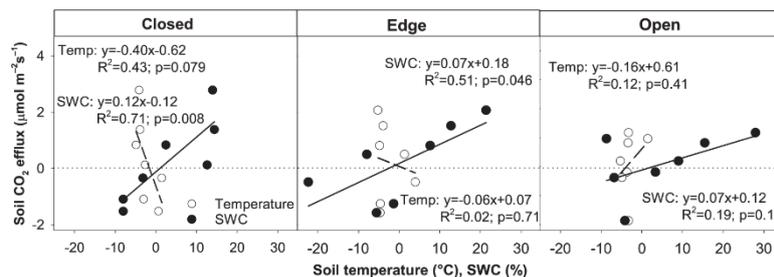


Fig. 5. Differences in soil CO_2 efflux during the campaign in 2023 from that during the campaign in 2022 over the differences in soil temperature and soil water content (SWC). Seven out of eight sites were included due to the inaccessibility of Site 1 in 2023.

et al. (2022), the magnitude of the warming effect on R_s can also be altered by other conditions, namely by soil properties, such as organic carbon content, microbial biomass, phosphorus content, and pH, which is in agreement with our results. We did not observe any significant effect of soil temperature on temporal or spatial variability in R_s , which was rather driven by SWC or soil properties.

Despite clearly increasing MAT, mean annual precipitation (MAP) at the study sites did not show any trend over the last fifty years (Supplementary Fig. 2). At sites 1–6, however, the summer precipitation during the last decade (2011–2020) were the lowest (Fig. Supplementary 3-B). This indicates that in future, these sites might be severely affected by summer droughts. Low SWC affects R_s directly through limited availability of water-diluted substrate (Or et al., 2007)

but long-term reduced or irregularly distributed precipitation during the growing season can reduce R_s also through reduced forest productivity (Davi et al., 2006), which drives the input of labile carbon into the soil (Caprez et al., 2012).

We did not observe any significant effect of SWC on the R_s variability between the forest sites. The dependence of the inter-annual R_s differences on SWC, however, shows that big actual SWC changes (like at sites 2 or 7; Fig. 1) could substantially influence temporal patterns in R_s . Therefore, we may expect that potential summer droughts may decrease soil activity and R_s , but the decrease will also depend on the precipitation distribution.

From all studied factors, soil properties (C and N content) had the biggest effect on the R_s variability among the sites. Despite the

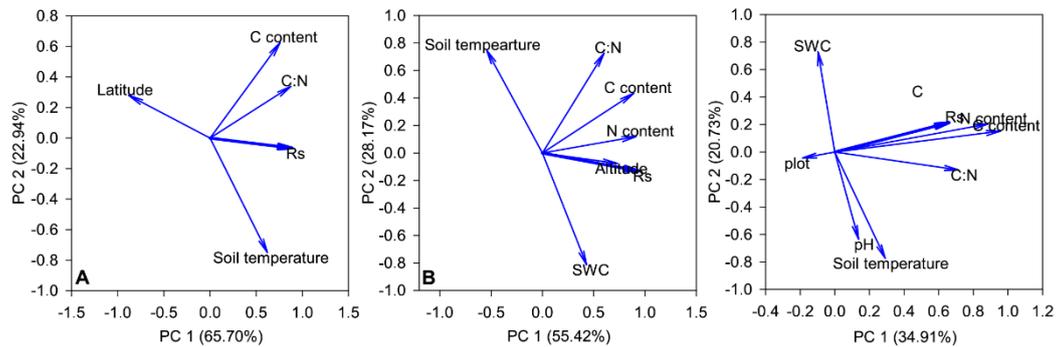


Fig. 6. The Loading Plots of Principal Component Analysis (PCA). The angle between arrows indicates direction of the relationship (positive, negative, or no relationship). A and B – analyses run for the closed canopy plots of the sites along the Carpathian arc in 2022 and 2023, respectively. The analyses were run for soil CO₂ efflux (Rs) and parameters which showed correlation coefficient with Rs $r > 0.5$. C – analyses for Rs, soil microclimatic parameters, and soil properties of all sites, plots (with the closed canopy, at the forest edge, and with the open canopy), and years (2022 and 2023). SWC – soil water content, C – carbon, N – nitrogen.

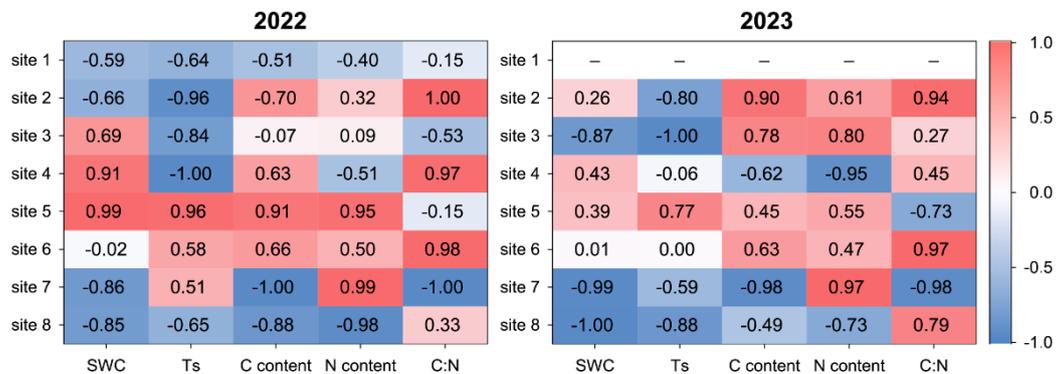


Fig. 7. Matrix of Pearson's correlations coefficients between soil CO₂ efflux on three plots (closed canopy, forest edge, and open canopy) at each site and corresponding soil properties (SWC – soil water content, Ts – soil temperature, carbon (C) content, nitrogen (N) content, and C:N).

differences in soil temperature and SWC between the two campaigns, Rs significantly increased with C:N in 2022 and with C and N content in 2023. We might, therefore, expect that changes in Rs in the future can be likely connected with changes in these soil properties. Soil C and N content and C:N depend substantially on new organic matter input through rhizodeposits and root and above-ground litter. Those are linked to photosynthesis and forest productivity which are expected strongly affected by the climate change (Boisvenue and Running, 2006; Kirschbaum, 2004). Photosynthesis is directly connected with actual production of rhizodeposits. Rhizodeposits represent low-molecular weight organic substrates which are mostly rapidly used by microorganisms and do not remain in the soil for long time (Pausch and Kuzyakov, 2018). The forest productivity can be associated with tree growth which is in great extent affected by MAT and MAP (Wang et al., 2023). Generally, warmer and wetter climate tends to increase the forest productivity, but the frequent dry periods during the growing season decrease it (Duan et al., 2018). Adamić et al. (2023) analysed beech and fir growth during the last 70 years on the same localities as our study. They confirmed different trends in growth for the studied species in dependence with geographical position. While fir showed a relatively steep increase in annual stem increment on the northern and decrease in the southern Carpathians, beech growth in both parts was consistent

during the last decades. Annual stem increment correlated negatively with summer air temperature but positively with summer precipitation. The sensitivity of the increment to these climatic conditions, however, varied between species and location showing fir as more sensitive to the climatic variables in the south part compared to the north, while the opposite was observed for the beech. We may expect a gradual decline in future growth of fir in the southern and better performance in the northern Carpathian regions.

Changing of the tree species contribution impacts litter C and N content and especially the litter C:N which is an important indicator of the litter decomposition rate (Li et al., 2020) and, therefore, soil respiration. Beech foliage has higher N content and lower C:N than fir (Cater and Diaci, 2017; Cools et al., 2014; Yang et al., 2022), even though the opposite was also observed by Kara et al. (2014). A bigger amount of nitrogen relative to carbon supports organic matter decomposition, so beech litter decomposes faster than firs. Conifer and broadleaf admixture supports soil organic carbon storage (Staszal et al., 2022). Therefore, smaller abundance of fir in the future in southern areas would decrease soil carbon storage.

According to our results, C:N ratio in the soil is an Rs indicator, as we observed increase in Rs with increasing C:N (Fig. 2). There are, however, contradicting results from the previous studies; while some found high

soil C:N was accompanied with reduced decomposition due to the limited availability of nitrogen for microbes (Xu et al., 2016), others showed similar results to ours (Klimek et al., 2021; Tian et al., 2019), where C:N may indicate soil organic carbon being more decomposed by microorganisms (Ngao et al., 2012).

4.2. Effect of canopy openness

The studied areas were difficult to access, so it would be difficult (or even impossible) to evaluate age of forest gaps. The gaps are integral to the forest ecosystems and their carbon budget but they have different microclimate and carbon and nutrient supply compared to the forest under the closed canopy. Opening canopy leads to a bigger amount of solar radiation and precipitation reaching the ground (Jianxin et al., 2016), resulting in more favourable conditions for soil microbial activity. This is in accordance also with our results as we observed in most cases higher temperature and SWC under the open canopy than under the closed canopy conditions (Fig. 3). Gaps, however, are exposed to smaller input of new organic matter due to smaller root density and litterfall (Griffiths et al., 2010; Kohout et al., 2018), which reduces Rs. However, the herbal plant development after canopy opening can, to some extent compensate this through their roots and litter (Don et al., 2012). Gaps also influence the diversity, biomass and ratio of bacteria and fungi in the soil (Chen et al., 2022; Han et al., 2020).

Canopy removal causes an initial increase in Rs due to improved micrometeorological conditions and decomposition of dead roots but then Rs gradually decreases (Ma et al., 2013; Darenova et al., 2016). For example, Cater et al. (2021) observed that it took about 17 and 28 months for Rs of harvested beech and firs stands, respectively, to return to the levels of unharvested stands. We observed variable differences in Rs under closed and open canopy (Fig. 3) from higher Rs under closed canopy, through no effect of canopy closure, to higher Rs under open canopy. The difference in Rs between gaps and closed canopy conditions varied also in the previous studies. Zhao et al. (2021) reported higher Rs in gaps, but higher Rs under closed canopy was observed by Saner et al. (2009) and Han et al. (2020). Similar variability in Rs for open canopy relative to closed canopy were observed also for the edge conditions despite Scharenbroch and Bockheim (2007) suggestion that the edges may provide optimal microclimate and substrate to enhance microbial activity within forest ecosystems. The correlations between Rs and different soil properties (soil temperature, SWC, C and N content) under closed and open canopy and the edge were not able to explain any uniform effect of these properties on Rs (Fig. 7). This can be due to a different strength of these factors depending, for example, on the gap age and size, microbial composition, local climate (Cater et al., 2021; Griffiths et al., 2010; Han et al., 2020; Lan and Ding, 2022).

5. Conclusions

On eight experimental plots along the Carpathian Mountains within beech-fir forests, the soil CO₂ variability efflux among the plots was driven by soil properties such as carbon and nitrogen content rather than by climatic conditions. Therefore, we may assume that climate effect on new organic matter input through forest productivity and species composition will have a big effect on soil organic matter decomposition and storage. No effect of temperature on soil CO₂ efflux was confirmed, but soil moisture affected the differences in CO₂ efflux between both measurement campaigns. We may assume that future summer droughts, which will likely occur at the studied sites, will decrease soil CO₂ efflux. Although forest gaps are integral to the forest ecosystems, they bring uncertainty to the estimation of the forest carbon balance. We did not find any uniform effect of the canopy openness on soil CO₂ efflux either. That could be a result of the different age of these gaps, which we were not able to estimate.

CRedit authorship contribution statement

Eva Darenova: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft. Pia Caroline Adamić: Data curation, Writing – review & editing. Matjaž Cater: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Eva Darenova reports financial support was provided by Global Change Research Institute Czech Academy of Sciences. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2024.107974>.

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2.3 RASTNI ODZIV NAVADNE BUKVE (*Fagus sylvatica* L.) IN BELE JELKE (*Abies alba* Mill.) NA KLIMATSKE DEJAVNIKE VZDOLŽ KOMPLEKSA KARPATOV

Adamič P. C., Levanič T., Hanzu M., Čater M. 2023. Growth response of European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) to climate factors along the Carpathian massive. *Forests*, 14, 7: 1318, <https://doi.org/10.3390/f14071318>

Izveček: Evropski gozdovi postajajo vse bolj ogroženi zaradi klimatskih sprememb in pogostejših sušnih razmer. Verjetni odziv vrst na podnebne spremembe bo različen, kar bo vplivalo na njihovo tekmovalno sposobnost, obstoj in posledično gozdnogojitvene odločitve in ukrepe. Ugotavljali smo vpliv klimatskih parametrov na debelinsko rast navadne bukve in bele jelke vzdolž Karpatov ter primerjali njun odziv. Izbrali in analizirali smo sedem lokacij z odraslimi sestoji jelke in bukve na nadmorski višini nad 800 m. Študija je potrdila različne odzive glede na vrsto in lokacijo. Na vzhodnih lokacijah je bil odziv debelinske rasti dreves na klimatske parametre izrazitejši, medtem ko je bil na južnih lokacijah statistično manj značilen ali neznačilen. Tako pri bukvi kot pri jelki je bila debelinska rast večja ob večjih julijskih padavinah in manjša ob večjih povprečnih in maksimalnih temperaturah v juniju opazovanega leta. Pri jelki smo potrdili pozitivno korelacijo med debelinsko rastjo in zimsko temperaturo, pri bukvi pa negativno korelacijo med debelinsko rastjo in poletno temperaturo. V obdobju med leti 1951 in 1960 sta bili povprečni širini branik pri jelki in bukvi največji na južnih lokacijah; od leta 2011 naprej je bila debelinska rast na južnih lokacijah najmanjša, na severnih lokacijah pa največja. Potrdili smo različen odziv jelke in bukve na podnebne spremembe, kar bo vplivalo na njuno prihodno tekmovalno sposobnost.



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Article

Growth Response of European Beech (*Fagus sylvatica* L.) and Silver Fir (*Abies alba* Mill.) to Climate Factors along the Carpathian Massive

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Abstract: European forests are becoming increasingly threatened by climate change and more frequent droughts. The likely responses of species to climate change will vary, affecting their competitiveness, their existence, and consequently, forest management decisions and measures. We determined the influence of climate on the radial growth of European beech and silver fir along the Carpathians to find similarities between the two species and the main differences. Along the Carpathian Mountains, seven sites with mature fir–beech stands above 800 m above sea level were selected and analyzed. Our study confirmed different responses depending on species and location. A more pronounced response of tree growth to climate was observed on the eastern side of the Carpathians, while it was less expressed or even absent on the southern sites. Both beech and fir show better radial growth with higher precipitation in July and slower growth with higher average and maximum temperatures in June of the current year. Fir demonstrates a positive correlation between radial growth and temperature in winter, while beech demonstrates a negative correlation between radial growth and temperature in summer. In the 1951–1960 decade, the average tree ring widths in fir and beech were largest at the southern sites compared to the other sites, but since 2011, the southern sites have had the lowest increase while northern sites have had the largest. Both species respond differently to climate and are likely to follow different competitive paths in the future.

Keywords: climate change; dendrochronology; radial growth response; meteorological parameters



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1. Introduction

Due to climate change and more frequent droughts, European forests are becoming increasingly threatened [1,2]. The dependency of tree growth on precipitation has increased during the last century, and drought has experienced an upward trend since the 1950s. The latitudinal progression of radial growth decline and the proportion of positive trends strongly support the rapid northward advance of the Mediterranean climate caused by global changes and its effect on tree ecology [3].

In our research, we focused on European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.), which are likely to be the two most important tree species for a large part of Europe's mid- and high-altitude forests in the future [4].

Beech is a dominant forest tree species in Europe [5], with a wide distribution range between Scandinavia and the Mediterranean [6]. Despite its functional adaptability and great ecological plasticity, it is affected by drought, as confirmed by studies of its response in southern Europe [7]. It thrives in pure and mixed stands with conifers, especially fir,

whose distribution is mainly limited to the area of the Alps and the Carpathians [8]. A long-term decline in radial growth at lower elevations in Central Europe since around the 1980s [9–11] suggests that it is sensitive to a warmer and drier climate [12].

Silver fir, as one of the most important conifers of European mountain forests, predominates in cold temperate areas [13]. Its regression over Europe, e.g., [14,15], affected its use and economic value [16]. Fir forms heterogeneous stand structures; its ecotypes show great variation in their resistance to frost, drought, and shade. Natural regeneration of fir is questionable when stands are managed with clearcutting and a short regeneration period [4]. Climate change is believed to have had an adverse impact on the growth performance of autochthonous fir populations in Europe in recent decades [17,18]. While causes of fir decline such as climate change, air pollution, and overbrowsing are difficult to control, silvicultural measures (e.g., creation of suitable stand climate, promotion with tending and preservation of seed trees) are becoming even more significant for its conservation.

In a study at the Balkan Peninsula along the Dinaric high karst, where different and well-expressed ecological factors intertwine at relatively short geographical distance (approx. 1000 km) [19], response of beech and fir from the southern, warmer, and dryer sites already served successfully as a most probable future prediction for the same species' response in currently less-extreme sites northward [20]. Carpathians at more complex sites comprise sufficient latitudinal and longitudinal gradients, connected with significant differences in temperature/precipitation as well as differences in their seasonal pattern [21].

The quality and future of fir–beech forests is in tight connection with our understanding of tree-responses to environmental parameters. Dendrochronological analyses of stand growth provides a historical retrospective of the response to climatic factors in different time series of mature trees [22]. In predicting the consequences of climate change on tree species, studying the response of species on a geographic gradient may highlight the crucial parameters important for tree growth on a larger scale, help to predict future responses, and optimize the future forest management.

In the presented study, we were interested in discerning if there are similar responses between tree species along the Carpathian arc. The aim was to determine the influence of climate on the growth of beech and fir along the geographical gradient (a), to find similarities or differences between the two species (b), and to compare responses in time with respect to eventual changes in the growth response (c).

2. Materials and Methods

Along the Carpathian Mountains, seven sites with mature fir–beech stands located between 820 and 1038 m above sea level were selected and analyzed (Figure 1 and Table 1). At the study sites, the average temperature is 7.3 °C and the average temperature in the growing season (from May to August) is 15.8 °C. The average precipitation is 60.7 mm per month and 91.5 mm per month from May to August. The meteorological data were calculated for the years 1950 to 2020 (Table 2).

At each site, 15 mature dominant fir and beech trees were double cored, which gave, in total, 105 sampled trees for fir and 105 sampled trees for beech. All sampled trees were healthy trees with no visible signs of stem damage or any kind of declining tree vitality. Tree cores were packed into plastic straws, marked, and transported to the dendrochronology laboratory.

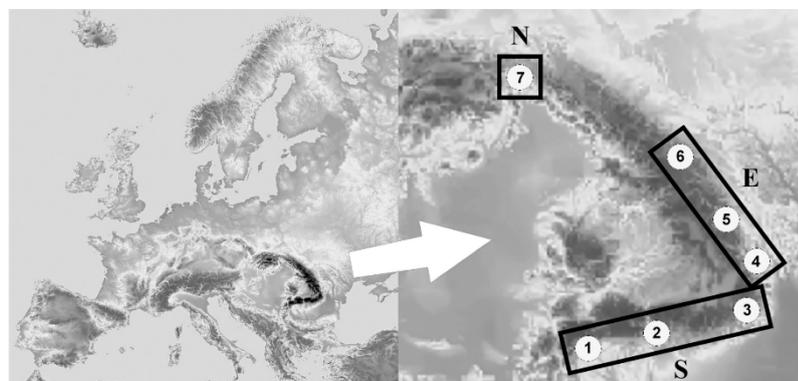


Figure 1. Location of research sites. The white arrow shows the enlarged area of the Carpathians; the numbers in the circles indicate the numbers of the plots, and the black squares show the plots grouped according to their exposure.

Table 1. Locations, forest label, altitude, and coordinates of research site locations.

No.	County	Plot	Managed/Old Growth Forest	Altitude (m)	E (DMS)	N (DMS)
1	Gorj	Tismana	managed	985	22°55'1.00"	45°10'10.00"
2	Arges	Arefu	managed	995	24°39'4.00"	45°27'37.00"
3	Buzau	Zagon	old growth	1038	26°13'44.00"	45°36'51.00"
4	Vrancea	Soveja	managed	830	26°36'14.00"	46°0'5.00"
5	Neamt	Tarcau	managed	950	26°10'6.00"	46°51'15.00"
6	Suceava	Frumosu	managed	850	25°40'60.00"	47°28'6.00"
7	Bardejov	Livovska huta	managed	880	21°0'59.62"	49°15'17.06"

Table 2. Meteorological data for southern (S), eastern (E), and northern (N) sites.

Group of Research Sites	Average Temperature (°C)	Temperature May to AUGUST (°C)	Average Precipitation (mm/Month)	Precipitation May to August (mm/Month)
S: site 1, 2, 3	7.7	15.9	65.1	96.4
E: site 4, 5, 6	7.1	16.0	53.9	84.1
N: site 7	7.2	15.5	63.1	94.0

The cores were dried under load for fourteen days to prevent decay. Each core was mounted and glued on a wooden support and sanded with progressively finer sandpaper with grid from 180 to 600. After sanding, the cores were cleaned of all particles with an air blaster. The cores were then scanned with an ATRICS [23] image capturing system, and annual radial increments were measured to within 0.01 mm using CooRecorder and CDendro software v. 9.8.1 (Cybis, Stockholm, Sweden), which also served as quality control for the measured tree-ring width (TRW) sequences. TRW sequences were visually and statistically synchronized with PAST-5 v. 5.0.610 (SCIEM, Vienna, Austria). Quality control was also performed by checking and correction. We calculated correlations between trees in CDendro and created a plot chronology that we compared to individual trees. Any tree ring width sequence that did not fit well into the plot chronology were corrected in CooRecorder and returned into data pool. In very rare cases with obvious tree ring width anomalies, cores were excluded from further processing. We paid attention to missing and false tree rings, as well as rotated sections of the cores. Individual TRW were standardized to remove long-term trends using a cubic smoothing spline of 67% with a frequency cutoff of 50% in R program's dplR library [24].

The expressed population signal (EPS) was used to assess the representativeness of a small sample relative to the signal of the total population. EPS values range from 0 to 1, with values greater than or equal to 0.85 considered high enough to indicate a common signal in the entire population [25]. This common signal may be associated with environmental or climatic factors; however, in many cases it is a climatic signal contained in the tree rings. In this study, EPS was used as a measure of common signal in site chronology.

TRW chronologies with detrended index, residual (RES), and standard (STD), were created for each site and tree species. Indexed TRW chronologies were compared to monthly mean temperatures, maximum temperatures, monthly sum of precipitation, and two drought indices using the bootstrapped resampling method and calculating the correlation coefficient in the treeclim library [26] of the R program. Temporal correlation was examined using monthly gridded temperature, precipitation, and drought data ($0.5 \times 0.5^\circ$ grids) from the CRU TS and CSIC database, available online in KNMI Climate Explorer (<http://climexp.knmi.nl>, accessed on 5 April 2023). Each tree-ring proxy was tested against monthly meteorological data or different combinations of seasonal variables to find the best possible combination of influencing climate variables. We analyzed the period from 1950 to 2016.

To show whether trees along the Carpathians respond similarly to meteorological data, correlation coefficients above 0.2 and below -0.2 were considered. If such a value was confirmed in at least three studied sites, we marked a particular month with a climate parameter as important for certain species.

The sites on different sides of the Carpathians were grouped into three clusters: southern group—sites 1, 2, 3; eastern group—sites 4, 5, 6 and northern site number 7. We calculated the average TRW for fir and beech by decades from 1950 on.

3. Results

3.1. General Climate Response

The expressed population signal [25] is high for both species (above 0.85; except for the fir chronology of site 1). This indicates that the calculation of the climate–growth relationship can be performed and that the results should have a reasonable statistical interpretation. Because of the high EPS value, we were able to perform a climate–growth analysis (Table 3).

Table 3. Expressed population signal (EPS) in site chronologies of beech and fir.

Site	<i>F. sylvatica</i>	<i>A. alba</i>
1	0.864	0.818
2	0.869	0.869
3	0.862	0.878
4	0.874	0.893
5	0.855	0.898
6	0.952	0.864
7	0.919	0.877

Above-average precipitation in July positively affected TRW of both species (Figure 2). Precipitation in June also had a positive effect on radial growth of beech. In contrast to fir, above-average September precipitation had a negative effect on beech radial growth. September growth is difficult to interpret because the growing season is over by this time.

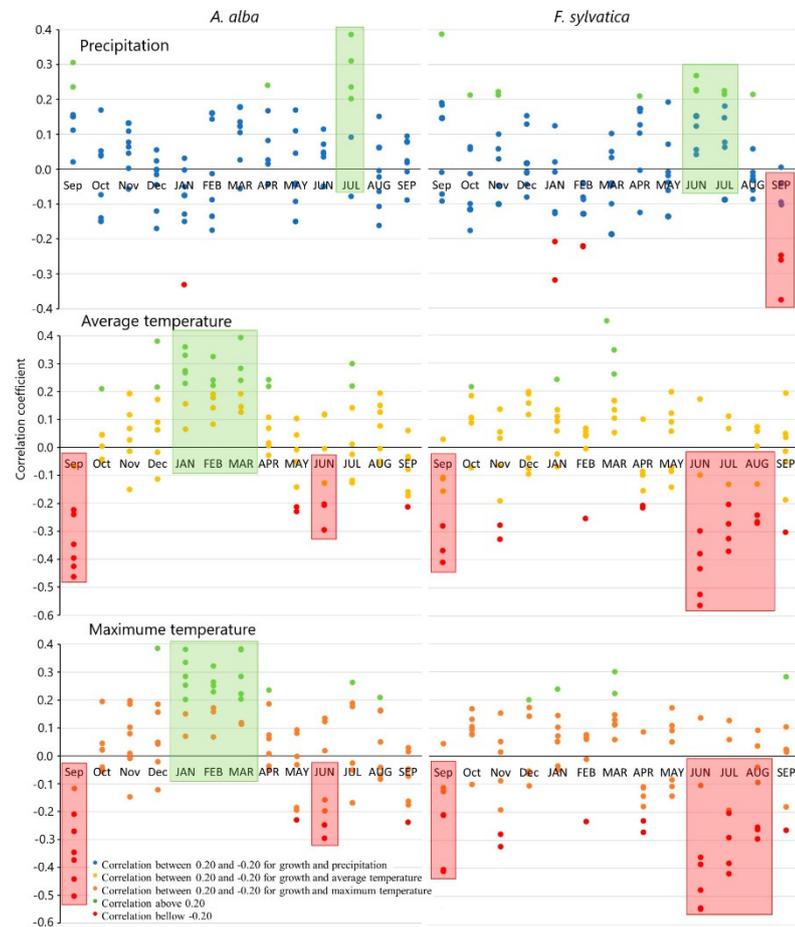


Figure 2. Correlation between fir and beech TRW and climate parameters (all sites). Transparent red and green rectangles mark months or group of months important for tree ring formation.

In both species, above-average temperatures in June and September of the preceding tree ring formation negatively affect TRW. Winter temperatures from January to March have a positive effect on fir growth. The correlation between the temperature during the September of the preceding tree ring formation and TRW is significant. Beech growth responds differently to climate than fir, although the trees were sampled at the same sites and in the same forest stands. Above-average temperatures in June have a more pronounced negative effect on beech growth, which continues during the summer in July and August. Unlike fir, no significant positive correlation on at least three sites between average or maximum temperature and TRW in beech was confirmed.

The influence of the average and maximum temperature for both species on radial growth of trees is similar. Winter temperatures from January to March have an even more significant positive influence on fir growth, and all other correlations with maximum temperature are similar to correlations with average temperature.

3.2. Comparison of Beech and Fir Climate Response between Southern, Eastern and Northern Carpathians

Our study showed different responses depending on species and location (Figure 3). Results are consistent with the response in Dinaric montane forests of fir and beech [20]. A more significant correlation between tree growth of both species and seasonal variables was observed on the eastern Carpathian sites, and a less or not significant correlation was observed on the southern sites. Fir on the northern site have even fewer significant correlations than on the southern sites, while beech on the northern site have more significant correlations than on the southern sites but fewer than on the eastern sites. Both species have the same number of significant correlations at the eastern sites, but fir has slightly more significant correlations at the southern sites.

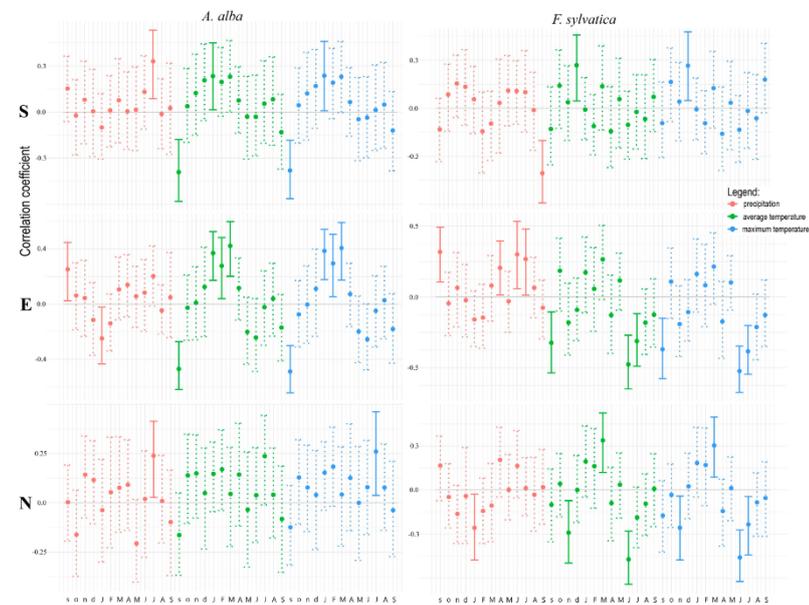


Figure 3. Correlation between fir and beech TRW and climate parameters for southern (S), eastern (E), and northern (N) sites. Solid vertical line shows significant and dotted vertical line insignificant correlations.

3.3. Growth Response of Beech and Fir in Time

Figure 4 shows average non standardized (age trend not removed) TRW of fir and beech for south, east, and north Carpathians by decades since 1951. We took a basic approach and are aware of the shortcomings of non-standardized data, but we wanted to show a growth trend (since the trees had similar ages) that standardization would otherwise cancel out. Beech on the southern sites shows consistent growth in time, while fir's growth is decreasing. Both tree species show an increasing average TRW on the eastern sites, which started decreasing in the last decade. Fir on the northern side shows the largest increase, while beech shows a relatively constant tree ring width for the last three decades. Compared to beech at southern sites, beech at eastern sites grew more slowly in the first decade (1951–1960) and at northern sites in the first two decades (1951–1970) (Figure 4, right panel). After 1961, beech began to grow better at eastern sites, followed by northern sites a decade later. After 1971, beech grew better on both the northern and eastern sites and continues to outgrow beech on the southern sites in the present.

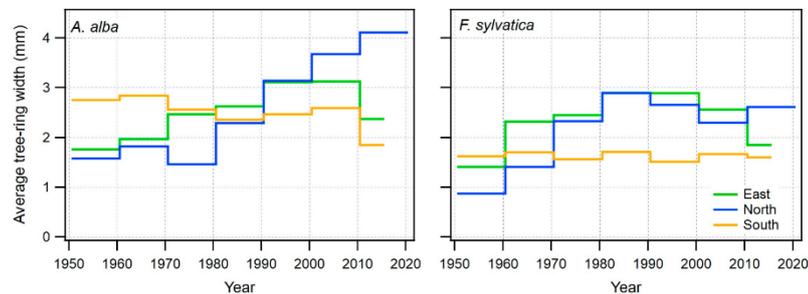


Figure 4. Average TRW of fir (left) and beech (right) by decades since 1950.

The decadal growth pattern of fir is similar to that of beech, but the average TRW of fir was higher on the southern sites compared to the northern and eastern sites until the decade 1981–1990, when the eastern sites began to grow better, and until the decade 1991–2000, when the northern sites also began to grow better (Figure 4, left). In the most recent decade (2011–2020), the southern and eastern sites have shown a decline in TRW, while TRW at the northern sites continues to increase.

3.4. Climate Response between South, East, and North Carpathians

Fir and beech responded differently on the studied sites over time (Figure 5). Fir on the eastern sites respond most consistently compared to the southern and northern parts, where the response became more pronounced after 1961, especially if we consider the above-average winter temperatures. On the southern sites, July precipitation significantly correlated with fir's radial growth since 1961, while on the eastern and northern sites, correlation became significant only after 1976. On the southern sites, only September precipitation had a negative effect on beech growth, while on the eastern and northern sites, above-average summer temperatures in both June and July negatively affected growth, which is becoming more pronounced over the years. Above-average March temperatures as well as June precipitation have positive effects on beech growth on the eastern sites.

When radial growth was compared with drought indices SPEI for 3 (SPEI-3) and 6 (SPEI-6) months, no patterns were apparent between sites and species (see Figure A1). At the southern sites, the drought index correlated significantly with the radial growth of fir only during the September of the preceding tree ring formation, while there was no correlation for beech. At the eastern sites, the drought index correlated positively with the radial growth of fir during September, October, and November, while it correlated negatively during February and March. The drought index in the September of the year preceding tree ring formation and the months October, November, June, July, and August correlated significantly with radial growth of beech. At the northern sites, fir radial growth had no correlation with either SPEI-3 or SPEI-6, while beech radial growth had a positive correlation with SPEI-3 in June and a negative in February and March and a negative correlation in March with SPEI-6.

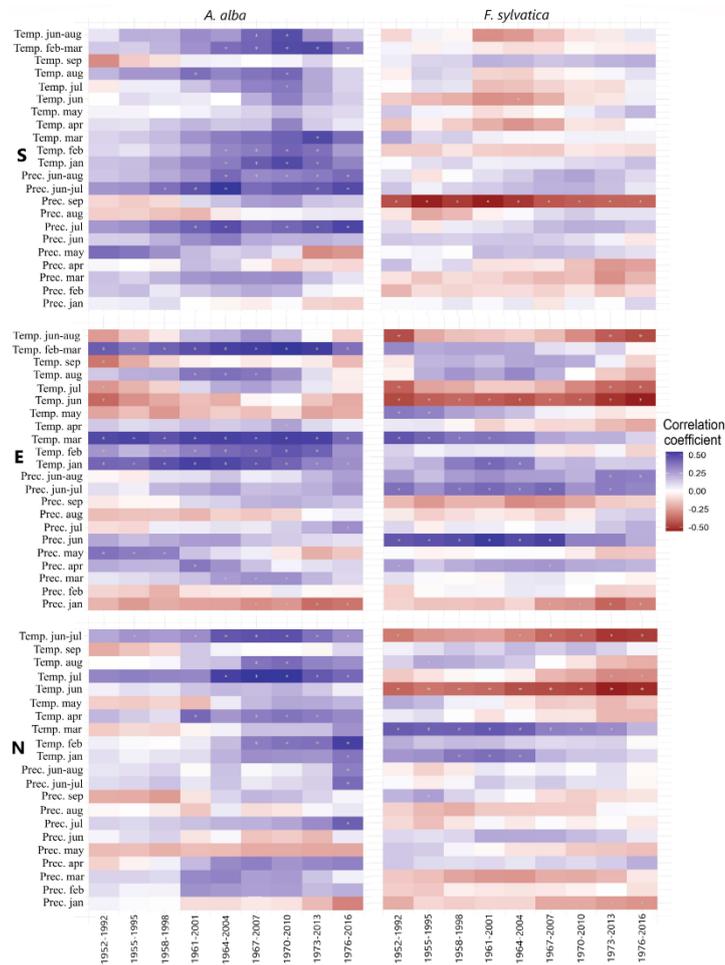


Figure 5. Temporal comparison between fir and beech TRW on different sites (southern (S), eastern (E), and northern (N) sites).

3.5. Comparison of Climate Response between Managed and Old Growth Forest

TRW in the old growth forest (site 3) was compared to TRW in the closest managed forest (site 4). The compared sites have different elevations of more than 200 m. Fir responded positively to precipitation in July at both sites and to precipitation in the September of the preceding tree ring formation in the managed forest. Precipitation in November of the preceding tree ring formation had a positive effect on beech growth at both sites, but only in the managed forest in June and July. Precipitation in September also has a negative effect on beech TRW in the old growth forest. Above-average temperatures in the September of the preceding tree ring formation had a negative effect on fir growth. In the old growth forest, above-average temperatures in June negatively affected fir growth, while in the managed forest, this is valid for May. In the managed forests, above-average winter temperatures in January, February, and March also had a positive effect on fir growth. Maximum temperatures had the same effect for fir and beech. In both the old growth and the managed

forests, above-average temperatures in September, June, July, and August had a negative effect on beech growth. The same response is seen in the old growth forest in April, and in the managed forest in September.

4. Discussion

We have achieved the stated objectives of the study, which were to determine the effect of climate on the growth of beech and fir along the geographic gradient, to determine similarities or differences between the two species, and to compare their responses over time to determine any changes in the growth response.

This study showed that a more significant correlation between tree growth and seasonal variables was observed on the eastern side of the Carpathian arc, while it was less evident or absent at sites on the southern side (sites 1, 2, 3). In comparable studies, the response to different climatic variables was decreasing or was absent on the south side of the studied transect due to genetic adaptability, phenotypic plasticity, or both [20]. The reason for the different response could also be that the eastern side of the Carpathians is affected by a climate with continental nuances and Baltic influences [27]. Fir and beech on northern sites react differently to meteorological parameters.

Above-average precipitation in July had a positive effect on radial growth in both species, and in beech also in June. In the course of climate change, we do not expect above-average precipitation in summer; on the contrary, we expect more summer drought.

Silver fir is an extremely demanding species regarding site conditions [28] and less tolerant to environmental change than the European larch or white pine [29,30]. In this study, we showed that fir responds negatively to above-average temperatures in the June and in September of the preceding tree ring formation, with above-average summer temperatures likely to become more frequent under climate change, while warmer winters increase fir radial growth. Above-average maximum winter temperatures from January to March have an even more significant positive influence on fir growth than above-average temperatures. Fir, as an evergreen tree species, enjoys warm winters, while beech, as a deciduous tree species, is not as affected by warm winter temperatures. Mihai et al. [31] showed high genetic variability within the silver fir studied in the Carpathians. They confirm that climate change could increase fir productivity at higher elevations, while climatically marginal environments and low elevations, such as edges of the Eastern Carpathians and the Banat region, may be exposed to higher risk [31] due to higher temperatures and lack of moisture.

Current fir populations have well-preserved genetic resources and relatively high genetic variability [32] but are threatened by pressure from herbivores, large-scale reforestation of old fir stands, inappropriate management practices [4], reductions in population density that can lead to fragmentation, self-pollination, genetic drift [7], and predicted climate change, and particularly increases in temperature and lack of precipitation [33].

Beech does not thrive in too-hot summers during the active growth phase, while this is not so pronounced in fir. Above-average temperature in the summer months had a negative effect on radial growth, so the higher summer temperatures may cause disturbances in beech growth. In the Eastern Carpathian region, changes in beech forests have been noted in recent decades [34], while old-growth beech forests in the Northwestern Carpathians were considered stable [35]. Martinez del Castillo et al. [36] predicted a substantial decline in beech growth across Europe, ranging from -20% to more than -50% by 2090, depending on the region and climate change scenario (CMIP6 SSP1-2.6 and SSP5-8.5).

A comparison of average TRW over decades shows the better growth of fir at the northern and eastern sites and a slight decrease at the southern sites. Beech demonstrates more consistent radial growth in the south, but its growth increases less than that of fir on the eastern and northern studied sites.

The effect of global warming becomes evident in comparison of fir and beech response in time. Since we wanted to know the recent growth trend due to climate change, we calculated the average TRW for fir and beech by decades from 1950 on. Fir on the southern side shows a decreasing trend in TRW over time, signaling that these sites are gradually

becoming unfavorable for fir. At the same time, the eastern and especially the northern sites are becoming more favorable for the growth of both species.

Of particular concern is the negative effect of above-average summer temperatures on beech growth, which is becoming more significant over the years, while July precipitation indicates an increasingly positive effect radial growth of fir. We may expect more frequent above-average summer temperatures and the absence of summer (July) precipitation, reflecting along both latitude and longitude; thus, future differences in the seasonal responsiveness of beech and fir may be expected. Extreme weather events and increasing average temperatures will also influence the future demographics of fir, i.e., to higher elevations and northward, as mentioned by Tinner et al. [37] and Klopčič et al. [38]. At the same time, a similar response of beech at the expense of fir and its general spread in Central Europe was observed by Šamonil [39], Vrška [40], and Janík [41]. Our results confirm the increasing dependence of trees on precipitation over the past century and coincide with the increasing drought events after 1951. The likely response of species to climate change will vary, affecting their competitiveness, their existence, and consequently, forest management decisions and measures [42].

In southwestern Europe, fir is more resilient to climatic extremes compared to other tree species [8]. At the same time, two fir populations have been distinguished in the Carpathian region: the eastern one, which is similar to the Balkan population; and the western one, which is less sensitive to summer droughts [8]. In the south-exposed areas of Eastern Carpathians, fir was the least sensitive of studied tree species [43]; its growth rate increased continuously and remained at a high level even in old individuals compared to Scots pine or Norway spruce. Fir growth was significantly and positively correlated with December temperatures and spring precipitation in April and May [43]. Although growing under the same conditions, European beech and silver fir have shown remarkably different growth patterns over the past half century. While fir has responded positively to recent warming, beech growth has declined at all examined sites, suggesting that fir is less susceptible to warmer and drier conditions than beech [8]. Long-term growth patterns and the growth–climate sensitivity of fir and beech did not differ significantly between managed and unmanaged forests.

5. Conclusions

Predicted forest productivity loss is mostly pronounced at the southern limit of beech's natural distribution, where drought intensity is expected to increase [36]. Our study confirmed different responses depending on species and location. A more pronounced response of tree growth to climate was observed on the eastern side of the Carpathians, while it was less pronounced or absent at the southern sites. Both beech and fir show better radial growth with higher precipitation in July and slower growth with higher average and maximum temperatures in June of the current year. Fir shows a positive correlation between radial growth and temperature in winter, while beech shows a negative correlation between radial growth and temperature in summer. In the 1951–1960 decade, average tree ring widths for fir and beech were largest at southern sites compared to other sites, but since 2011, the increase has been smallest at the southern sites and greatest at the northern sites. Despite the adaptive diversity of beech populations, the survival of beech and other temperate tree species in the future is uncertain as the rate, uniformity, and intensity of climate change vary among different sites. We may expect strong climate variability in the future in the southern forest ecoregion, while northern sites still exhibit stability and structural resistance. Temporal changes in species composition led to minor fluctuations in stand parameters that do not threaten the long-term coexistence of beech and fir [44]. Beech populations at the edge of the species' range have great adaptive potential, and their persistence appears to contribute to forest stability throughout Europe, which requires the adaptation of forest management and conservation policies [45–47].

Author Contributions: Conceptualization, P.C.A., T.L. and M.Č.; methodology, P.C.A., T.L. and M.Č.; validation, P.C.A., T.L. and M.Č.; formal analysis, P.C.A. and T.L.; investigation, P.C.A., T.L., M.H. and M.Č.; resources, T.L. and M.Č.; data curation, P.C.A., T.L. and M.Č.; writing—original draft preparation, P.C.A., T.L. and M.Č.; writing—review and editing, P.C.A., T.L. and M.Č.; visualization, P.C.A. and T.L.; supervision, M.Č.; project administration, M.Č.; funding acquisition, T.L. and M.Č. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The non-meteorological datasets presented in this study are available on request from the corresponding author. Publicly available meteorological datasets were analyzed in this study.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

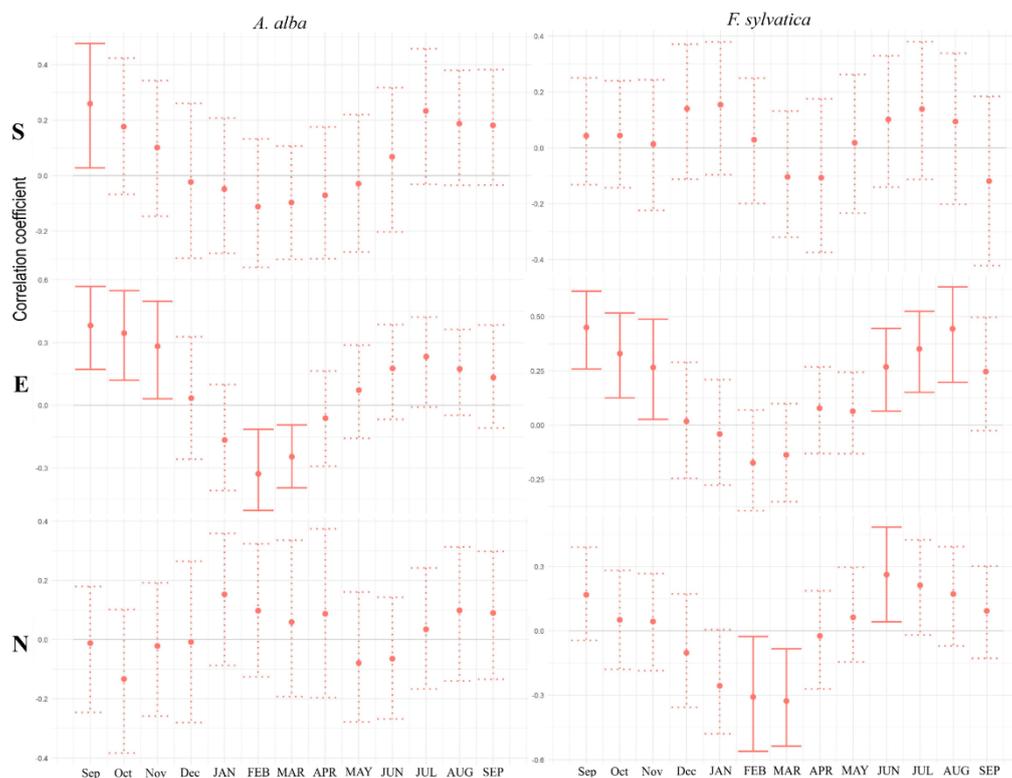


Figure A1. Correlation between fir and beech TRW and SPEI 3 indices for southern (S), eastern (E), and northern (N) sites. Solid vertical line shows significant and dotted vertical line insignificant correlations.

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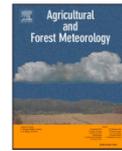
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2.4 PODNEBNE OMEJITVE RASTI NAVADNE BUKVE IN BELE JELKE VZDOLŽ KOMPLEKSA KARPATOV - NEDAVNO STANJE IN OBETI ZA PRIHODNOST

Kašpar J., Král K., Levanič T., Adamič P.C., Čater M. 2025. Climate growth limitations of European beech and silver fir along the Carpathian arc – the recent state and future prospects. *Agricultural and Forest Meteorology*, 361: 110323, <https://doi.org/10.1016/j.agrformet.2024.110323>

Izvleček: Temperaturne in padavinske spremembe vplivajo na podnebne omejitve rasti drevoja. Podnebne spremembe vplivajo na posamezne drevesne vrste različno, njihov vpliv se krajevno razlikuje. V Karpatih, ki predstavljajo obsežno gorsko območje Evrope, uspeva veliko bele jelke (*Abies alba* Mill.) in navadne bukve (*Fagus sylvatica* L.), ki se kljub podobnim ekološkim nišam na podnebje odzivata različno. Z raziskavo smo želeli določiti učinke podnebnih sprememb v Karpatih in napovedati prihodnjo dinamiko rasti jelke in bukve na tem območju. Izbrali smo osem lokacij vzdolž Karpatov na podobnih nadmorskih višinah in s podobnimi edafskimi razmerami ter dendrokronološko vzorčili in izmerili 15 dominantnih odraslih dreves obeh vrst. S procesnim modelom Vaganov-Šaškin smo modelirali debelinsko rast in določali spremenljivke rastne sezone ter temperaturne in vlažnostne omejitve. Kalibracija modela je zajemala obdobje od leta 1985 do 2015. Uporabili smo klimatološke podatke iz E-OBS-a za obdobje od 1985 do 2022, za napovedi od leta 2023 do 2050 pa smo uporabili prilagojen scenarij RCP 4,5. Z raziskavo smo potrdili tri različna območja v Karpatih, vsako z različnimi podnebnimi omejitvami za debelinsko rast: severno, jugozahodno in jugovzhodno območje. Na severnih območjih predstavljajo omejitve nizke temperature, na južnih območjih omejuje debelinsko rast nezadostna vlaga; njen primanjkljaj se proti vzhodu še stopnjuje. Jelka na severnih območjih kaže statistično značilne omejitve zaradi nizkih temperatur in se v primerjavi z bukvijo izraziteje odziva na klimatske parametre. Nasprotno kaže bukev večje omejitve rasti zaradi primanjkljaja vlage kot jelka, kar potrjuje boljšo prilagodljivost jelke na sušnejše razmere. Razlike med nedavnimi in prihodnjimi obdobji so bile v večini primerov statistično neznačilne. Opazili smo, da se po podnebnih omejitvah rasti severna rastišča postopno približujejo jugozahodnim rastiščem.



Climate growth limitations of European beech and silver fir along the Carpathian arc – the recent state and future prospects

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ABSTRACT

Changing temperature and precipitation patterns are shaping tree climate-growth limitations. The influence of climate change affects individual tree species differently, and can also differ across extensive geographical regions. The Carpathians, a vast mountainous area of Europe, host significant numbers of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.), both of which exhibit distinct climate-growth responses despite sharing similar ecological niches. Our study aims to discern the effects of climate change across Carpathians and forecast the future growth trajectories of silver fir and European beech within this area. We selected eight sites along the Carpathian arc at similar elevations and edaphic conditions, dendrochronologically sampled and measured 15 mature canopy trees of both species. Using the Vaganov-Shashkin process-based model, we simulated radial growth and computed growing season variables as well as temperature and moisture limitations. Model calibration covered the period from 1985 to 2015. E-OBS data were then used to simulate the period between 1985 and 2022, while the bias-corrected prediction of the RCP 4.5 scenario was utilized for predictions from 2023 to 2050. Our research revealed three distinct regions in the Carpathians, each with varying climate-growth limitations: the northern, south-western, and south-eastern areas. Northern sites primarily experienced limitations due to cold temperatures, while southern sites were predominantly constrained by insufficient moisture, intensifying eastward. Silver fir in northern sites exhibited significant low-temperature limitations and showed a higher response to climate conditions compared to European beech. Conversely, European beech consistently showed higher moisture-driven growth limitations than silver fir, indicating a better adaptability of silver fir to dryer conditions. Differences between recent and future periods were non-significant in most cases. However, there was a gradual convergence of northern sites to climatically limited growth in south-western sites.

1. Introduction

The extent of temperature and moisture limitation significantly influences tree growth (Tumajer et al., 2021), and contribute to the critical role of forests as the most important terrestrial carbon sink (Pan et al., 2011). However, the growth and physiological responses of different tree species to climate vary considerably (Čater and Levanič, 2019; Kašpar et al., 2021; Zang et al., 2014), among individual species as well as across large geographical regions (Bošela et al., 2016a; Gazol et al., 2015; Klesse et al., 2020; Martínez del Castillo et al., 2022). Climate change exacerbates these fluctuations by significantly altering the growth patterns of tree species (Kašpar et al., 2024b; Pretzsch et al.,

2023), affecting overall forest productivity (Boisvenue and Running, 2006; Ciaia et al., 2005; Trotsiuk et al., 2020) and potentially reshaping the future distribution of tree species (Buras and Menzel, 2019; Martín-Benito et al., 2010). Anticipating these changes requires comprehensive analyses allowing deeper insights into climate-induced limitations of tree growth across large geographic regions, encompassing both current and predicted climate conditions.

The radial growth of trees (hereafter growth) predominantly depends on the number of growing days given by favourable climate conditions (Etzold et al., 2022). However, the influence of individual climate factors and their combinations to tree growth at daily and sub-daily scales is non-linear (Tumajer et al., 2021; Wilmking et al.,

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2020). Therefore, advanced statistical methods must be used to elucidate the effects of individual climate factors. One of such method is the process-based Vaganov-Shaskin model (VS model, Vaganov et al. 2006). The VS model works exclusively with climatic inputs and simulates tree growth on the basis of daily temperature and precipitation data. Recent applications of the model include the simulation of cambial activity (Popkova et al., 2018; Tumajer et al., 2021) and the exploration of climate-growth limitations in both conifers (Tychkov et al., 2019) and broadleaves (Kašpar et al., 2021). By including predicted climate conditions, simulations by the VS model can be extended to the prediction of climate-induced growth limitations.

The Carpathian Mountains comprise a large mountainous area that stretches across Eastern Europe and crosses different biogeographical zones (Kholiavchuk et al., 2024). This region has experienced a notable rise in annual temperatures, with increases of 1.2–2.1 °C in the period 1961–2021 (Kholiavchuk et al., 2024), and is predicted to experience further significant increases in the future compared to pre-industrial levels (Kholiavchuk et al., 2024; Lewis et al., 2019). Silver fir (*Abies alba* Mill. – hereafter fir) and European beech (*Fagus sylvatica* L. – hereafter beech) are the two key tree species in the Carpathians (Kholiavchuk et al., 2024). Although they share a common ecological niche (Paluch, 2007), they differ in terms of physiological characteristics, growth timing, plasticity and climate growth limitations (Cater et al., 2024; Cater and Levanic, 2019; Etzold et al., 2022; Kašpar et al., 2024a, 2021; Martinez del Castillo et al., 2018; Zang et al., 2014).

Recent observations have found an unprecedented increase in the growth of fir, suggesting that it is well adapted to the current Central European climate conditions (Kašpar et al., 2024b, 2021; Zang et al., 2014). Conversely, fir in Mediterranean region and Southern Carpathians, fir has been reported to be susceptible to drought (Bošela et al., 2016a; Carrer et al., 2010; Gazol et al., 2015, 2019). Beech, in comparison with fir, has also shown accelerated radial and population growth at the end of the 20th and beginning of the 21st centuries (Janik et al., 2016), which can be attributed to increased nitrogen depositions and the reduced effects of sulphur depositions in the 1970's and 80's (Oulehle et al., 2022). However, recent studies suggest that beech has reached its limits due to increasing drought (Charru et al., 2010; Gazol et al., 2019; Gennaretti et al., 2020; Klesse et al., 2024; Martinez del Castillo et al., 2022; Muffler et al., 2020). Nevertheless, at higher elevations in Central Europe, both species show predominantly positive growth trends (Kašpar et al., 2024b; Trotsiuk et al., 2020), with an expected growth acceleration of beech at elevations above 1000 m in the future (Klesse et al., 2024).

In the Carpathians, the climate-growth responses of beech and fir show considerable variability (Adamić et al., 2023). This may be potentially attributed to genetic differences between the northern and southern populations (Bošela et al., 2016a), to the significant variance in climatic conditions across the geographical range of the Carpathians (Kholiavchuk et al., 2024) or to combination of both. In this study we attempt to extend the results of the study by Adamić et al. (2023) and explore growth limitations at the seasonal level in both recent (1985–2022) and future (2023–2050) periods. Based on recent observations (Kašpar et al., 2024b, 2021; Zang et al., 2014), we expect significant differences in the climate growth limitations of both beech and fir. Specifically, we expect a better adaptability of fir to dryer conditions and thus better adaptability to future climate conditions. To support this hypothesis, we modelled the upcoming climate-induced changes in beech-fir forests in different parts of the Carpathian arc, while first (i) calculating the climate-growth limitations of beech and fir based on recent data; then (ii) extending the simulations based on a future climate scenario to identify potential effects of climate change on long-term growth trends and climate limitations of both species; and finally (iii) quantify the growth limitations of beech and fir given by low temperature and low moisture along the north-south gradient of the Carpathians in the recent period and under projected climate conditions.

2. Methods

2.1. Study sites

Our study included eight sites (Fig. 1) located along a gradient spanning the Carpathians from the south-west through the south-east to the north-west. All sites were located above 800 m a.s.l. to amplify differences across the large geographical gradient in climate and environmental conditions. Each of these sites is characterised by a predominance of beech and fir in the mature canopy stand, and a minor share of Norway spruce (*Picea abies* (L.) Karst.) at some sites. The mean growing season temperature (April–September) in the period 1985–2015 varied from 4.6 (Arg) to 7.7 °C (Gor). Growing season precipitation totals varied from 538 (Vra) to 1095 mm (Bes). Climate data was taken from the E-OBS database (database version 27.0e; for details see Cornes et al. 2008; Figure A1). The detailed soil sampling was conducted by Darenová et al. (2024) classifying the soil type at all sites as Cambisol.

2.2. Data sampling and measurement

At each site, we selected and sampled from 14 to 17 healthy dominant mature canopy trees for each studied species (246 trees and 472 cores; FASY 120 trees, 234 cores; ABAL 126 trees, 238 cores). Dominant trees were selected to amplify the climate signal. All samples were collected using a Pressler borer at breast height (1.3 m) above the stem base. Each core was air-dried, mounted, and sanded with progressively finer sanding paper to increase the visibility of tree rings (Stokes and Smiley, 1996). After sanding, the cores were cleaned and digitized using an ATRICS system or WINDENDRO (Levanic, 2007; Régent instruments). Tree-ring widths were measured using CooRecorder (Cybis, Stockholm, Sweden) or WINDENRO software (Régent instruments) with a precision of 0.01 mm. Each tree-ring series was statistically and visually crosschecked using PAST-5 software (SCIEM, Vienna, Austria). In the case of synchronization errors, appropriate corrections were made.

Individual tree-ring width (TRW) series were detrended following Cook and Peters (1981), to emphasize the effects of climate on tree growth, as a prerequisite for the VS model (Vaganov et al., 2006), and remove long-term trends related to tree ontogeny (Cook and Peters, 1981). Most of selected forests are natural without direct human influence, so it was also necessary to minimize the effect of stand dynamics. To achieve this, we used a 67 % cubic smoothing spline with a 50 % frequency cut-off in the dplR library (Bunn, 2010) developed for the R statistical software (R Core Team, 2023). To isolate the climate effect of each growing season, we removed autocorrelation in the tree-ring width data (Cook and Holmes, 1997) by calculating the residual chronology for each site and species using pre-whitened values from an autoregressive model whose selection was based on the minimum Akaike criterion.

2.3. Climate data

Daily mean temperatures and precipitation totals spanning from 1985 to 2022 were obtained from the E-OBS database of gridded meteorological data with a 0.1° resolution across Europe (database version 27e; Cornes et al., 2018).

Predicted climate data covering the period from 2006 to 2050, based on the RCP 4.5 climate scenario, were obtained from the Swedish Meteorological and Hydrological Institute on behalf of the Copernicus Climate Change Service database accessible within Copernicus database (Berg et al., 2021). RCP 4.5 was selected as a reasonable representation of the ongoing climate development. Bias-corrected daily precipitation and temperatures data at resolution 0.11° were used. To address minor disparities between datasets, adjustments were made to the projected climate data to align it with the E-OBS dataset and minimize the differences. These adjustments were specifically based on the mean

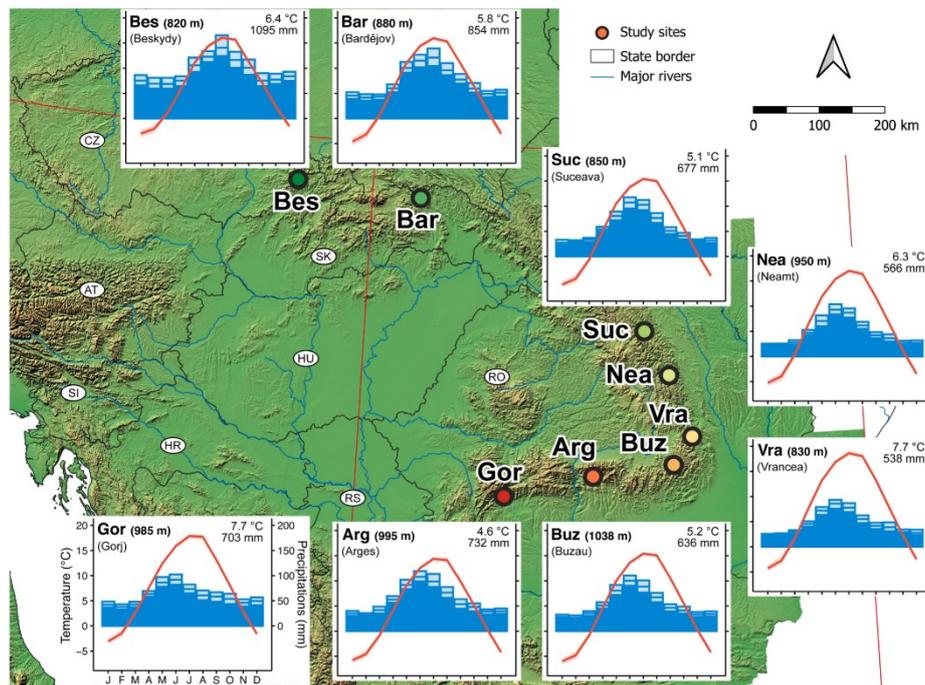


Fig. 1. The study area and climate characteristics of individual study sites. The mean annual temperature and precipitation totals for sites extracted from the E-OBS database are presented in the accompanying climadiagrams. Individual sites are colour coded. Individual colours are further used in the following figures to facilitate the connection between individual figures.

growing season temperatures and precipitation totals from the 2006–2022 period (Figure S3).

Datasets were combined for simulating tree growth. We utilized E-OBS data to simulate tree growth under recent climate conditions (1985–2022) and predicted climate data for simulating tree growth under future climate conditions (2023–2050).

2.4. Tree growth modelling

To simulate the growth limitations imposed by individual meteorological variables, the Vaganov-Shashkin model (VS model) was employed. This model is a purely climatic-driven, process-based model (Vaganov et al., 2006) designed to simulate tree-growth including limiting factors. The model incorporates a site's latitude to determine day length, and utilizes daily climate data, including mean temperatures and precipitation totals. Additionally, the model requires calibration using several metrics (Table A4, for detailed descriptions see Vaganov et al. 2006).

To calibrate the model, we utilized both climate and tree-growth data spanning from 1985 to 2015. This timeframe was chosen: (i) to avoid air pollution period in the 1970s, which could potentially skew the calibration of northern sites (Elling et al., 2009; Rydval and Wilson, 2012), (ii) to use climate data that are as reliable as possible, especially those from the southern part of study region, (iii) to ensure a consistent study period across all sites (the oldest samples were collected in summer 2016, when tree-rings were not yet completed), and (iv) to satisfy the requirements of the VS model for a minimum calibration period of 30-years. During the calibration process, we determined the most common thresholds for the individual climate metrics, adjusting them

against the climate data to achieve optimized correlations with the residual chronology (Figure A4). The calibration aimed to minimize the root mean square error and maximize the correlation coefficient and Gleichläufigkeit index (Eckstein and Bauch, 1969), ensuring the thresholds were within a realistic range as supported by the literature (see the final values in Table A4). A comparison of real and simulated curves for the period 1985–2016 is given in the supplementary material (Figure A5). Following calibration, the model was used to run simulations based on the combined climate datasets up to the year 2050.

The VS model calculates daily partial growth responses to temperature ($Gr_{T(d,y)}$) and soil moisture ($GM_{M(d,y)}$) for each day (d) and calendar year (y) through a pair of non-linear response functions. By imputing temperature and moisture data, the model employs a hydrological model to calculate soil moisture (Thornthwaite and Mather, 1955). These inputs are further translated into growth responses on a scale from 0 to 1 (Fig. 2A). The configuration of these response functions is individually tailored for each climate metric, defined by four parameters that establish minimal (T1 and M1), maximal (T4 and M4) and optimal (T2-T3 and M2-M4) temperature (T) and moisture (M) thresholds (Table A4). The model then applies Liebig's law of the minimum, where the lower value derived from the response functions is adjusted by the day length relative to the longest day ($Gr_{s(d)}$; Fig. 2B). Subsequently, the model calculates the daily growth rate and identifies the primary limiting factor for a given day (Fig. 2C-E; Vaganov et al. 2006). The model accumulates individual growth rates to estimate annual cumulative growth, which is then expressed as a percentage of complete growth (Fig. 2F).

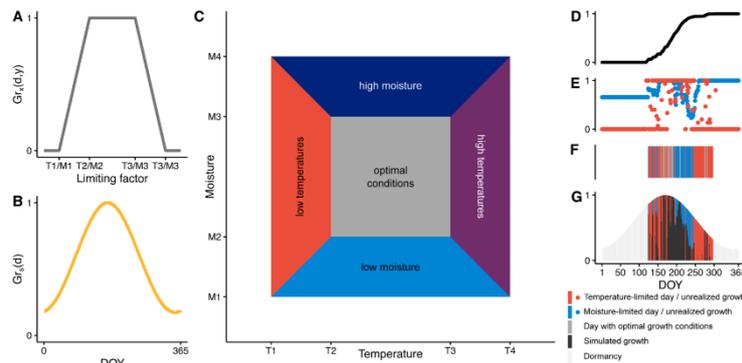


Fig. 2. The methodological approach used in this study for simulating climate-growth limitations. A – the response function's shape depicting the relationship between temperature/precipitation and partial growth response; B – the response function's shape illustrating the relationship between growth rate and day duration; C – computation of specific daily growth rates; D – daily growth rates with emphasis on the predominant limiting factor (low moisture and/or low temperatures; E – representation of the growing season's progression categorized by the dominant limiting factor; F – visualization of tree-ring formation throughout the growing season; G – simulation of realized growth and growth not realized due to insufficient temperature and moisture conditions.

2.5. Statistical analysis

To test differences between recent and future period for one species we used the Wilcoxon Signed-Rank test, while the differences between beech and fir in the same period were tested using the Kruskal-Wallis test. To investigate trends in the length and onset of the growing season, and changes in the number/proportion of days limited by temperatures or soil moisture, we constructed a generalized linear model (GLM), using the formula variable~calendar year. For proportion data (ranging from 0 to 1), quasi binomial regression model was used. For the growing season start, duration and simulated growth rates, we employed a gamma regression model with log link due to the non-normal and skewed distribution of the fitted data. The changes in time were derived based on predicted values. Trends along the geographical gradient of the Carpathians were assessed based on their position from the southwest to the southeast and to the north (see Fig. 1). For this we also utilized linear regression, with the explanatory variable (position) included as a spline with two degrees of freedom. To reveal similarities in climate-growth relationships between individual sites, a Principal Component Analysis (PCA) was performed using data on the proportion of temperature, moisture and unlimited simulated growth and growth not realized due to insufficient temperature and moisture conditions. The proportions were calculated from potential growth (Fig. 2G) and aggregated into decades to capture decadal trends. All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023).

3. Results

The growing season onset of fir and beech showed no significant differences between recent (1985–2022) and predicted (2023–2050) periods, except for beech at Vra and Bes, where growth started earlier (Fig. 3A). Projected growing seasons were generally longer ($p < 0.05$), except for beech at Arg and Buz (Fig. 3B). The proportion of temperature-limited days remained mostly constant ($p > 0.05$), with significant ($p < 0.05$) decrease at northern sites (Bes and Bar; Figs. 3C). In contrast, the proportion of moisture-limited days, increased significantly ($p < 0.05$) at half of the sites, notably for fir at Arg, Bes and Bar, and beech at Arg and Suc (Fig. 3D). Significant increases in simulated growth rates were observed at Arg and Nea for fir, and beech at Gor and Nea (Fig. 3E). There were no significant ($p > 0.05$) differences in the absolute number of temperature-limited days, except for beech at Vra and Nea (Figure A6A). The total number of moisture limited days

increased for fir at Arg, Suc, Bar and Bes and for beech at all sites except Nea and Bes (Figure A6B).

There were generally no significant differences between fir and beech in the start and duration of the growing season. However, significant ($p < 0.05$) differences were found in the proportion of temperature-limited (Gor, Vra, Nea, Bar and Bes) and moisture-limited (Gor, Buz, Vra, Nea, Suc, Bar and Bes) days, as well as in simulated growth rates, consistent across both periods (Fig. 3A-D). Fir showed lower moisture and higher temperature limitations, except at south-eastern sites (Vra, Nea, Suc; Figure A6A,B). The simulated growth of fir and beech differed at all sites except Buz and Suc (Fig. 3E).

Though non-significant, the change in the start of the growing seasons (1–2 days per decade), indicates a consistent earlier start of the growing seasons (Figs. 4A). Trends in the delayed cessation also resulted in a prolongation of the growing season by 3–5 days per decade, which was statistically significant for both studied tree species at all sites (Fig. 4B). This prolongation is reflected in a reduced proportion of temperature-limited days, particularly at south-western and northern sites (1.5–3.3 % and 1.5–2.0 % of days per decade for fir and beech; Fig. 4C). At south-eastern sites, trends varied, with changes up to ± 1.0 % per decade (Fig. 4C). In contrast, the proportion of moisture-limited days increased significantly for fir at Arg, Buz and Bar, and for beech at Arg, Bar and Bes, with the highest trend observed at northern sites for fir (3.4 % per decade; at Bes and Bar) and south-western sites for beech (2 % per decade; Gor, Arg, and Buz; Figs. 4D). The highest increase in simulated growth was observed at southern sites, decreasing northwards (Fig. 4G). These findings highlight site-specific variations in simulated annual growth between periods. Comprehensive details on the growing season onset, duration, climate-growth limitations, and simulated growth from 1985 to 2050 are in the supplementary material (Figure A7 and A8).

The PCA confirmed a shift from temperature-limited to low moisture limited growth, noting that 2011–2020 was the driest period. Based on the PCA, sites were clustered by climate-growth limitations (Fig. 5A and A9): (i) low temperature limited sites (fir at the northern sites - Bes, Bar, plus Gor and beech at Bes and Gor); (ii) low moisture limited sites (south-eastern sites - Suc, Nea, and Vra); and (iii) sites with mixed limitations (southern sites, close to 0 at both PC axes; for fir Arg and Buz and for beech Arg, Buz and Bar).

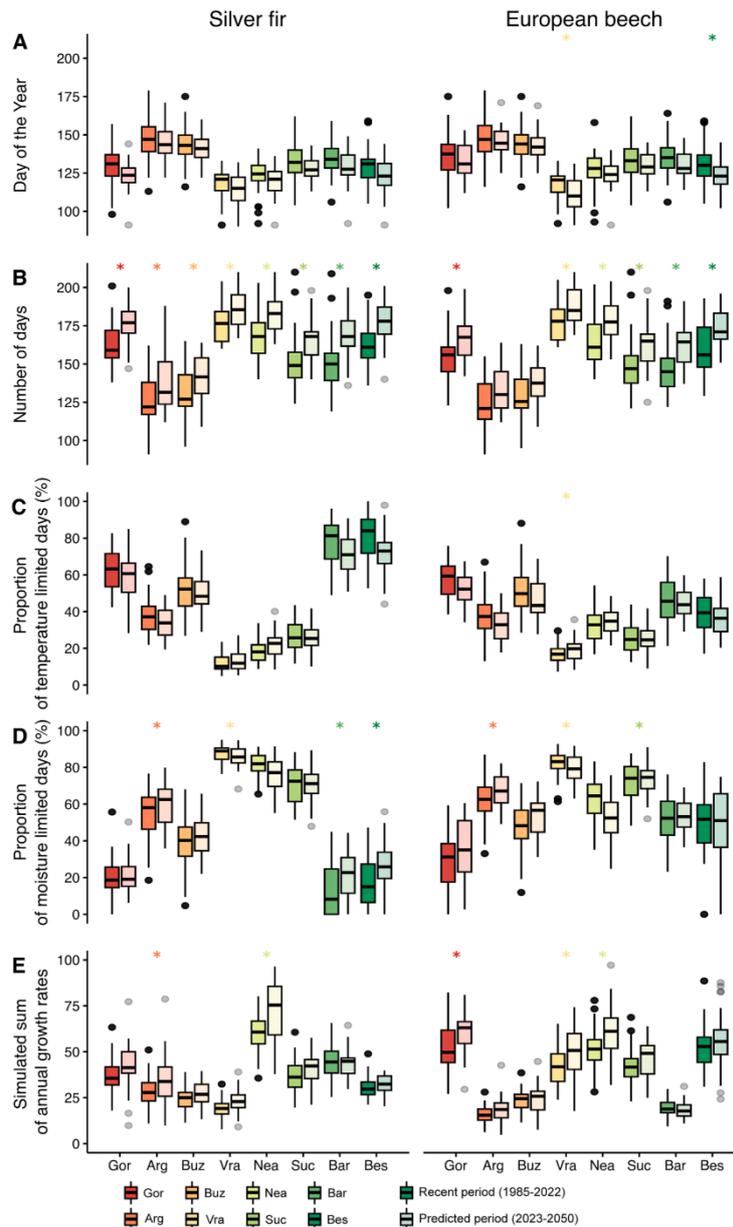


Fig. 3. Growing season parameters and climate growth limitations at individual sites and tree species in the recent and predicted periods. A – start of the growing season; B – duration of the growing season; C – percentage of the growing season limited by temperatures; D – percentage of the growing season limited by moisture conditions; E – simulated growth rates. The boxplots denote 25th, 50th and 75th percentiles. Whiskers illustrate “reasonable” minimum and maximum, and dots represents outliers. For each site, the boxplot with the darker colour depicts the recent period (1985–2022) and the boxplot with the lighter colour the predicted period (2023–2050). Asterisks denote statistically significant differences ($p < 0.05$) between recent and future periods.

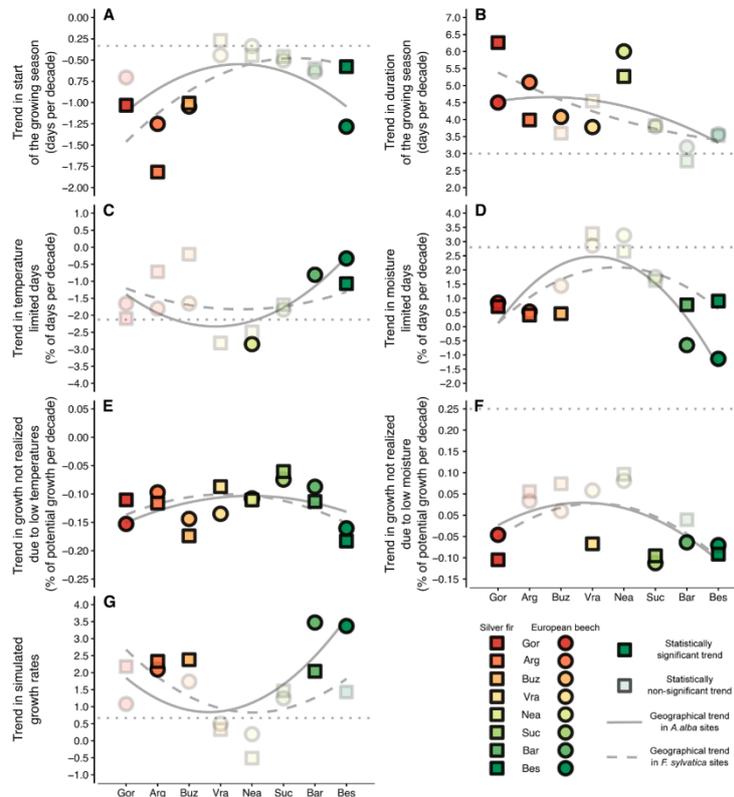


Fig. 4. Trends (slopes of linear regressions in the study period) in growing season parameters and climate-growth limitations of fir and beech at individual sites. All sites are ordered based on their geographical positions (see Fig. 1). A – start of the growing season; B – length of the growing season; C – proportion of the growing season limited by temperatures; D – proportion of the growing season limited by moisture; E – growth not realized due to temperature conditions; F – growth not realized due to moisture conditions; G – simulated growth rates.

4. Discussion

Our study, based on the climate-growth limitations and timing of the growing season determined by the VS model, revealed significant differences in the climate-growth limitations of fir and beech across the Carpathians. In the south-eastern regions, we observed higher recent growth limitations due to low moisture conditions. Towards the future, the lengthening of the growing season and changing proportion of growing days limited by low moisture and low temperature will likely lead to a gradual convergence of climate-growth limitations across the Carpathians. This shift is primarily driven by an increased proportion of the growing season being limited by drought, particularly in the northern compared to the south-western or south-eastern regions. In both cases, the decreasing number of temperature-limited days is expected to promote growth despite increasing moisture limitations (Bošela et al., 2023; García-Duro et al., 2021). Still, the differences between northern and south-eastern and south-western sites might persist through 2050.

4.1. Growth limitation patterns across the Carpathian arc

For fir we found three groups of sites exhibiting similar climate-

growth responses along the Carpathians (Fig. 5A), confirming the previous result of Adamić et al. (2023). In the northern part (Bes and Bar) and in the Gor site, growth is primarily limited by low temperatures, while the proportion of the growing season limited by low moisture increased towards the south-eastern sites. Similar differences were found by Bošela et al. (2016a), who attributed this to differences in the genetic predispositions of fir given by the different post-glacial origin of northern and southern fir populations. During the 1985–2015 period, however, the proportion of the moisture-limited growing season in the northern sites and Gor remained below 40 %, which is significantly lower than in both southern regions (Fig. 6B). The increasing part of the growing season limited by low moisture rather than by low temperatures is behind the increased growth detected in the northern Carpathians and Central Europe in the last decades (Bošela et al., 2018; Kašpar et al., 2024b). In addition, southern fir sites (Arg and Buz) showed a similar climate growth limitation to Bar and Bes, suggesting that fir in the Carpathians reflects the difference in the proportion of temperature- and moisture-limited days during the growing season rather than its population differences. Therefore, the distinct response compared to southern sites cannot be fully attributed to different genetic predispositions as suggested by Bošela et al. (2016a), but is rather a manifestation of phenotypic plasticity to local conditions (Leites and Benito Garzón,

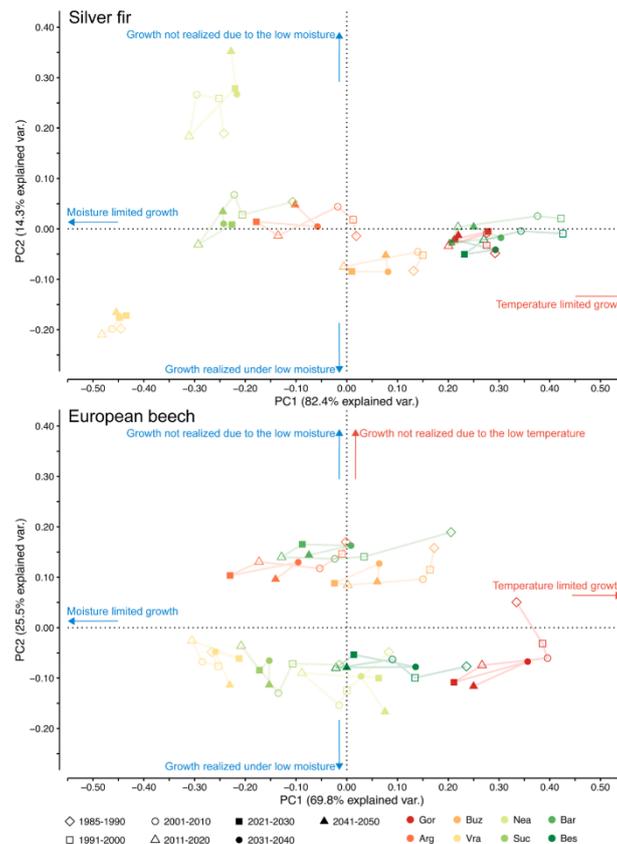


Fig. 5. Principal Component Analysis of growth limitations at investigated sites A – fir and B – beech.

2023).

In contrast to fir, beech displayed a more uniform growth response across the gradient (Fig. 5B), with unclear clusters delimited from both a statistical and geographical perspective. In addition, the individual PC axis correlated mainly with moisture limitation, indicating a high susceptibility of beech to low moisture (Gennaretti et al., 2020; Hackett-Pain et al., 2016; Muffler et al., 2020). This is also supported by a decreasing TRW due to an increasing proportion of growing days limited by low moisture (Fig. 6B). The lower phenotypic plasticity of beech leads to a concentration of its growth into a relatively narrow time window during the year (Etzold et al., 2022; Martínez del Castillo et al., 2018), which has ultimately resulted in decreasing growth rates in the recent period (Figure A10). Unlike fir, this trend remains consistent across the entire Carpathians, so this characteristic might disadvantage beech in mutual coexistence with fir, as indicated by other studies (Kašpar et al., 2021; Zang et al., 2014).

Our data did not confirm an accelerated growth of either fir (Figure A6C; except at the northern sites Bar and Bes) or beech in the recent period, in contrast to some other studies (Bošela et al., 2018, 2016a, 2016b; Gazol et al., 2015). Rather, our study showed that growth trends were mostly insignificant ($p > 0.05$ in the case of fir) or even negative (in the case of beech; Figure A10B). In the case of fir at the northern sites, the unprecedented growth increase in recent decades can

be explained by recovery from high sulphur depositions in the 1970's and 80's in Central Europe, to which fir was the most sensitive (Hánová, 2020; Oulehle et al., 2022; Rydval and Wilson, 2012).

4.2. Growth of fir and beech in the Carpathians in future climate conditions

When comparing the recent and predicted periods, the main differences resulting from the VS model were the lengthening of the growing season and increasing proportion of growing season days limited by low soil moisture at the expense of the proportion of temperature-limited days. Since our study sites were located at higher elevations, with low temperature as the main limiting factor (except at south-eastern sites), the increasing temperatures predicted by the RCP 4.5 scenario resulted in increasing growth rates. This has also been observed and reported in other studies (Klesse et al., 2024). The VS model also showed that most of the growth is realised at the beginning of the growing season (Figure A11), when expected adequate moisture conditions favour growth (Lindner et al., 2014). This should ultimately mitigate the drought limitations expected in the later part of the growing season (Figure A11). On the other hand, the growing season starts during days with a shorter photoperiod, which may not allow for the mitigation of potential growth depressions in the later part of the growing season

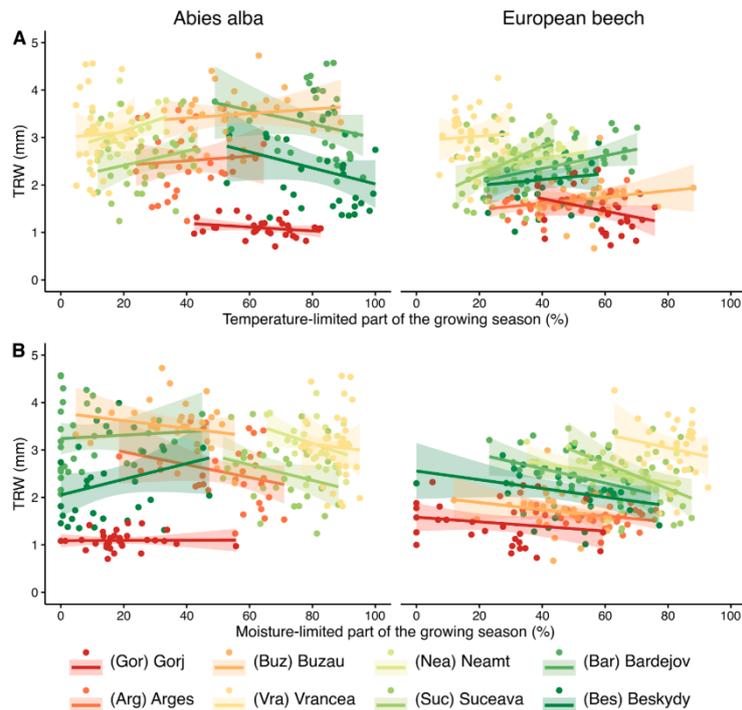


Fig. 6. Relationships between TRW and the proportion of growing season limited by climatic factors. A – TRW and the proportion of temperature-limited days; B – TRW and the proportion of moisture-limited days. Lines represent linear regressions between TRW and the proportion of temperature/moisture-limited growing seasons. The confidence interval represents the standard error. Individual sites are colour coded.

(Jezfk et al., 2021; Rossi et al., 2016). Increasing winter temperatures are also anticipated to promote growth due to reductions in the risk of winter embolism (Gazol et al., 2019; Principe et al., 2017; van der Maaten, 2012), but an earlier start of the growing season significantly increases the probability of late frost damage (Marquis et al., 2022), which can be more critical for beech than for fir (Fischelli et al., 2014). Consequently, growth performance during the middle of the growing season is expected to be significantly influenced by species-specific growth plasticity and their adaptability to projected future climate conditions (Kašpar et al., 2021; Martínez del Castillo et al., 2018; Zhang et al., 2024). Based on current knowledge, the above-mentioned constraints are more relevant for beech than for fir. Therefore, forthcoming climate conditions in the Carpathians are anticipated to favour fir over beech (Figure A10), as indicated elsewhere in Europe (Buras and Menzel, 2019; García-Duro et al., 2021; Kašpar et al., 2021; Zang et al., 2014).

Considering the upward trends in days limited by low moisture, there appears to be gradual convergence of climatic limitations affecting both beech and fir population across northern and southern Carpathians, which is slowly diminishing the disparities between these two regions; see also (Adamić et al., 2023; Bošel'a et al., 2016a). Based on the medium climate scenario (RCP 4.5), it is plausible that after the 2040s the northern sites will experience climate-growth limitations similar to those observed in the south-western sites in the 1990s. However, this estimation may be accelerated due to faster warming trends as reported by the IPCC (2022). Notably, our simulations do not account for unprecedented drought events like those experienced in 2000, 2003 and

2018 (Buras et al., 2020), which could potentially induce substantial growth reductions or alter growth trends (Charru et al., 2010; Kašpar et al., 2024b). If we consider the differences between studied sites, especially when the proportion of the moisture-limited part of the growing seasons of fir exceeds 40% (Fig. 6B), the marked acceleration of growth acceleration of fir observed in the northern Carpathians at the beginning of the 20th century will continue. Similarly, trends in beech, which faces moisture limitation during the growing season, show a steadily decreasing growth rate with an increasing proportion of moisture-limited days (Fig. 5D), which will likely lead to growth declines across the Carpathians (García-Duro et al., 2021; Gennaretti et al., 2020; Martínez del Castillo et al., 2022).

Recent studies have reported a decoupling of tree growth between lower and higher elevations (Kašpar et al., 2024b; Trotsiuk et al., 2020). Our study sites were mostly located above 800 m (Table A1), which is slightly below the expected elevation (1000 m ASL) where there is a reduction of beech growth in south-eastern Europe (Klesse et al., 2024). On the other hand, most of our study sites (except Vra, Nea and Gor) are colder than the 6 °C threshold suggested by Klesse et al. (2024). Still, based on the results calculated for recent period, beech in the Carpathians will likely have lower growth rates at elevations around 850 m a. s.l. in the future.

4.3. Limitations of the study

The determination of a growing season's start, length and the growth rates of fir and beech are theoretical values derived from input climatic

variables (Vaganov et al., 2006). However, the VS model simulated an increase in growth rates at both the beginning and end of the growing season (Figure A11). This leads to several significant challenges for such a model: the short photoperiod (Ježik et al. 2021; Rossi et al. 2016; Huang et al., 2023), growth plasticity inherent to individual tree species (Kašpar et al., 2024a; Leites and Benito Garzón, 2023; Martínez del Castillo et al., 2018), growth convergence of the onset of growing season due to increasing winter temperatures (Zhang et al., 2024) and, particularly for beech, the interplay of physiology (Klein, 2014). For that reason, predicting the extent to which specific tree species will be able to capitalize on this potential becomes difficult. On the other hand, studies based on recent data (Kašpar et al., 2021; Popkova et al., 2018; Tyehkov et al., 2019) showed valid results when compared with actual data.

Another limitation of our study is that it focuses on dominant trees, to capture the effect of climate on present and near future forest, and omits young individuals, whose reactions might slightly differ from older ones. For instance, young fir in the Carpathians appears to be more sensitive to low moisture conditions when compared to beech as well as young fir in the same light conditions along in Balkan region (Cater et al., 2024).

Future climate scenarios used in our study did not account for extreme climatic events such as significant (long lasting) droughts, whose frequency and severity have increased in the Carpathians and elsewhere in the Europe in recent decades (Kholiavchuk et al., 2024) and are expected to continue increasing in the future (Lindner et al., 2014; Prudhomme et al., 2014; Spinoni et al., 2018). Intense droughts may cause significant growth depressions lasting several years (Buras et al., 2020) or disrupt growth stationarity in both trajectory and magnitude (Kašpar et al., 2024b; Tumajer et al., 2023). However, climate projections simulated more precipitation events (compared to E-OBS data in period 2006–2015; Micu et al., 2014), which might lead to over-estimations of simulated growth, particularly for beech, which is notably susceptible to prolonged droughts (Gennaretti et al., 2020). Consequently, the most significant factor changing over time seems to be the rising temperature that escalates evaporative demands (Spinoni et al., 2015). Therefore, in our attempt to carefully interpret our results within the context of changing climate and climate-growth limitations, we presented our results as long term linearly trends. We believe that this has allowed us to project likely trends in growth limitation for both fir and beech in the Carpathians over the next few decades.

5. Conclusion

In recent times, climate growth limitations in the Carpathians have delineated three distinct regions. The northern part has experienced significant limitations given by low temperature, whereas the south-western and south-eastern regions have encountered limitations from low moisture, intensifying towards the east. Notably, differences in the temperature limitations of fir across the Carpathians (especially significant in the north) have highlighted the distinct response of fir to drought conditions between northern and southern regions. Increasing moisture limitations at northern sites have paradoxically led to increased growth rates due to the decreasing temperature limitations that have hindered growth at northern sites. However, these differences are expected to be reduced due to the anticipated convergence of climate-growth limitations between the northern and south-western parts driven by climate change. Nonetheless, distinctions among these clusters are anticipated to persist into the future under the RCP 4.5 scenario. Present trends in the climate-growth limitations of beech and fir suggest that the northern sites will exhibit climate limitations similar to what the south-western part underwent in the second half of the 1980s (when our model simulation started) during the mid-21st century. Under the RCP 4.5 scenario, our results suggest increased growth rates of beech and fir in future decades, likely due to the prolonging growing season. Beech exhibited consistently more pronounced moisture limitations across the entire Carpathians, indicating a potentially higher

susceptibility to future droughts due to its limited growth plasticity compared to fir, which appears to show better adaptability to future conditions, particularly in the north.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT 4.0 in order to improve grammar. After using ChatGPT 4.0, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article. The final text was also checked by a native speaker.

CRedit authorship contribution statement

Jakub Kašpar: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Kamil Král:** Writing – review & editing, Project administration, Funding acquisition. **Tom Levanič:** Writing – review & editing, Funding acquisition, Data curation. **Pia Caroline Adamič:** Writing – review & editing. **Matjaž Cater:** Writing – review & editing, Project administration, Funding acquisition.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2024.110323](https://doi.org/10.1016/j.agrformet.2024.110323).

Data availability

Data will be made available on request.

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2.5 VPLIV PODNEBNIH SPREMEMB NA LESNO-ANATOMSKE ZNAČILNOSTI JELKE IN BUKVE IZ TREH LOKACIJ V KARPATIH, ROMUNIJI

Adamič P.C., Prislán P., Levanič T., Jevšenak J., Kašpar J., Čater M. 2025. The impact of climate change on anatomical characteristics of silver fir and European beech wood from three sites in the Carpathians, Romania. *Forests*, 16, 9: 1497, <https://doi.org/10.3390/f16091497>

Izvleček: Strukturne prilagoditve lesa na okoljske dejavnike imajo odločilno vlogo pri določanju hidravličnih in mehanskih lastnosti lesa ter posledično vplivajo na konkurenčnost in obstoj jelke in bukve. Analizirali smo vpliv podnebnih razmer (temperature in količine padavin) na določenem območju na širino branik in lesno-anatomske značilnosti jelke in bukve v Karpatih. Vzorce smo odvzeli iz treh jelovo-bukovih sestojev (lokacij) na Karpatih z različnimi podnebnimi režimi. Za obdobje od leta 1980 do 2016 smo izdelali kronologije povprečnih širin branik (MRW), povprečne površine celic (MLA), gostote celic (CD), relativne prevodne površine (RCTA) in za jelko tudi srednje debeline tangencialnih celičnih sten (CWTTAN). Primerjave povprečnih širin branik in lesno-anatomskih značilnosti ter korelacije s podnebnimi dejavniki – najmanjše in največje dnevne temperature ter vsote padavin iz dnevnih podnebnih podatkov E-OBS – kažejo na razlike med proučevanimi lokacijami. Bukev in jelka se na izbranih rastiščih odzivata na podnebne parametre različno, kar kaže na prilagojenost lokalnim razmeram. Zlasti bukev se je pokazala kot bolj občutljiva, saj ima težave s pretoplimi poletji, medtem ko je jelka odpornejša. Študije rasti in lesne anatomije so bistvene za razumevanje plastičnosti jelke in bukve v različnih okoljskih pogojih in predstavlja prvi korak k napovedovanju njunih odzivov na prihodnje podnebne scenarije.



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Article

The Impact of Climate Change on Anatomical Characteristics of Silver Fir and European Beech Wood from Three Sites in the Carpathians, Romania

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Abstract

Structural adaptations of wood to environmental conditions play a crucial role in shaping its mechanical and hydraulic properties, which are vital for the performance and survival of fir and beech. In this study, we investigated how site-specific climatic conditions influence tree-ring widths and wood-anatomical traits of fir and beech in the Carpathians. Increment cores were collected from three forest stands across the Carpathians, each characterized by distinct climate regimes. We developed chronologies for mean tree-ring width (MRW), mean lumen area of vessels/tracheids (MLA), cell density (CD), relative conductive tissue area (RCTA), and, for fir, mean tangential cell wall thickness (CWTIAN), covering the period from 1980 to 2016. By comparing MRW and wood-anatomical traits with climatic variables—daily minimum and maximum temperatures and daily precipitation sums from E-OBS climate data—we identified clear differences among the three sites. The relationships between tree-ring widths and wood-anatomical traits varied between fir and beech, reflecting species-specific responses to local climate conditions. Notably, beech appeared more sensitive to warm summer temperatures, while fir was comparatively less affected. Evaluating the variability in radial growth and wood anatomy is essential for understanding the plasticity of fir and beech under diverse environmental conditions, and represents a first step toward predicting their responses to future climate scenarios.

Keywords: *Abies alba*; *Fagus sylvatica*; dendrochronology; radial growth response; wood anatomy



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1. Introduction

The anatomy of xylem provides insights into the allometry and ecophysiological performance of trees that cannot be inferred from conventional parameters such as ring width or wood density [1]. Although general anatomical features are species-specific and

genetically determined, their actual characteristics vary across different parts of the xylem rings due to diverse external influences [2]. Trees respond to environmental conditions through structural modifications in the wood, which significantly affect their mechanical and hydraulic properties, thereby influencing tree performance and survival [3,4]. While numerous studies have examined the impact of environmental factors on the radial growth of fir and beech, limited knowledge exists regarding how temperature and precipitation variability influence xylem structure in these species [5–8].

Growth dynamics under drought conditions often manifest as reduced tree-ring width, resulting from reduced cell division rates or premature cessation of cambial activity [9–12]. Anatomical changes in the wood, such as alterations in cell lumen and wall morphology, also occur under drought stress [13,14]. However, the implications of these anatomical changes for wood structure and tree function under increasing climate variability remain largely unexplored.

The Carpathian Mountains represent one of Europe's most complex mountain landscapes, shaped by the interplay of numerous environmental factors. Global warming presents significant challenges to mountain ecosystems and their associated services, as these regions are particularly vulnerable to climate change. This underscores their importance in environmental research as sensitive indicators of biodiversity shifts [15,16]. During the twentieth century, mountain ecosystems experienced above-average warming [17], with projections indicating continued warming and increased climate extremes. According to Micu et al. [16], the most pronounced temperature rise is expected during summer, with most Carpathian regions anticipated to be 2.5–3.0 °C warmer in 2021–2050 compared to 1961–1990. In terms of precipitation, winters are projected to become significantly drier, while autumns may experience increasing trends.

European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) are expected to remain dominant tree species in mid- and high-elevation European forests [18]. Despite its ecological plasticity and functional adaptability, beech is sensitive to drought, as evidenced by studies conducted in southern Europe [19]. Recent research using provenance trials has investigated the variability of beech anatomical traits across Europe [5,20]. Climatic conditions influence not only ring width and vessel size in beech, but also vessel arrangement. Humid conditions promote wider rings and larger vessels, whereas dry conditions have the opposite effect. Under high precipitation, vessel area typically increases in the early part of the tree-ring, remains stable, and then declines sharply toward the end. In contrast, under water deficit, beech wood exhibits a semi-ring porous structure, with vessel area peaking at approximately 25% of the ring width before rapidly decreasing [9]. Consequently, projected changes in temperature and precipitation under climate change scenarios are expected to affect both tree-ring width and wood structure in beech [7].

Silver fir, a key conifer species in European mountain forests, is prevalent in cold temperate zones [21]. Its ecotypes exhibit considerable variation in resistance to frost, drought, and shade [17]. Unlike beech, the anatomical responses of fir remain relatively understudied. Larysch et al. [22] found that fir was unaffected by spring drought and demonstrated a strong capacity to respond rapidly to improved growing conditions, highlighting the plasticity of wood formation in conifers under extreme environmental stress [23–25]. However, summer drought severely disrupted cell enlargement, with rates significantly reduced. Prolonged drought negatively impacted cell wall area throughout the growing season, with both wall thickening and duration declining for several weeks. Drought conditions also led to reduced cell production, limiting the conductive area for water transport, and resulting in smaller cells due to low turgor pressure [22].

Under normal climatic conditions, the formation of typical tree-ring structures in conifers is only marginally influenced by climate, suggesting a strong developmental

control over xylogenesis [26]. Cuny et al. [27] introduced new quantifications and mechanistic models of wood formation kinetics that explain tree-ring structure formation in Norway spruce, Scots pine, and silver fir. Similar studies on other conifers, such as those by Ziaco et al. [28], demonstrated that drought significantly affects cell enlargement and final tracheid size in pine and spruce species. Tracheid morphogenesis—comprising cell enlargement and wall thickening—occurs sequentially during the growing season and is influenced by climatic conditions in successive periods, indicating that distinct morphogenetic mechanisms govern different tracheid traits [29].

Warming tends to increase lumen area in conifers, enhancing water transport efficiency but also elevating the risk of cavitation, whether induced by drought in summer or freezing in winter. The combined effects of warming and elevated CO₂ alter tracheid dimensions, with more pronounced changes in latewood, thereby affecting wood density, mechanical support, and stem water-holding capacity [30]. Studies on spruce and beech confirm high interannual variability and sensitivity of xylem ring width to temperature and precipitation, with species- and site-specific responses. Water availability emerged as the most critical factor influencing tissue- and species-specific responses to local weather conditions [31].

This study builds upon a broader research initiative investigating the responses of fir and beech to climate variability in the Carpathians [32–35]. In this study, we focus specifically on wood-anatomical adaptations in both species, providing an additional perspective on how fir and beech respond to environmental conditions in this region. The primary objective is to examine the influence of site-specific climatic factors—particularly temperature and precipitation—on wood-anatomical traits in fir and beech.

We anticipate that fir and beech will exhibit distinct responses to climatic variables across the selected sites. Previous research has emphasized beech's vulnerability to drought, whereas conifers typically adopt more conservative water-use strategies and possess xylem anatomical characteristics—such as smaller conduit diameters and thicker cell walls—that confer greater resistance to drought-induced cavitation [36]. Accordingly, we hypothesize the following: (H1) wood-anatomical traits (e.g., cell size, cell wall thickness, density, and distribution of water-conducting cells) differ between the selected sites for both species; (H2) relationships between tree-ring width and wood-anatomical traits are consistent across sites for each species; (H3) fir and beech respond differently to climatic variables, with fir exhibiting greater drought tolerance than beech.

Evaluating the variability in radial growth and wood-anatomical traits across different sites is essential for assessing the plasticity of these species under diverse environmental conditions. This represents a critical step toward predicting their responses to future climate scenarios.

2. Materials and Methods

2.1. Study Site and Climate Data

In the Carpathian Mountains, three sites with mature fir–beech stands—Gorj, Vrancea, and Suceava—located between 830 and 985 m above sea level, were selected and analyzed. All sites are situated in managed forests with natural regeneration of both species and represent optimal growing conditions for silver fir and European beech. The favorable ecological conditions of these areas are reflected in their rich biodiversity and high diversity of plant and animal species [37]. Positioned at the intersection of Atlantic and continental climate zones, the region is predominantly influenced by a western climate type characterized by anticyclonic weather patterns [38]. For detailed information on weather conditions, study sites, and sampled trees, see Figure 1 and Table 1. Geologically, flysch dominates the eastern and outer Western Carpathians, while crystalline and volcanic rocks are typical of the inner band, and metamorphic rocks prevail in the Southern Carpathians [39,40]. The

easternmost site, Vrancea, is steeper and rockier than the others, resulting in shallower soils. Detailed soil sampling conducted by Dařenová et al. [34] classified the soil type at all sites as Cambisols.

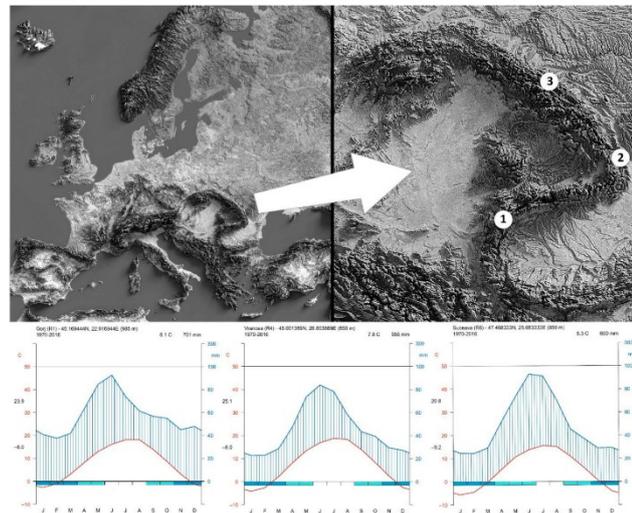


Figure 1. Geographical locations and climate diagrams of selected sites, i.e., 1—Gorj, 2—Vrancea, 3—Suceava. Climate diagrams are based on E-OBS daily climate datasets for the period from 1970 to 2016.

Table 1. Characteristics of the research site locations, representing the local site conditions (CGP—canopy gap fraction, MAT—mean annual air temperature, and MAP—mean annual precipitation), as well as sampled tree characteristics (N—number of trees and DBH—mean diameter at breast height).

County	Plot	Elevation (m)	Latitude	Longitude	Slope Inclination (%)	Exposure	CGP (%) *	MAT (°C)	MAP (mm)	N	A. alba	F. sylv.	Average DBH (cm)	A. alba	F. sylv.
Gorj	Tismana	985	45°10'10"	22°55'11"	10–15	E-SE	7.04	8.1	701	15	15	63.9	63.7		
Vrancea	Soveja	830	46°0'5"	26°36'14"	20–25	SE	8.75	7.8	556	16	15	56.9	54.2		
Suceava	Frumosu	850	47°28'6"	25°40'60"	15–20	SW	7.18	5.3	600	16	15	78.9	54.0		

* Canopy gap fraction was estimated in 2023 from hemispherical photographs according to Dařenová et al. [34].

We used E-OBS daily climate data (version 30.0e) on a 0.1° regular grid [38] to extract mean, minimum, and maximum daily temperatures, as well as daily precipitation sums from the nearest grid points. All sites receive between 550 and 700 mm of annual precipitation, with a peak in June and a minimum in January. Gorj, the southernmost site, experiences the highest average temperatures and the greatest precipitation. The E-OBS climate database is based on daily climate data collected from ground-based observation stations operated by national meteorological services between January 1950 and December 2019 [41]. For this study, we extracted climate data from 1980 to 2016 for further analysis.

2.2. Sample Collection and Preparation

Samples (cores) of beech and fir were collected in 2017 from healthy trees with no visible signs of stem damage or any kind of declining tree vitality. The criteria for the selection of trees were as follows: (1) adult trees of the second (dominant trees) and third class (co-dominant trees) according to Kraft classes; (2) they must form the canopy of the stand; (3) the trunk must be free of visible damage up to a height of at least 4–5 m;

and (4) crown transparency must not exceed 30%. At each site, 15 mature dominant fir and beech trees were sampled using a standard 5 mm increment borer (Haglöf Sweden, Långsele, Sweden). Two cores were taken from each tree and carefully placed in straws for transport.

The cores were dried under load for fourteen days to prevent bending, mounted and glued to a wooden support, and sanded with increasingly finer sandpaper with a grit of 180 to 600. The cores were scanned using the ATRICS [42] imaging system, and the annual radial increments were measured to the nearest 0.01 mm using CooRecorder and CDendro software, which also served as quality control for the measured tree-ring widths. Sampled trees were from at least 91 to 234 years old for fir and 124 to 260 years old for beech. In general, the trees in Gorj were the oldest and the trees in Suceava the youngest, with the beech being older than the fir on all sites. The MRW sequences were visually and statistically synchronized with PAST-5. Quality control was also performed by verification and correction. We calculated correlations between trees in CDendro and created a plot chronology that we compared with individual trees. Any tree-ring width sequence that did not fit into the plot chronology was corrected in CooRecorder and returned to the data pool. In three cases with obvious anomalies in tree-ring width, the cores were excluded from further processing. We paid attention to missing and false tree rings and rotated sections of the cores.

2.3. Laboratory Methods and Quantitative Analysis of Wood Anatomy

Quantitative wood anatomy analysis was performed on five to six randomly selected cores per site. We used random selection with the goal of capturing population-level anatomical variability, acknowledging the trade-off with climate signal strength. The small sample size, which can be explained by the relatively high effort required to obtain such data, has nevertheless been reported in several studies to have meaningful and robust correlations with environmental parameters for both wood anatomy and shrub-ring data [43]. Since the same cores were used for MRW measurements, they were first soaked in water before removal from the wooden holders. The samples were prepared for imaging under a transmitted light microscope at the Laboratory for Wood Anatomy at the Slovenian Forestry Institute according to the protocol suggested by von Arx et al. [44], i.e., each core was split into subsamples of similar length to fit on the microscope slide.

From each beech subsample, 15 to 20 μm thick transverse sections were cut with a sledge microtome using OLFA-80 \times 9 mm replacement blades [45]. Fir samples were dehydrated in a graded series of ethanol and infiltrated with UltraClear (Avantor Performance Materials, Deventer, the Netherlands) and paraffin (Paraplast plus, Leica Biosystems, Richmond, CA, USA) and embedded in paraffin blocks to stabilize the samples for further processing [46]. Embedding the samples in paraffin helps to prevent damage to the cell structures during cutting, and as the fir samples were brittle, different protocols were used compared to the beech. Transverse sections of 20 μm thickness were cut with a LeicaRM 2245 rotary microtome (Leica Microsystems, Wetzlar, Germany) using Leica 819 Low Profile Microtome blades (Leica Biosystems, Nussloch, Germany). The sections of both species were transferred to object glasses, and the paraffin was subsequently washed out with UltraClear and ethanol. The sections were stained with a water mixture of safranin and Astra blue. After staining, sections were dehydrated and permanently fixed between two glass slides with Euparal mounting medium. To prevent the sections from buckling, which impairs a uniform focus when capturing an image, a small magnet was placed on the top of the slide with the coverslip to keep the sections flat and avoid air bubbles during drying. High-resolution images (beech: 0.514 pixel/ μm , fir: 2.056 pixel/ μm) of the sections were obtained using a Leica DM 4000 B light microscope (Leica Microsystems, Wetzlar,

Germany) at 50× magnification, a Leica DFC 280 digital camera (Leica Microsystems, Wetzlar, Germany), and LAS image analysis software (Leica Application Suite). The image sequences of the xylem rings were acquired with at least 25% of the overlapping area and then stitched together using PTGui v11.16 Pro (New House Internet Services B.V., Rotterdam, The Netherlands). The panoramic images were then processed using Image-Pro Plus 7.1 image analysis software and ROXAS (v3.0.437) [44,47], which provides cell (vessels for beech and tracheids for fir) dimensions (e.g., lumen size, cell wall thickness) and relative position within the dated growth ring for all selected cells [29].

Based on this, we calculated chronologies of (1) mean tree-ring width (MRW), (2) mean vessel/tracheid lumen area (MLA), (3) tracheid or vessel density (CD), (4) relative conductive area (RCTA), and (5) for fir also mean thickness of tangential cell walls (CWTTAN) for a minimum of the last 39 years and then used the period between 1980 and 2016 for the analyses with climate variables.

2.4. Statistical Analysis

Individual MRW were standardized to remove long-term trends using a cubic smoothing spline of 67% with a frequency cutoff of 50% in the R program's `dplR` library [48]. All other wood-anatomical chronologies were also standardized, resulting in detrended series: MRWi, MLAi, CDi, RCTAi, and CWTTANi. Raw chronologies were used to assess differences in wood-anatomical characteristics between sites.

To test for significant differences in tree-ring characteristics, i.e., mean tree-ring width (MRW), mean vessel/tracheid lumen area (MLA), tracheid or vessel density (CD), relative conductive area (RCTA), and mean tangential cell wall thickness (CWTTAN), either parametric or non-parametric statistical tests were applied depending on the distribution and variance homogeneity of the data. Specifically, linear mixed-effects models (LMMs) with site as a fixed effect and year as a random effect were used when the assumptions of normality and homoscedasticity were satisfied. In cases where these assumptions were violated, the non-parametric Friedman test was applied. Post hoc pairwise comparisons were corrected using the Bonferroni adjustment for multiple testing.

To assess the influence of site-specific climatic conditions on wood-anatomical traits and tree-ring widths, we applied repeated measures ANOVA (rm-ANOVA). This statistical approach was used to evaluate differences in mean tree-ring width (MRW), cell density (CD), relative conductive tissue area (RCTA), tangential cell wall thickness (CWTTAN), and mean lumen area (MLA) across the three study sites. The rm-ANOVA allowed us to account for within-subject variability over time and test for site-specific effects while considering the repeated nature of the measurements taken from individual trees over multiple years.

To examine relationships between wood-anatomical traits, we used LMMs fitted with the `lmerTest` package in R. Analyses were based on yearly averages per site to ensure consistent temporal resolution. Each model included site (Gorj, Suceava, Vrancea) as a fixed effect and year as a random intercept to account for temporal dependency. To assess site-specific relationships, we estimated marginal slopes (trends) and pairwise contrasts using the `emtrends()` function from the `emmeans` package. All statistical analyses were conducted in R version 4.5.1.

Correlations between climate variables and growth parameters were assessed using the `daily_response()` function from the R (version 4.5.1) package `dendroTools` [49], applied independently to each species and tree-ring parameter. Daily values of precipitation, maximum temperature, and minimum temperature were considered and aggregated into seasonal windows ranging from 7 to 60 days, covering the period from the previous June to the current October. Pearson's correlation coefficients were calculated for the

years 1980–2016 using 1000 bootstrap samples. Only correlations with $p < 0.05$ were retained to infer statistically significant relationships between climate and wood-anatomical characteristics.

3. Results

3.1. Differences in Wood-Anatomical Characteristics Between Sites

Chronologies of MRW were similar at the Suceava and Vrancea sites, with some peaks and declines matching well, while the Gorj site has a very different chronology for both species and generally has the lowest MRW (Figure 2; Table 2). All MRW chronologies appear to be declining between 1980 and 2016, except for beech at the Gorj site, which has been increasing since 2002. In Vrancea, there has been the largest decrease in MRW for both species in recent years. In Suceava, the MRW of beech was significantly lower than that of fir, while the MRW in Vrancea and Gorj is similar for both species. CD and RCTA of vessels are lower than those of tracheids, while the MLA of vessels is higher than that of tracheids. CWTTAN of tracheids increases with time and is therefore inversely proportional to the MRW of the fir.

Table 2. Mean ring width (MRW), relative conductive area (RCTA), cell density (CD), mean lumen area (MLA), and tangential cell wall thickness (CWTTAN) of fir and beech with descriptive statistics across sites.

Species	Site	Wood-Anatomical Characteristics	Mean	±SD	ACI
<i>Abies alba</i>	Suceava	MRW	4654.9	916.3	0.706
		RCTA	43.3	2.8	0.556
		CD	882.9	59.3	0.510
		MLA	515.5	56.1	0.568
		CWTTAN	5.8	0.3	0.520
	Vrancea	MRW	2262.8	913.0	0.764
		RCTA	39.5	3.5	0.485
		CD	1017.1	121.3	0.680
		MLA	417.5	69.2	0.583
		CWTTAN	5.8	0.4	0.535
	Gorj	MRW	1159.4	322.5	0.751
		RCTA	41.7	2.8	0.365
		CD	836.5	59.4	0.548
		MLA	517.1	59.5	0.475
		CWTTAN	6.1	0.3	0.329
<i>Fagus sylvatica</i>	Suceava	MRW	2638.5	518.1	0.421
		RCTA	18.3	1.4	0.493
		CD	113.1	5.8	0.344
		MLA	1627.4	98.8	0.439
	Vrancea	MRW	2301.6	780.9	0.662
		RCTA	20.5	1.8	0.532
		CD	119.4	10.3	0.545
		MLA	1726.8	102.7	0.396
	Gorj	MRW	1340.8	600.1	0.698
		RCTA	22.3	2.1	0.577
		CD	134.8	15.3	0.581
		MLA	1689.5	135.5	0.461

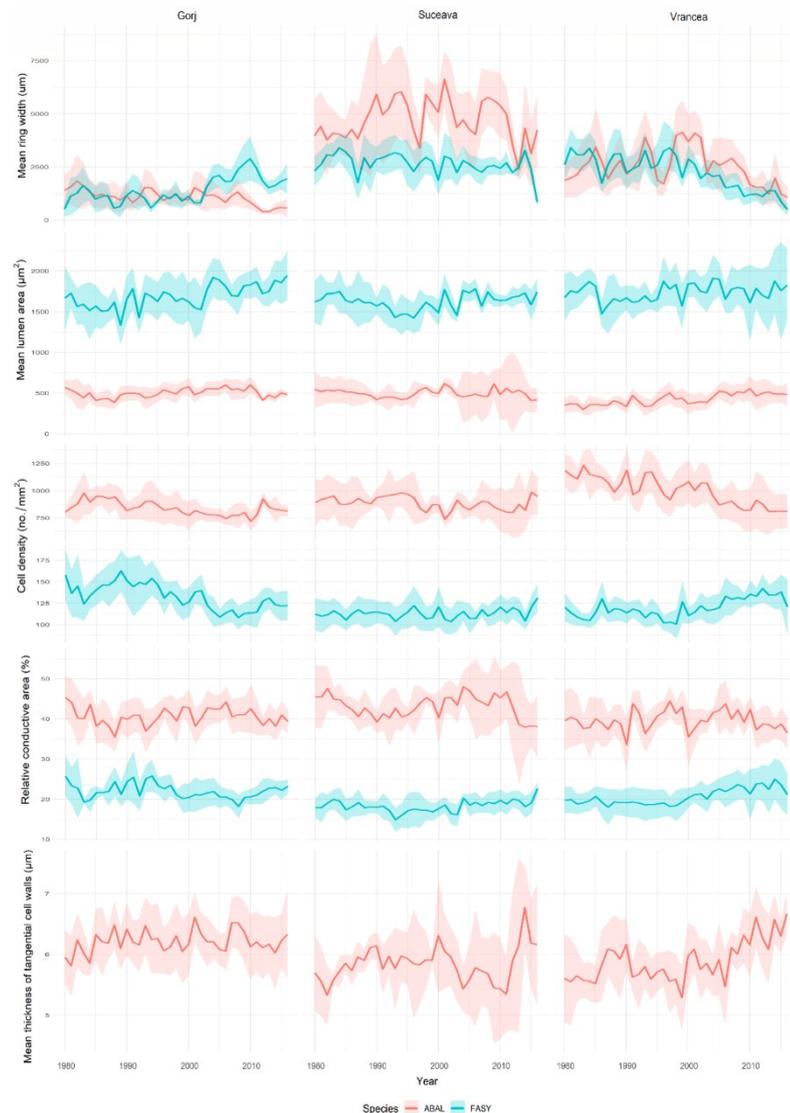


Figure 2. Chronologies of mean tree ring width and wood-anatomical characteristics in fir (ABAL) and beech (FASY) at studied sites.

The widest MRW for fir was measured in Suceava, followed by Vrancea and Gorj; all differences were statistically significant (Figure 3A). MLA of tracheids was similar in Suceava and Gorj, but significantly lower in Vrancea (Figure 3B). RCTA was comparable in Vrancea and Gorj, but significantly higher in Suceava (Figure 3C). CD differed significantly across all sites, with the highest values measured in Vrancea, followed by Suceava, and the lowest in Gorj (Figure 3D). CWTTAN was highest in Gorj, but significantly lower in Suceava and Vrancea (Figure 3E).

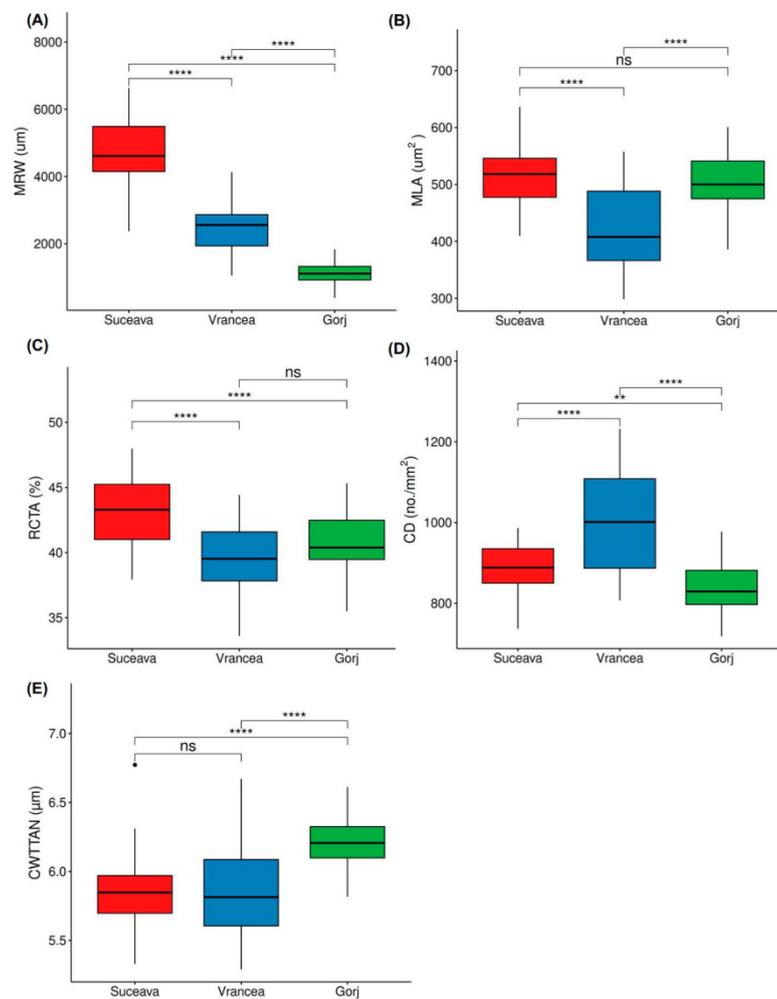


Figure 3. Differences among the sites in (A) mean ring width (MRW), (B) mean lumen area (MLA), (C) relative conductive area (RCTA), (D) cell density (CD), and (E) tangential cell wall thickness (CWTTAN) in fir analyzed by *rm*-ANOVA or the Friedman test. The significance level of the differences in tree-ring characteristics between sites is marked by ns—not significant. ** $p < 0.01$, and **** $p < 0.0001$. For summary of statistical tests, see Table A1.

The differences between sites in MRW of beech were similar to the differences in MRW of fir—statistically significant, highest in Suceava and lowest in Gorj (Figure 4A). MLA of vessels was similar in Vrancea and Gorj, but significantly lower in Suceava (Figure 4B). CD and RCTA values of beech differed significantly at all sites, with the highest values in Gorj and the lowest in Suceava (Figure 4C,D).

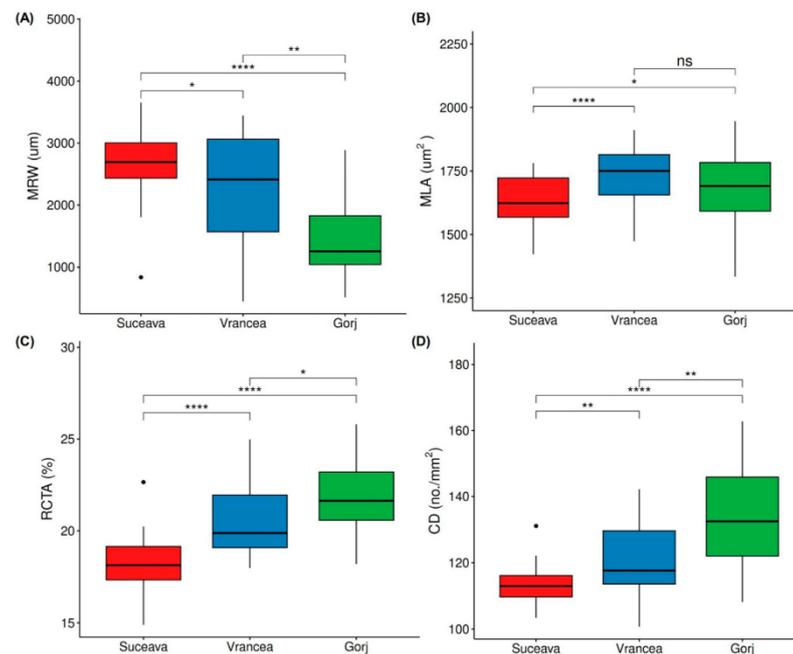


Figure 4. Differences among the sites in (A) mean ring width (MRW), (B) mean lumen area (MLA), (C) relative conductive area (RCTA), and (D) cell density (CD) in beech analyzed by rm-ANOVA or the Friedman test. The significance level of the differences in tree-ring characteristics between sites is marked by ns—not significant, * $p < 0.05$, ** $p < 0.01$, and **** $p < 0.0001$. For summary of statistical tests, see Table A1.

The correlation between CD and MRW in fir was significant and positive only in Vrancea (Figure 5A; detailed descriptions of the models in Tables A2 and A4), while the correlation between CWTTAN and MRW was significantly negative in Vrancea and positive in Gorj (Figure 5D). The relationships between RCTA vs. MRW and CD vs. MRW in fir showed no significant correlations (Figure 5B,C). The analysis revealed a significant negative correlation between RCTA vs. CD, MLA vs. CD, and CWTTAN vs. RCTA at all sites (Figure 5E,F,I). In Vrancea, there is a significant negative correlation between CWTTAN and CD (Figure 5G) and a significant positive correlation between CWTTAN and MLA, while in Suceava, there is a negative correlation between CWTTAN and MLA (Figure 5H).

The measured vessel traits in beech generally showed more significant correlations between wood-anatomical traits and MRW than those of fir (Figure 6; detailed descriptions of the models in Tables A3 and A5). A negative relationship between MRW and CD and between MRW and RCTA was observed at all sites, suggesting that narrower rings contain higher density vessels and have a larger relative conducting area (Figure 6A,B). Consequently, RCTA and CD showed a significant positive relationship at all sites; higher CD resulted in higher RCTA (Figure 6C), which is in contrast to the correlation in fir. Gorj was the only site where there was a significant positive correlation between MRW and MLA and a significant negative correlation between CD and MLA, suggesting that vessels are larger and density is lower in wider rings, reflecting a trade-off between vessel density and size as would be expected hydraulically (Figure 6D,E).

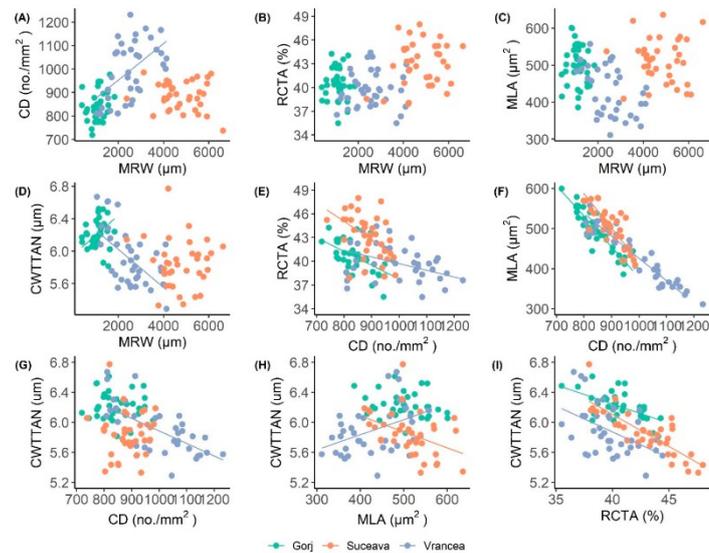


Figure 5. Relationships between wood-anatomical traits in fir at three sites (Gorj, Suceava, and Vrancea): (A) cell density (CD) vs. mean tree-ring width (MRW), (B) relative conductive area (RCTA) vs. MRW, (C) mean lumen area (MLA) vs. MRW, (D) mean tangential cell wall thickness (CWTTAN) vs. MRW, (E) RCTA vs. CD, (F) MLA vs. CD, (G) CWTTAN vs. CD, (H) CWTTAN vs. MLA, and (I) CWTTAN vs. RCTA. Lines represent site-specific slopes derived from linear mixed-effects models (LMMs) including year as a random effect. Only statistically supported relationships are shown. For model summaries and slope estimates, see Table A2 (LMM results) and Table A4 (emtrends results).

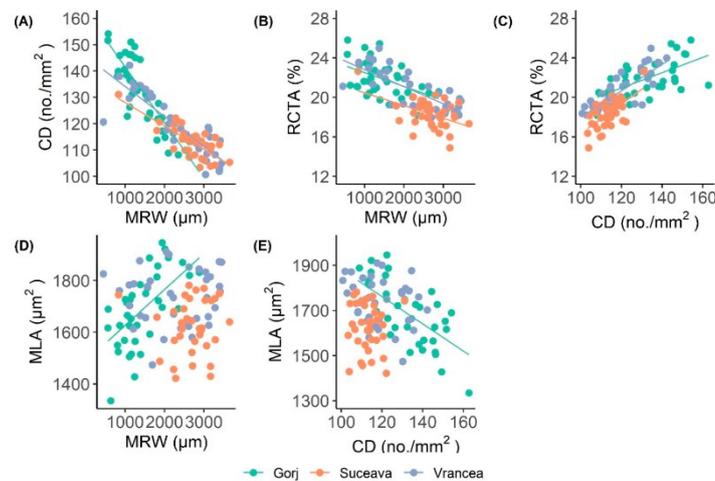


Figure 6. Relationships between wood-anatomical traits in beech at three sites (Gorj, Suceava, and Vrancea): (A) cell density (CD) vs. mean tree-ring width (MRW), (B) relative conductive area (RCTA) vs. MRW, (C) RCTA vs. CD, (D) mean lumen area (MLA) vs. MRW, (E) MLA vs. CD. Lines represent site-specific slopes derived from linear mixed-effects models (LMMs) including year as a random effect. Only statistically supported relationships are shown. For model summaries and slope estimates, see Table A3 (LMM results) and Table A5 (emtrends results).

3.2. The Effect of Climate Variables on Tree-Ring and Vessel Parameters

The correlation analysis between long-term daily climate data and the investigated wood-anatomical parameters in beech and fir revealed strong and statistically significant associations with temperature and precipitation across all study sites. Overall, precipitation and maximum temperature emerged as the most influential climatic factors affecting tree-ring characteristics, whereas minimum temperature showed weaker correlations, with only a few notable exceptions.

Correlations between the climate variables and the fir tree-ring characteristics were strongest in Vrancea (Figure 7). Interannual variability in MRWi was primarily influenced by winter conditions (from previous November to April—start of current growing season), with both maximum and minimum temperatures showing positive correlations. This means that tissue formation in the following year is influenced by preconditioning winter conditions. The strongest negative correlation was observed in Vrancea between maximum temperature at the beginning of the current growing season (April and May) and MLAi, as well as CDi, while RCTAi exhibited a positive correlation in this period. MLAi and CDi were positively correlated with precipitation in July and August, while CDi also showed a positive correlation with minimum temperature. CWTTANi displayed positive correlations with both minimum and, more notably, maximum temperatures in February at all sites (at Gorj also in January and at Suceava also in March). Increased wall thickness in response to warmer February temperatures implies better xylem safety, which increases resistance to drought-induced cavitation.

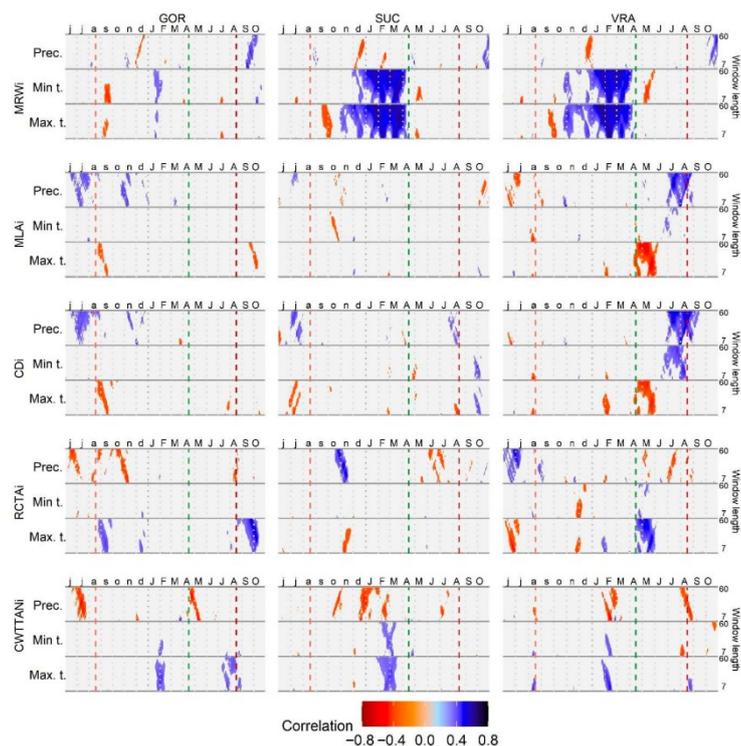


Figure 7. Correlations between standardized tree-ring chronologies for fir (mean ring width—MRWi, mean lumen area—MLAi, cell density—CDi, relative conductive area—RCTAi, and mean tangential

cell wall thickness—CWTANi) and maximum and minimum daily temperature and daily precipitation sums at Gorj (GOR), Suceava (SUC), and Vrancea (VRA), using a time window spanning between 7 and 60 days. Vertical dashed lines from left to right depict the approximate timing of the growing season based on previous data [46]: end of previous growing season (orange), start (green), and end (red) of current growing season.

Correlations between climate variables and tree-ring characteristics in beech differed from those in fir, generally showing stronger negative relationships (Figure 8). The correlations for MRWi varied across sites: Gorj showed the weakest correlations, Suceava exhibited a negative correlation with maximum temperatures in June–July and minimum temperatures in preceding July, while Vrancea had a negative correlation with the maximum and minimum temperatures in March–April (beginning of the growing season) and July. The strongest correlations were observed in Suceava, where interannual variability in MLAi was primarily influenced by current May and June conditions, with maximum and minimum temperatures showing negative correlations. The highest positive correlation was observed in Suceava between maximum and minimum temperature in December and Cdi. In contrast, correlations were least pronounced in Gorj, where the strongest positive relationships were observed between MLAi and precipitation as well as minimum temperatures in October and November.

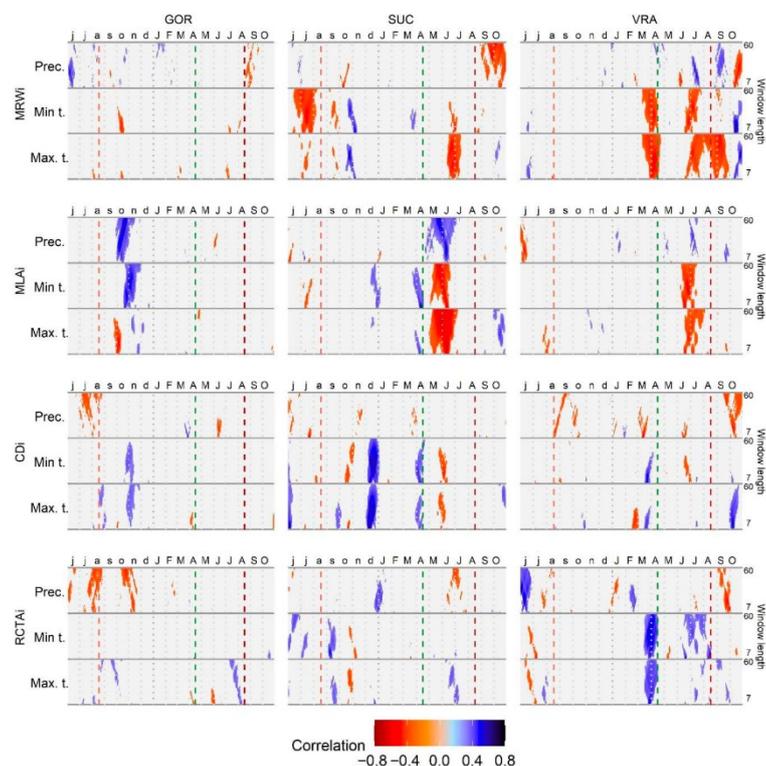


Figure 8. Correlations between standardized tree-ring chronologies for beech (mean ring width—MRWi, mean lumen area—MLAi, cell density—Cdi, and relative conductive area—RCTAi) and maximum and minimum daily temperature and daily precipitation sums at Gorj (GOR), Suceava (SUC),

and Vrancea (VRA), using a time window spanning between 7 and 60 days. Vertical dashed lines from left to right depict the approximate timing of the growing season based on previous data [46]: end of previous growing season (orange), start (green), and end (red) of current growing season.

4. Discussion

Our results show differences in wood-anatomical characteristics (e.g., MRW, CD, RCTA, CWTTAN, and MLA) at the selected sites for both investigated species, thus confirming our first hypothesis. The second hypothesis is rejected as the relationships between tree-ring widths and wood-anatomical characteristics are not similar for fir and beech at the selected sites. The third hypothesis, that beech and fir respond differently to climate variables at the selected sites, with fir being more drought-tolerant than beech, can be confirmed with significance.

4.1. Wood-Anatomical Characteristics of Fir and Beech Differ Between the Selected Sites

A comparison of MRW and wood-anatomical characteristics and their relationship to climatic factors revealed differences between three Carpathian sites that differ in their climatic regimes. In fir, significant differences in MRW and CD were found at all sites, in MLA at Vrancea, in RCTA at Suceava, and in CWTTAN at Gorj. The widest MRW for fir was measured in Suceava, the northernmost site, where there is also the greatest difference between the growth of fir and beech, with fir having a much wider MRW. The narrowest MRW was found in Gorj, the southernmost site. MLA is statistically lowest in Vrancea, the driest site with the lowest rainfall. In dry habitats, community mean conduit diameters are much narrower than in humid habitats. Narrower vessels are favored in drier environments as they are more resistant to the formation of embolism [50]. RCTA is highest in Suceava, where the water transport efficiency is the best. Wall thickness of the tracheids is significantly greater at the southernmost site, Gorj, which increases their resistance to drought-induced cavitation.

In beech, significant differences in MRW, RCTA, and CD were found at all sites. MLA is statistically lowest in Suceava, the northernmost site. The differences between sites in MLA, RCTA, and CD are not similar for fir and beech. However, the same pattern of MRW differences among sites is observed in beech, where the widest MRW is found in Suceava and the narrowest in Gorj. This could indicate that the southern areas of distribution of both species are less favorable for their growth. Statistically, RCTA and CD are highest in Gorj and lowest in Suceava. As beech has similar MLA values, it increases RCTA at a narrower MRW to maintain hydraulic capacity at a higher level. In the site chronologies, RCTA values increase slightly in Suceava and even more in Vrancea, a drier site. This means that the effect of the higher RCTA could be an effect of the production of smaller MRW due to the low humidity, which does not allow the production of a larger amount of new tissue. This means that in beech, the increasing amount of moisture can be traced from chronologies of wood-anatomical features (mainly RCTA). No such observation could be made for fir.

4.2. Relationships Between Tree-Ring Widths and Wood-Anatomical Traits

The relationships between the wood-anatomical features differ between fir and beech. The correlation between RCTA and CD is negative for fir and positive for beech at all sites. The only similar—negative—correlation is between MLA and CD in Gorj. In fir, MRW shows no significant relationship with RCTA and MLA. The analysis shows a significant negative correlation between RCTA-CD, MLA-CD, and CWTTAN-RCTA at all sites. At Vrancea, there was a significant negative correlation between CWTTAN and CD and a significant positive correlation between CWTTAN and MLA, suggesting that the tracheid

structure of fir is different under drier conditions—when the cell walls are thicker, the CD is lower and the MLA is greater. This does not apply to Suceava, where the correlation between CWTTAN and MLA was significantly negative.

The measured vessel traits in beech showed significant correlations with MRW, consistent with previous studies [5–7,51], which reported that CD and RCTA were generally smaller in wider tree rings. Consequently, a significant positive relationship between RCTA and CD was observed. Prislán et al. [52] demonstrated that CD depends on MRW and varies significantly between sites, being approximately 30% higher at the high-elevation site, where beech trees exhibited 54% narrower xylem rings. Similarly, Oladi et al. [51], studying oriental beech (*Fagus orientalis* Lipsky), found that wider tree rings contained slightly larger but substantially fewer vessels per mm², resulting in a negative correlation between MRW and RCTA.

In diffuse-porous beech, vessels from multiple years contribute to water transport, meaning the influence of a single tree ring on total hydraulic capacity is only partial [53]. However, a higher RCTA value in narrower rings suggests that water transport may take precedence over mechanical support, as the need for additional strength diminishes in adult trees—both ring width and density tend to decrease with increasing number of rings from the pith outward [54]. Oladi et al. [51] proposed that CD and MRW are highly influenced by environmental conditions, whereas mean lumen area (MLA) and RCTA are more endogenously regulated and thus exhibit less interannual variability [55].

Arnič et al. [7] reported similar correlations between MRW and CD, MRW and RCTA, and CD and RCTA, but found no significant relationship between MRW and MLA or between CD and MLA in beech. In contrast, our results from Gorj, the southernmost site, revealed a significant positive correlation between MRW and MLA and a significant negative correlation between CD and MLA. Beech trees appear to compensate for external environmental influences by adjusting their anatomical traits [51]. During the mature growth phase, MRW in beech is strongly influenced by external factors. Cornelius [56] and Zobel and Jett [57] argued that wood properties—and thus wood structure—are more closely linked to genetic predisposition than to tree-ring width, suggesting that genetic influence on MRW is generally limited.

The first anatomical trait to respond to changes in MRW is CD, with both being affected by the same environmental factors to which beech is particularly sensitive [58,59]. CD has also been shown to correlate more strongly with exogenous variables such as precipitation and temperature [60], as well as fluctuations in groundwater levels [61]. In contrast, vessel size and porosity are relatively stable traits, exhibiting limited variation and being primarily governed by genetic factors.

4.3. Fir and Beech Respond Differently to Climatic Variables

We used daily response functions to examine the effect of weather conditions on the tree-ring widths and vessel features. The fir show site-specific responses to climate variables. The only similar response is between MRWi and the maximum and minimum daily temperature and daily precipitation totals in Suceava and Vrancea. The comparison of fir tree-ring width with climatic variables revealed that MRWi variability is mainly influenced by winter and early spring (from November to April) conditions, with maximum and minimum temperatures showing positive correlations. As an evergreen species, fir benefits from warmer winters (with winter photosynthesis) [62], whereas beech, a deciduous species, is less affected by warm winter temperatures [32]. Correlations between the climate variables and the fir tree-ring characteristics were strongest in Vrancea, which is the driest site. The strongest negative correlation was observed in Vrancea between maximum temperature at the beginning of the current growing season (April and May) and MLAi, as

at the beginning of cambial activity is mainly controlled by internal factors. Precipitation in the previous summer and autumn and in the current May had only a minor influence. Vessel formation towards the end of cambial activity is strongly influenced by precipitation in July and is thus more strongly determined by external factors [64].

Increased summer temperatures have a negative effect on radial growth, which can lead to growth disturbances in beech trees. This is consistent with previous observations that the beech forests in the Eastern Carpathians have changed in recent decades [65], while the old-growth beech forests in the Northwest Carpathians have remained relatively stable [66]. Martinez del Castillo et al. [67] predicted a significant decline in beech growth across Europe, ranging from -20% to more than -50% by 2090, depending on the region and climate change scenario (CMIP6 SSP1-2.6 and SSP5-8.5). Under a moderate climate change scenario (CMIP6 SSP2-4.5), beech growth will decline in the near future (2021–2050) in most parts of its range: by 12–18% in northwestern Central Europe and by 11–21% in the Mediterranean region. Climate-induced growth increases are limited where the historical mean annual temperature was below $\sim 6\text{ }^{\circ}\text{C}$: a growth increase of 3% to 24% in the high-altitude areas of the Alps and the Carpathian Arc, with a northward range shift limited by water availability [68]. In contrast, Prislan et al. [52] found no significant correlation between intra-annual weather conditions and conduit characteristics of beech. Therefore, they assumed that precipitation is not a limiting factor for xylem growth and cell differentiation at sites with similar weather conditions in Europe.

With rising temperatures and constant precipitation, trees have a greater water deficit, which means that they must have higher water efficiency [69] and, consequently, adapt the anatomical properties of the wood. Provenance trials of beech confirmed that provenances from drought-prone sites cope better with water scarcity and show no negative response of mean or cumulative vessel area to summer drought [5]. Site conditions influence the climate sensitivity of beech, which is more pronounced in marginal locations or in extreme years [31]. Small vessels are generally less susceptible to cavitation [70], which can be an advantage under frequent drought conditions. However, as the smaller vessel area is not compensated by a higher vessel density, the water transport capacity is significantly lower [5]. The decrease in overall hydraulic capacity could then be behind the negative growth trends of beech predicted under future climate scenarios [67,68]. In locations where water supply is likely to be limited, drought-tolerant provenances could be planted to minimize the impact of drought on the growth of beech forests [31]. Populations growing at the southern limit of the distribution show considerable phenotypic plasticity, leading them to adjust anatomical and physiological traits in response to narrow ranges of environmental parameters. However, the distribution of beech appears to be limited to areas with at least 400 mm of precipitation during the growing season and a vapor pressure deficit (VPD) of $< 3\text{ kPa}$, which may represent the main environmental thresholds that severely limit beech growth and thus affect its ability to cope with future environmental conditions [71]. Diaconu et al. [6] provide new insights into the plastic response of beech wood anatomy to warmer climatic conditions and showed that thinning of forest stands alters the water-conducting system to make it more resistant to hydraulic failure. Kašpar et al. [35] concluded that beech has consistently higher moisture limits throughout the Carpathians, suggesting a potentially higher vulnerability to future droughts due to its limited growth plasticity compared to fir, which appears to be better able to adapt to future conditions, especially in the north. In Central Europe, fir showed recently more increasing growth trends than beech [72]. The likely response of species to climate change will vary, which will affect their competitiveness, their existence, and, consequently, forest management decisions and measures [73].

The novelty of the study is that we monitored coexisting fir and beech on three different sites in the Carpathians. Fir and beech always respond differently to climate variables at the same locations. Interestingly, both species showed the weakest climate-growth correlations in Gorj (especially with MRWi), suggesting that climatic limitations may be less pronounced at this site. Our results provide a more detailed understanding of the effects of complex climatic conditions on the productivity of temperate mixed forests.

5. Conclusions

This study is part of a broader research initiative examining the responses of fir and beech in the Carpathians [33,34,74], and provides an additional analysis of their climate-related adaptations [32,35]. Our primary objective was to investigate how site-specific climatic conditions—namely, temperature and precipitation—influence tree-ring widths and wood-anatomical traits in beech and fir.

By comparing mean tree-ring width (MRW) and wood-anatomical characteristics (e.g., MRW, cell density [CD], relative conductive tissue area [RCTA], tangential cell wall thickness [CWTTAN], and mean lumen area [MLA]) across three Carpathian sites with distinct climate regimes, we identified clear differences in species-specific responses. The relationships between tree-ring widths and wood-anatomical traits varied between fir and beech, reflecting their differing sensitivities to local climate conditions. Our findings align with previous dendrochronological studies, confirming that beech is more vulnerable to extremely warm summers, whereas fir exhibits greater tolerance.

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Abbreviations

The following abbreviations are used in this manuscript:

MRW	Mean tree-ring width
MLA	Mean vessel/tracheid lumen area
CD	Cell (tracheid or vessel) density
RCTA	Relative conductive area
CWTTAN	Mean thickness of tangential cell walls
LMM	Linear mixed model

CGP Canopy gap fraction
 MAT Mean annual air temperature
 MAP Mean annual precipitation
 N Number of trees
 DBH Mean diameter at breast height

Appendix A

Appendix A.1

Table A1. Summary of statistical tests assessing differences in xylem traits among three sites (Suceava, Vrancea, Gorj) for *Abies alba* (ABAL) and *Fagus sylvatica* (FASY). Tree-ring characteristics included: (I) mean tree-ring width (MRW); (II) mean vessel/tracheid lumen area (MLA); (III) tracheid or vessel density (CD); (IV) relative conductive area (RCTA); and (V) mean thickness of tangential cell walls (CWTTAN). Depending on data distribution and variance homogeneity, either the Friedman rank sum test or a linear mixed model (LMM) was applied. Test statistics and degrees of freedom (df) are reported. Pairwise comparisons between sites were corrected for multiple testing. Significance codes: **** $p < 0.0001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

Species	Tree-Ring Characteristic	Test (Statistic, df)	p-Value	Pairwise Comparison	Adjusted p	Significance
ABAL	MRW	Friedman ($\chi^2 = 74$, df = 2)	<0.0001	SUC-VRA	<0.0001	****
				SUC-GOR	<0.0001	****
				VRA-GOR	<0.0001	****
	CD	Friedman ($\chi^2 = 31.3$, df = 2)	<0.0001	SUC-VRA	<0.0001	****
				SUC-GOR	<0.01	**
RCTA	LMM (F = 30.47, df = 2, 72)	<0.0001	VRA-GOR	<0.0001	****	
			VRA-GOR	0.07	ns	
MLA	LMM (F = 31.81, df = 2, 72)	<0.001	SUC-VRA	<0.0001	****	
CWTTAN	Friedman ($\chi^2 = 32$, df = 2)	<0.0001	SUC-GOR	1.00	ns	
			VRA-GOR	<0.0001	****	
FASY	MRW	Friedman ($\chi^2 = 26.32$, df = 2)	<0.0001	SUC-VRA	0.023	*
				SUC-GOR	<0.0001	****
				VRA-GOR	<0.01	**
	CD	Friedman ($\chi^2 = 19.68$, df = 2)	<0.0001	SUC-VRA	0.009	**
				SUC-GOR	<0.0001	****
RCTA	Friedman ($\chi^2 = 42$, df = 2)	<0.0001	VRA-GOR	0.002	**	
			VRA-GOR	<0.0001	****	
MLA	LMM (F = 11.03, df = 2, 72)	<0.0001	SUC-VRA	<0.0001	****	
CWTTAN	LMM (F = 11.03, df = 2, 72)	<0.0001	SUC-GOR	0.027	*	
			VRA-GOR	0.149	ns	

Appendix A.2

Table A2. Summary of linear mixed-effects models (LMMs) assessing the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA, CWTTAN) and their interactions with site in fir. All models include year as a random effect. For each fixed-effect term, the estimate, standard error, degrees of freedom (df), t-value, and p-value are reported. Marginal and conditional R² values represent the variance explained by fixed effects alone and by the full model, respectively.

Model	Term	Estimate	Std. Error	df	t Value	Pr (> t)	R ² Marginal	R ² Conditional
CD ~ MRW * site	(Intercept)	854.19	39.46	97.49	21.647	0.000	0.47	0.73
	MRW	0.01	0.03	91.70	-0.372	0.711		
	siteSuceava	27.26	66.61	76.63	0.409	0.683		
	siteVrancea	-57.82	47.89	72.11	-1.207	0.231		
	MRW:siteSuceava	0.01	0.03	80.76	0.404	0.687		
	MRW:siteVrancea	0.09	0.03	78.88	2.662	0.009		
RCTA ~ MRW * site	(Intercept)	41.68	1.23	98.88	33.800	0.000	0.27	0.55
	MRW	0.00	0.00	95.47	-0.973	0.333		
	siteSuceava	-1.36	2.13	79.92	-0.638	0.525		
	siteVrancea	-1.72	1.54	74.91	-1.118	0.267		
	MRW:siteSuceava	0.00	0.00	84.44	1.481	0.142		
	MRW:siteVrancea	0.00	0.00	82.32	0.881	0.381		
CWTTAN ~ MRW * site	(Intercept)	5.95	0.13	98.40	45.240	0.000	0.39	0.64
	MRW	0.00	0.00	94.33	2.151	0.034		
	siteSuceava	0.16	0.23	78.36	0.728	0.469		
	siteVrancea	0.54	0.16	73.35	3.332	0.001		
	MRW:siteSuceava	0.00	0.00	82.90	-2.615	0.011		
	MRW:siteVrancea	0.00	0.00	80.78	-4.160	0.000		
MLA ~ MRW * site	(Intercept)	488.66	30.67	99.45	15.932	0.000	0.34	0.57
	MRW	0.01	0.03	96.81	0.393	0.696		
	siteSuceava	53.70	53.54	81.23	1.003	0.319		
	siteVrancea	36.27	38.77	76.00	0.936	0.352		
	MRW:siteSuceava	-0.02	0.03	85.91	-0.613	0.542		
	MRW:siteVrancea	-0.05	0.03	83.68	-1.773	0.080		
RCTA ~ CD * site	(Intercept)	55.20	4.19	92.09	13.167	0.000	0.42	0.68
	CD	-0.02	0.00	91.70	-3.508	0.001		
	siteSuceava	8.50	5.85	78.28	1.453	0.150		
	siteVrancea	-7.06	4.50	75.44	-1.568	0.121		
	CD:siteSuceava	-0.01	0.01	78.37	-0.870	0.387		
	CD:siteVrancea	0.01	0.01	77.16	1.745	0.085		
MLA ~ CD * site	(Intercept)	1142.87	52.17	92.24	21.905	0.000	0.87	0.92
	CD	-0.76	0.06	91.87	-12.365	0.000		
	siteSuceava	126.68	72.97	77.99	1.736	0.086		
	siteVrancea	-157.42	56.16	74.96	-2.803	0.006		
	CD:siteSuceava	-0.09	0.08	78.08	-1.052	0.296		
	CD:siteVrancea	0.21	0.06	76.74	3.189	0.002		
CWTTAN ~ CD * site	(Intercept)	6.50	0.54	99.75	12.075	0.000	0.40	0.52
	CD	0.00	0.00	99.68	-0.525	0.601		
	siteSuceava	-0.79	0.78	88.07	-1.016	0.312		
	siteVrancea	1.05	0.61	82.50	1.738	0.086		
	CD:siteSuceava	0.00	0.00	88.17	0.549	0.584		
	CD:siteVrancea	0.00	0.00	84.53	-1.924	0.058		
CWTTAN ~ MLA * site	(Intercept)	6.28	0.39	96.84	16.167	0.000	0.37	0.52
	MLA	0.00	0.00	96.55	-0.153	0.879		
	siteSuceava	0.66	0.52	90.21	1.273	0.206		
	siteVrancea	-1.24	0.45	83.25	-2.739	0.008		
	MLA:siteSuceava	0.00	0.00	90.46	-1.963	0.053		
	MLA:siteVrancea	0.00	0.00	82.76	2.234	0.028		
CWTTAN ~ RCTA * site	(Intercept)	8.28	0.72	101.94	11.442	0.000	0.56	0.57
	RCTA	-0.05	0.02	101.94	-2.860	0.005		
	siteSuceava	1.23	0.91	96.24	1.357	0.178		
	siteVrancea	0.35	0.96	91.94	0.360	0.720		
	RCTA:siteSuceava	-0.03	0.02	96.46	-1.565	0.121		
	RCTA:siteVrancea	-0.02	0.02	91.96	-0.751	0.455		

Appendix A.3

Table A3. Summary of linear mixed-effects models (LMMs) assessing the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA) and their interactions with site in beech. All models include year as a random effect. For each fixed-effect term, the estimate, standard error, degrees of freedom (df), t-value, and p-value are reported. Marginal and conditional R² values represent the variance explained by fixed effects alone and by the full model, respectively.

Model	Term	Estimate	Std. Error	df	t Value	Pr (> t)	R ² Marginal	R ² Conditional
CD ~ MRW * site	(Intercept)	162.74	2.72	101.85	59.839	0.000	0.80	0.83
	MRW	-0.02	0.00	101.51	-12.086	0.000		
	siteSuceava	-25.77	6.06	101.81	-4.251	0.000		
	siteVrancea	-17.19	4.07	96.27	-4.223	0.000		
	MRW:siteSuceava	0.01	0.00	100.02	4.591	0.000		
	MRW:siteVrancea	0.01	0.00	91.75	4.470	0.000		
RCTA ~ MRW * site	(Intercept)	23.91	0.63	102.00	37.840	0.000	0.63	
	MRW	0.00	0.00	102.00	-3.442	0.001		
	siteSuceava	-2.16	1.40	102.00	-1.548	0.125		
	siteVrancea	0.63	0.92	102.00	0.684	0.496		
	MRW:siteSuceava	0.00	0.00	102.00	0.185	0.853		
	MRW:siteVrancea	0.00	0.00	102.00	-0.665	0.507		
MLA ~ MRW * site	(Intercept)	1487.43	47.89	101.47	31.062	0.000	0.27	0.41
	MRW	0.14	0.03	100.19	4.513	0.000		
	siteSuceava	103.95	107.06	101.97	0.971	0.334		
	siteVrancea	201.45	72.59	98.27	2.775	0.007		
	MRW:siteSuceava	-0.13	0.05	101.20	-2.676	0.009		
	MRW:siteVrancea	-0.12	0.04	94.63	-3.015	0.003		
RCTA ~ CD * site	(Intercept)	11.61	1.96	100.83	5.924	0.000	0.69	0.72
	CD	0.08	0.01	100.77	5.280	0.000		
	siteSuceava	-10.24	4.55	101.87	-2.249	0.027		
	siteVrancea	-7.08	3.07	97.58	-2.303	0.023		
	CD:siteSuceava	0.07	0.04	101.81	1.836	0.069		
	CD:siteVrancea	0.06	0.02	97.48	2.303	0.023		
MLA ~ CD * site	(Intercept)	2486.75	159.75	99.07	15.567	0.000	0.31	0.41
	CD	-6.04	1.20	98.90	-5.032	0.000		
	siteSuceava	-726.43	371.74	100.74	-1.954	0.053		
	siteVrancea	-407.60	252.84	100.30	-1.612	0.110		
	CD:siteSuceava	4.84	3.20	100.55	1.513	0.133		
	CD:siteVrancea	3.18	2.02	100.25	1.571	0.119		

Appendix A.4

Table A4. Estimated site-specific slopes and pairwise contrasts of marginal trends (emtrends) extracted from linear mixed-effects models (LMMs). The models assess the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA, CWTTAN) and site-specific differences in these relationships in fir. For each model, estimated slopes are reported separately for each site (Gorj, Suceava, Vrancea), followed by Tukey-adjusted pairwise contrasts between sites. Columns include estimates, standard errors (SE), degrees of freedom (df), confidence intervals (CL), t-ratios, and p-values.

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	p Value		
CD ~ MRW * site	Estimated slope	Gorj	-0.013	0.035	92.17	-0.081	0.056	-0.401	0.915		
		Suceava	0.001	0.013	93.70	-0.025	0.027				
		Vrancea	0.078	0.014	94.60	0.050	0.106				
	Pairwise contrast	Gorj-Suceava	-0.014	0.034	81.62					-2.646	0.026
		Gorj-Vrancea	-0.091	0.034	79.80						
		Suceava-Vrancea	-0.077	0.017	72.17						
RCTA ~ MRW * site	Estimated slope	Gorj	-0.001	0.001	95.54	-0.003	0.001	-1.469	0.311		
		Suceava	0.001	0.000	96.87	0.000	0.001				
		Vrancea	0.000	0.000	97.63	-0.001	0.001				
	Pairwise contrast	Gorj-Suceava	-0.002	0.001	84.62					-0.875	0.658
		Gorj-Vrancea	-0.001	0.001	82.52						
		Suceava-Vrancea	0.001	0.001	73.79						

Table A4. Cont.

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	p Value
CWTAN ~ MRW * site	Estimated slope	Gorj	0.000	0.000	94.77	0.000	0.000		
		Suceava	0.000	0.000	96.16	0.000	0.000		
		Vrancea	0.000	0.000	96.97	0.000	0.000		
	Pairwise contrast	Gorj-Suceava	0.000	0.000	83.87			2.594	0.030
		Gorj-Vrancea	0.000	0.000	81.83			4.130	0.000
		Suceava-Vrancea	0.000	0.000	73.36			3.157	0.006
MLA ~ MRW * site	Estimated slope	Gorj	0.011	0.027	96.86	-0.043	0.064		
		Suceava	-0.006	0.010	98.04	-0.026	0.014		
		Vrancea	-0.038	0.011	98.71	-0.060	-0.016		
	Pairwise contrast	Gorj-Suceava	0.017	0.028	86.04			0.60729	0.81653
		Gorj-Vrancea	0.048	0.028	83.81			1.75874	0.18986
		Suceava-Vrancea	0.032	0.013	74.64			2.3563	0.05433
RCTA ~ CD * site	Estimated slope	Gorj	-0.017	0.005	91.92	-0.027	-0.007		
		Suceava	-0.023	0.005	89.24	-0.034	-0.013		
		Vrancea	-0.008	0.003	92.26	-0.014	-0.003		
	Pairwise contrast	Gorj-Suceava	0.006	0.007	78.79			0.86429	0.66428
		Gorj-Vrancea	-0.009	0.005	77.59			-1.7357	0.19852
		Suceava-Vrancea	-0.015	0.006	79.90			-2.6893	0.02343
MLA ~ CD * site	Estimated slope	Gorj	-0.765	0.063	92.42	-0.889	-0.641		
		Suceava	-0.853	0.065	89.77	-0.983	-0.724		
		Vrancea	-0.560	0.033	92.76	-0.625	-0.495		
	Pairwise contrast	Gorj-Suceava	0.089	0.085	79.19			1.04513	0.55084
		Gorj-Vrancea	-0.205	0.065	77.90			-3.1705	0.0061
		Suceava-Vrancea	-0.294	0.069	80.32			-4.258	0.00016
CWTAN ~ CD * site	Estimated slope	Gorj	0.000	0.001	99.64	-0.002	0.001		
		Suceava	0.000	0.001	98.39	-0.001	0.002		
		Vrancea	-0.002	0.000	99.79	-0.002	-0.001		
	Pairwise contrast	Gorj-Suceava	0.000	0.001	87.95			-0.543	0.85032
		Gorj-Vrancea	0.001	0.001	84.26			1.90759	0.14282
		Suceava-Vrancea	0.002	0.001	89.16			2.47074	0.04039
CWTAN ~ MLA * site	Estimated slope	Gorj	0.000	0.001	96.80	-0.002	0.001		
		Suceava	-0.002	0.001	95.91	-0.004	-0.001		
		Vrancea	0.002	0.001	97.18	0.001	0.003		
	Pairwise contrast	Gorj-Suceava	0.002	0.001	90.96			1.93827	0.13387
		Gorj-Vrancea	-0.002	0.001	83.52			-2.2133	0.07477
		Suceava-Vrancea	-0.004	0.001	87.88			-4.486	6.5 × 10 ⁻⁵
CWTAN ~ RCTA * site	Estimated slope	Gorj	-0.051	0.018	101.94	-0.087	-0.015		
		Suceava	-0.085	0.013	101.93	-0.111	-0.059		
		Vrancea	-0.069	0.016	101.95	-0.101	-0.037		
	Pairwise contrast	Gorj-Suceava	0.034314	0.02226	96.3681			1.54184	0.27611
		Gorj-Vrancea	0.017945	0.02422	91.7898			0.74098	0.73981
		Suceava-Vrancea	-0.01637	0.02081	94.0712			-0.7866	0.71217

Appendix A.5

Table A5. Estimated site-specific slopes and pairwise contrasts of marginal trends (emtrends) extracted from linear mixed-effects models (LMMs). The models assess the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA) and site-specific differences in these relationships in beech. For each model, estimated slopes are reported separately for each site (Gorj, Suceava, Vrancea), followed by Tukey-adjusted pairwise contrasts between sites. Columns include estimates, standard errors (SE), degrees of freedom (df), confidence intervals (CL), t-ratios, and p-values.

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	p Value
CD ~ MRW * site	Estimated slope	Gorj	-0.021	0.002	101.52	-0.025	-0.018		
		Suceava	-0.009	0.002	100.88	-0.013	-0.005		
		Vrancea	-0.011	0.001	101.66	-0.014	-0.009		
	Pairwise contrast	Gorj-Suceava	-0.012	0.003	100.05			-4.517	0.000
		Gorj-Vrancea	-0.010	0.002	91.89			-4.384	0.000
		Suceava-Vrancea	0.002	0.002	89.47			1.089	0.524
RCTA ~ MRW * site	Estimated slope	Gorj	-0.001	0.000	102.00	-0.002	-0.001		
		Suceava	-0.001	0.000	102.00	-0.002	0.000		
		Vrancea	-0.002	0.000	102.00	-0.002	-0.001		
	Pairwise contrast	Gorj-Suceava	0.000	0.001	97.14			-0.183	0.982
		Gorj-Vrancea	0.000	0.001	84.13			0.653	0.791
		Suceava-Vrancea	0.000	0.001	94.74			0.815	0.694

Table A5. Cont.

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	p Value
MLA – MRW * site	Estimated slope	Gorj	0.139	0.031	100.63	0.077	0.201		
		Suceava	0.012	0.035	99.16	–0.057	0.081		
		Vrancea	0.021	0.021	100.98	–0.022	0.063		
	Pairwise contrast	Gorj–Suceava	0.127	0.048	101.40			2.632	0.026
		Gorj–Vrancea	0.118	0.040	96.35			2.957	0.011
		Suceava–Vrancea	–0.009	0.039	86.14			–0.220	0.974
RCTA – CD * site	Estimated slope	Gorj	0.078	0.015	101.09	0.048	0.107		
		Suceava	0.150	0.037	100.65	0.077	0.222		
		Vrancea	0.134	0.019	101.07	0.096	0.173		
	Pairwise contrast	Gorj–Suceava	–0.072	0.040	101.86			–1.802	0.174
		Gorj–Vrancea	–0.057	0.025	98.64			–2.255	0.067
		Suceava–Vrancea	0.015	0.041	98.66			0.369	0.928
MLA – CD * site	Estimated slope	Gorj	–6.044	1.220	99.85	–8.464	–3.624		
		Suceava	–1.208	2.986	98.91	–7.133	4.717		
		Vrancea	–2.869	1.583	99.80	–6.009	0.272		
	Pairwise contrast	Gorj–Suceava	–4.836	3.253	101.00			–1.487	0.302
		Gorj–Vrancea	–3.175	2.064	100.79			–1.539	0.277
		Suceava–Vrancea	1.661	3.353	96.37			0.495	0.874

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3 RAZPRAVA IN SKLEPI

3.1 RAZPRAVA

Mešani jelovo-bukovi gozdovi predstavljajo glavno komponento gozdnih ekosistemov srednje in jugovzhodne Evrope (Dobrowolska in sod., 2017). Nedavne raziskave potrjujejo, da se gozdna vegetacija Karpatov spreminja z različno intenziteto in v različnih smereh, kar lahko pripišemo različnim procesom (Šamonil in Vrška, 2007), kot so onesnaževanje zraka, zakisovanje tal (Hédl in sod., 2011) in konkurenčnosti mladja (Łysik, 2009). Vprašanje je, kako se bo ekološko in gospodarsko pomembna jelka, odzivala na spreminjajoče se podnebne trende (Maiorano in sod., 2013; Tinner in sod., 2013).

Višje zimske temperature naj bi pospeševale rast zaradi manjšega tveganja zaradi embolije (Gazol in sod., 2019; Príncipe in sod., 2017; van der Maaten, 2012), vendar lahko zgodnejši začetek raste sezone znatno poveča verjetnost poškodb zaradi poznih zmrzali (Marquis in sod., 2022), ki je za bukev bolj kritična kot za jelko (Fisichelli in sod., 2014). Na uspešnost rasti sredi rastnega obdobja bo pomembno vplivala plastičnost in prilagodljivost vrst na predvidene podnebne spremembe (Kašpar in sod., 2021; Martinez del Castillo in sod., 2018; Zhang in sod., 2024). Na podlagi sedanjih ugotovitev so podnebne omejitve za rast bolj omejujoče za bukev kot za jelko, zato lahko pričakujemo, da bodo prihodnje podnebne razmere v Karpatih ugodnejše za jelko kot za bukev, kar potrjujejo podobne raziskave v Evropi (Buras in Menzel, 2019; García-Duro in sod., 2021; Kašpar in sod., 2021; Zang in sod., 2014).

Prvo hipotezo, o vplivu geografske širine na spremembo asimilacijskega odziva jelovega in bukovega mladja na različno intenziteto svetlobe zavrnamo, saj so imeli večji vpliv klimatski parametri. Vrednost asimilacijske učinkovitosti za obe vrsti se je v Karpatih zmanjševala z naraščajočo povprečno letno temperaturo in povečevala s povečujočo količino padavin, posebno pri jelki.

Drugo hipotezo, o neznačilnih razlikah med vrstama v asimilacijskem odzivu mladja na intenziteto svetlobe zavrnamo, saj sta sencozdržnost jelke in bukve različni. Asimilacijska učinkovitost jelke se z večanjem sence oz. zastora odraslega sestoja povečuje, učinkovitost bukve pa se obratno, povečuje z vse manjšo zastrtostjo.

Tretjo hipotezo, o neznačilnih odzivih jelke in bukve med gospodarskimi gozdovi in pragozdnimi rezervati zavrnamo; razlike med obema kategorijama gozdov v Karpatih so značilne, vendar manj izrazite kot razlike v Dinaridih. Potrdili smo, da je asimilacijski odziv v pragozdu pri svetlobni kategoriji »rob« bolj podoben kategoriji »odprto«, v gospodarskem gozdu pa so odzivi razporejeni bolj enakomerno. Razlik v rastnem odzivu jelke in bukve med gospodarskimi gozdovi in pragozdovi ne moremo potrditi, saj se dolgoročni vzorci rasti med obema kategorijama niso značilno razlikovali.

Četrto hipotezo, o različnih prirastnih odzivih jelke in bukve na klimo potrdimo, saj smo z dendrokronološko raziskavo potrdili različne odzive glede na vrsto in lokacijo. Pri jelki smo

potrdili pozitivno korelacijo med debelinsko rastjo in temperaturo pozimi, pri bukvi pa negativno korelacijo med debelinsko rastjo in temperaturo poleti. Čeprav smo potrdili podoben odziv ob večjih julijskih padavinah in višjih povprečnih in maksimalnih temperaturah v juniju, se v drugih mesecih vrsti odzivata na klimo različno.

Zadnjo, peto hipotezo, da lesno-anatomske značilnosti ne kažejo povezave z geografsko širino ali dolžino zavrnejo, saj je primerjava povprečnih širin branik in lesno-anatomskih značilnosti ter njihove korelacije s podnebnimi dejavniki potrdila razlike med tremi lokacijami na Karpatih. Pri bukvi smo potrdili statistično pozitivno korelacijo med povprečnimi širinami branik in povprečno površino celic le na eni lokaciji. Vrsti se na izbranih rastiščih različno odzivata na podnebne parametre, kar kaže tudi na specifično prilagojenost lokalnim razmeram.

S proučevanjem svetlobnih odzivov smo ovrednotili sencozdržnost, opredelili odziv jelke in bukve v gospodarskih sestojih in pragozdu ter primerjali odziv vzdolž dveh večjih geografskih gradientov (Čater in sod., 2024). Relativno kratkoročni odzivi jelke in bukve v treh zaporednih rastnih obdobjih potrjujejo konsistentne odzive v različnih svetlobnih intenzitetah; sencozdržnost jelke in bukve sta različni, asimilacijska učinkovitost jelke se z večanjem zastrtosti povečuje, učinkovitost bukve pa zmanjšuje. V pragozdu je svetlobna kategorija »rob« bolj podobna kategoriji »odprto«; v gospodarskem gozdu so odzivi razporejeni enakomerneje. Odzivi bukve na padavine so v Dinaridih in v Karpatih podobni: večanje temperatur zmanjšuje učinkovitost bukve, pri jelki se učinkovitost zmanjšuje v Karpatih, na Balkanu pa povečuje. Razliko povezujemo z večjo količino padavin v rastnem obdobju v Dinaridih in posledično ugodnejšo razpoložljivostjo vode kot v Karpatih, kjer je dejavnik minimuma. Rezultati dajejo vpogled v dejanski odziv dveh ključnih drevesnih vrst na podnebne spremembe v prihodnje, kar bo vplivalo na njuno konkurenčnost, obstoj in posledično gozdnogojitvene odločitve ob pričakovanih klimatskih spremembah.

Dihanje tal na lokacijah vzdolž Karpatov je bilo bolj odvisno od talnih lastnosti (vsebnosti ogljika in dušika), kot od podnebnih razmer (Dařenova in sod., 2014). Domnevamo, da bodo podnebne spremembe izrazito vplivale na razgradnjo in skladiščenje organske snovi v tleh. Vpliva temperature na dihanje tal nismo potrdili, je pa vplivala na razlike v dihanju tal med meritvami različna vlažnost tal v dveh zaporednih letih. Predvidevamo, da bodo prihodnje poletne suše, ki se bodo najverjetneje stopnjevale, zmanjšale dihanje tal, vse večje temperature in ekstremi pa delovale v obratni smeri in ga povečevale. Čeprav so gozdne vrzeli sestavni del gozdnih ekosistemov, vnašajo negotovost v oceno bilance ogljika v gozdu. Enotnega vpliva zastrtosti krošenj na dihanje tal nismo potrdili, najverjetneje zaradi različne starosti vrzeli, katerih s tem obsegom dela nismo mogli določiti.

Predvidena izguba gozdne produktivnosti je najizrazitejša na južni meji naravne razširjenosti bukve, kjer naj bi se intenzivnost suše v prihodnosti povečala (Martinez Del Castillo in sod., 2022). Največ statistično značilnih korelacij med debelinsko rastjo in klimatskimi parametri smo potrdili na vzhodnih lokacijah Karpatov, medtem ko jih je bilo na južnih lokacijah manj ali pa jih sploh ni bilo (Adamič in sod., 2023). Nadpovprečne količine padavin v juliju so pozitivno vplivale na debelinsko rast pri obeh vrstah, vendar v prihodnje, v času podnebnih

sprememb poleti ne pričakujemo nadpovprečnih padavin. Obe vrsti se negativno odzivata na večjo povprečno in maksimalno temperaturo v juniju. Nadpovprečne temperature v poznih zimskih mesecih (od januarja do marca) vplivajo pozitivno na debelinsko rast jelke, kar lahko pomeni, da bodo, zaradi podnebnih sprememb, toplejše zime povečale njeno priraščanje. Nadpovprečna temperatura v poletnih mesecih (od junija do avgusta) vpliva negativno na debelinsko rast bukve. Prihodnje poletne visoke temperature bodo najverjetneje vplivale negativno na bukev.

Povprečne širine branik po desetletjih od leta 1950 naprej kažejo pri jelki na južnih lokacijah trend zmanjševanja, kar nakazuje, da postajajo ta rastišča postopoma neugodna za njeno rast. Pri obeh drevesnih vrstah se je debelinska rast povečevala na vzhodnih rastiščih Karpatov, v zadnjem desetletju pa se je začela zmanjševati. Na severnih lokacijah jelka izkazuje največjo rast; širina branik bukev v zadnjih treh desetletjih je bila enakomerna. Severna rastišča postajajo za rast obeh vrst ugodnejša, zlasti za jelko. Jelka na severnih rastiščih je v obdobju 1970 do 1980 slabše priraščala, rast se je izboljšala po letu 1980. Upad rasti lahko povežemo s prirastno depresijo v 60-ih letih, ki ji je sledilo izboljšanje prirastka v 80-ih letih in so jo potrdili pri jelki v vsej Evropi. Prirastno depresijo in diferenciacijo jelove populacije je povzročil splet zaporednih neugodnih vremenskih razmer, onesnaževanje ozračja z SO₂ kot glavni vzrok in neprimerno gospodarjenje z gozdom (Levanič, 1997; Elling in sod., 2009; Čavlović in sod., 2015).

V raziskavi podnebnih omejitev za rast jelke in bukve v Karpatih smo določili tri različna območja: severni predeli se soočajo z omejitvami zaradi nizkih temperatur, jugozahodne in jugovzhodne predele Karpatov pa omejuje premajhna količina padavin in posledično nezadostna vlaga, katere primanjkljaj se proti vzhodu še stopnjuje (Kašpar in sod., 2025). Razlike v temperaturnih omejitvah jelke v Karpatih (pomembne zlasti na severu) so potrdile različne odzive jelke na sušo med severnimi in južnimi lokacijami. Kljub vse večjim omejitvam vlage na severnih lokacijah se tam rast povečuje zaradi manjših temperaturnih omejitev. V bodoče lahko pričakujemo vse manjše razlike v omejitvah rasti med severnimi in jugozahodnimi lokacijami Karpatov, čeprav se bodo razlike po scenariju RCP 4.5 kljub temu najverjetneje ohranile. Modelne napovedi kažejo, da bodo na severnih lokacijah v sredini 21. stoletja podnebne omejitve za rast podobne tistim, na jugozahodnih lokacijah v drugi polovici 1980-ih let. Po scenariju RCP 4.5 napovedujemo v prihodnjih desetletjih povečano rast bukve in jelke predvsem zaradi podaljševanja rastnega obdobja. Bukve je pokazala konsistentne omejitve rasti zaradi primanjkljaja vlage na celotnem območju Karpatov, kar kaže večjo dovzetnost za prihodnje suše v primerjavi z jelko, ki je bolj prilagojena na spremembe, zlasti na severu.

Lesno-anatomska analiza predstavlja dodaten vpogled v odzive jelke in bukve na podnebne razmere, kjer smo vzporejali temperature in količino padavin s širinami branik in lesno-anatomskimi značilnostmi obeh vrst na Karpatih. Primerjava povprečnih širin branik in lesno-anatomskih značilnosti ter njihove korelacije s podnebnimi dejavniki (najmanjše in največje dnevne temperature ter vsote padavin iz dnevnih klimatskih podatkov E-OBS) potrjujejo razlike med tremi proučevanimi lokacijami Karpatov. Pri bukvi smo potrdili statistično pozitivno

korelacijo med povprečnimi širinami branik in povprečno površino celic le na eni lokaciji. Bukev in jelka se na analiziranih lokacijah odzivata na podnebne parametre različno, kar kaže na prilagojenost lokalnim razmeram. Raziskava je skladna z zaključki dendrokronološkega in ekofiziološkega sklopa, ki kažejo, da se bukev težje prilagaja toplimi poletjem, medtem ko je jelka nanje odpornejša.

3.1.1 Smernice in usmeritve za gospodarjenje z jelovo-bukovimi gozdovi v Sloveniji

Kljub prilagoditveni sposobnosti bukovih sestojev je preživetje bukve in drugih drevesnih vrst zmerne pasu v prihodnosti negotovo, saj se hitrost in intenziteta podnebnih sprememb na različnih območjih razlikujeta. V južnih delih Karpatov lahko v prihodnje pričakujemo večje spremembe temperatur in razporeditve ter količine padavin, medtem ko gozdovi severnega dela še vedno odražajo stabilnost in strukturno odpornost. Spremembe vrstne sestave so povzročile manjša nihanja v parametrih sestojev, ki dolgoročno ne ogrožajo sobivanja bukve in jelke (Petritan in sod., 2015). Kljub omejujočim dejavnikom suše in poletne vročine za jelko, pa še vedno najdemo primere v južnem delu njenega areala po Evropi, kjer se kaže nasprotno. Jelka v sestojih na Biokovu in Veliki Kapeli (južna Hrvaška) raste v zelo toploljubni združbi skupaj s črnim gabrom, malim jesenom, trikrpim javorjem in mokovcem v sestojih asociacije *Ostryo-Abietetum* (Dakskobler in Marinšek, 2009). Bukove populacije na robu območja razširjenosti vrste imajo velik prilagoditveni potencial, njihova ohranitev lahko znatno prispeva k stabilnosti gozdov po vsej Evropi z ustreznim prilagojenim gospodarjenjem in politikami ohranjanja gozdov (Máttyás in sod., 2009; Lefèvre in sod., 2014; Fady in sod., 2016).

Učinkovita obnova gozdov po motnjah je predpogoj za njihovo sposobnost obstoja in delovanja v času. Pod pritiskom vse večjih motenj in predvidenih okoljskih sprememb, ki bodo verjetno vplivale na gozdne ekosisteme - tako s postopnimi spremembami povprečnih podnebnih razmer kot s povečanjem pogostosti in obsegom ekstremnih vremenskih dogodkov (IPCC, 2018) - je njihova odpornost ključna. Z vidika blaženja prihodnjih vplivov podnebnih sprememb in krepitve sposobnosti prilagajanja gozdov na ekstremne vremenske pojave je vse več zanimanja za mešane gozdove, saj so ekološko odpornejši od gozdov s prevladujočo eno drevesno vrsto (Griess in sod., 2012; Griess in Knoke, 2013; Lebourgeois in sod., 2013). Obnova gozdov po veliko površinskih motnjah je lahko manj zahtevna za države s prevladujočim golosečnim načinom gospodarjenja in umetno obnovo, saj je le-ta dobro uveljavljena, drevesa pa so prilagojena mikroklimatskim razmeram na odprtih območjih. Ker je v številnih srednjeevropskih državah golosečnja precej omejena (Pommerening in Murphy, 2004; Schütz in sod., 2016), je tudi celoten sistem umetne obnove manj razvit.

Sencodržne vrste kot sta bukev in jelka, so povezane s številnimi fiziološkimi, morfološkimi in strukturnimi prilagoditvami, ki dajejo prednost učinkoviti sečnji pri zmerni oz. majhni odprtosti sestojev (Ellsworth in Reich, 1992; Walters in Reich, 1996; Walters in Reich, 1999). Sencodržnost obenem vključuje zmanjšano fotosintetsko zmogljivost in povečano dovzetnost za fotoinhibitorne poškodbe pri večjih svetlobnih jakostih (Tucker et al., 1987; Henry in Aarssen, 1997), kar lahko vodi v nepopravljivo poškodbo reakcijskih centrov po obsežnih motnjah, kot sta žled ali vetrolom zaradi posledično hitrih presvetljenosti (Ruban, 2014).

Prilagoditev vključuje spremembe in fiziološke prilagoditve obstoječega listja/ iglic, kot npr. zmanjšano alokacija dušika, sintezo več fotozaščitnih spojin itd., ali nastanek novega, fiziološko spremenjenega listnega aparata s prilagojeno anatomsko strukturo (Givnish, 1988; Wyka in sod., 2007). Zlasti jelka ima največ težav in omejitev pri hitrem fotosintetskem privajanju na večjo intenziteto svetlobe, saj je njeno prilagajanje postopno (Robakowski in sod., 2004). Medtem ko je za gospodarjenje z gozdom značilno postopno nadzorovano odpiranje zastora, naravne motnje povzročijo takojšnjo spremembo gozdne klime (Schütz in sod., 2016). Ker motnjam pogosto sledi sanitarna sečnja, lahko učinek kratkoročno privede do precej ekstremnih okoljskih razmer. To lahko vpliva na zmanjšanje učinkovitosti fotosinteze in produktivnosti mladja (Ruban, 2009), kar lahko upočasni naravno obnovo, povzroči upad sencozdržnih vrst in prispeva k slabim odločitvam glede obnove gozda (Čater in Diaci, 2017).

Študije odziva pospešene obnove po naravnih motnjah (Čater in sod., 2014; Čater in Diaci, 2017; Čater, 2021) kažejo, da se regeneracijska učinkovitost jelke in bukve po velikopovršinskih motnjah zaradi spremenjenih rastiščnih razmer razlikuje – bukev kaže večjo tekmovalno moč in sposobnost obnove v naravnem mladju kot jelka. Splošno je boljša prilagodljivost listavcev po motnjah lahko tesno povezana z njihovim letnim razvojem listja v primerjavi z iglavci in dolgoživostjo iglic jelke. Prisotnost mladja ima pomembno vlogo pri razvoju novih sestojev po velikih in intenzivnih motnjah (Szwagrzyk in sod., 2018), zlasti vetrolomih, ki navadno ne prizadene mladja (Franklin in sod., 2007). Zmanjšanje števila sadik jelke po žledolomu je bila posledica hitre izpostavljenosti svetlobi po motnjah, objedanja in naravnega osipa začetnega števila sadik. Uspešna aklimatizacija dreves po velikopovršinskih motnjah je povezana z njihovo sposobnostjo razvoja asimilacijskih površin prilagojenih na večje intenzitete in amplitude sevanja. Večja pogostost motenj bo vplivala v bodoče na uspešnost obnove, zlasti v gozdovih s pretežno sencozdržnimi vrstami. Trend sestave drevesnih vrst v odraslih mešanih gozdovih kaže na množično širitev bukve tudi na račun drugih vrst (Janík in sod., 2014; Keren in sod., 2014; Parobeková in sod., 2018), zato sta obnova in prihodnost jelke vprašljivi, zlasti po obsežnih motnjah. Njeno preživetje na presvetljenih delih sestojev po ujmi je ogroženo in omejeno le na zastrte dele sestojev, k zmanjševanju številčnosti pa poleg svetlobnega stresa največ prispeva objedanje divjadi (Čater in Diaci, 2017).

Čeprav je Slovenija v primerjavi z drugimi evropskimi državami znana po trajnostnem konceptu gospodarjenja in velikem deležu ohranjenih in varovanih gozdov, se število gozdnogojitvenih problemov povečuje; naravno obnovo ovirajo prenamnoženi parkljarji, očitno je neravnovesje med razvojnimi fazami, nega pa se izvaja nepopolno. Stroški gospodarjenja naraščajo, prav tako pritiski ter zahteve po povečanju varovalnih in socialnih funkcij gozdov, opazna so tudi odstopanja od načrtovanih in izvedenih gozdnogojitvenih del (Čater in Diaci, 2020). Slovenski gozdovi so v zadnjih letih doživeli velike spremembe v strukturi in sestavi (Kutnar in sod., 2021). Naravne motnje in sanitarne sečnje so povzročile precejšnje motnje v gozdovih in tudi na gozdnih tleh. Posledica motenj je velik delež degradiranih gozdov s številnimi odprtini, kjer se pojavljajo mlajše razvojne faze. Različni dejavniki delujejo na spremembo vrstne sestave gozdov v smeri povečanega deleža listavcev. V zadnjih dveh desetletjih se je v slovenskih gozdovih skupno zmanjšal delež treh prevladujočih drevesnih vrst – bukve, smreke in jelke (Kutnar in sod., 2021). Čeprav se je

povečal delež bukve v skupni lesni zalogi, zaradi zmanjševanja deleža smreke in jelke, se za Slovenijo (Kutnar in Kobler, 2011; 2014) in Evropo (Hanewinkel in sod., 2013) predvideva, da bo tudi bukev v drugi polovici 21. stoletja začela izgubljati svoj delež. Druge vrste gozdov in drevesne vrste z manjšo gospodarsko vrednostjo in večjo požarno ogroženostjo, npr. toploljubni širokolistni in na sušo odporni gozdovi, se bodo verjetno v Sloveniji razširili (Kutnar in Kobler, 2011) in Evropi (Hanewinkel in sod., 2013).

Toplejše razmere bodo najbrž povečale rast jelke, vendar težko predvidevamo posledice zaradi povečane pogostosti podnebnih ekstremov in naravnih motenj (Kutnar in sod., 2021). Ponekod se še vedno ukvarjamo z neavtohtono smreko, ki vse bolj kaže neprilagojenost podnebnim spremembam in smernicami, ki stremijo k nadomestitvi smrekovih monokultur z mešanimi sestoji jelke in bukve (Bošela in sod., 2019). Hkrati pa vse bolj pomembno postaja za gozdarje vprašanje, katere drevesne vrste moramo spodbujati glede na prihajajoče razmere (Thurm in sod., 2018). Predvsem želimo vedeti, v kolikšni meri in na katerih rastiščih lahko trenutno prevladujoče drevesne vrste ohranijo vitalne populacije v prihodnjih desetletjih in v katerih primerih bi morali razmisliti o alternativnih vrstah (Vitasse in sod., 2019, Thurm in sod., 2018). V pričakovanju podnebnih sprememb se vse bolj upošteva tudi nekatere tujerodne iglavce z boljšo prilagodljivostjo na sušo kot smreka, npr. navadna ameriška duglazija (*Pseudotsuga menziesii* (Mirb.) Franco), kljub temu pa bo potrebno opredeliti provenience, ki so bolj prilagojene prihodnjim razmeram. Za duglazijo sicer velja podobno kot za jelko, da je močno izpostavljena objedanju in škodi zaradi divjadi tako na njenem naravnem območju razširjenosti kot v Evropi (Nicolescu in sod., 2023).

Možnosti za ohranjanje jelke lahko izboljšamo z nekaterimi gojitvenimi ukrepi: s prebiralnim redčenjem, s katerim lahko omogočimo socialni vzpon jelk v dozrajšjih enomernih sestojih, in z nego mlajših sestojev, v katerih lahko z uravnavanjem zmesi in pozneje s pozitivno izbiro povečujemo delež jelke v sestojih (Westergren in sod., 2010). K preraščanju jelke je mogoče prispevati z ohranjanjem vitalne in mlajše nadstojne jelke na površinah, pomlajenih z bukvi. Pomemben ukrep je lahko prebiralno redčenje, s katerim omogočamo posameznim jelkam vrst v streho sestoja, mestoma je lahko aktualna tudi saditev jelk pod zastorom, npr. v smrekove kulture. Pri povečevanju naravne tekmovalne moči jelke je ključno postopno odpiranje odraslega sestoja in zaščita jelovega mladja (kolektivna zaščita z ograjo), vendar izkušnje kažejo, da je zaradi dolgih pomladitvenih dob potrebno ograje obnavljati ali postavljati na novo, kar povečuje stroške gospodarjenja (Bončina in sod., 2009). Predlagana je fragmentirana struktura gozdnega roba z večjim deležem zastrtosti. Bodoče ohranjanje jelke brez zaščite in intenzivnejših vlaganj tako ne bo mogoče zaradi povečevanja števila ekstremnih dogodkov, manjše tekmovalne moči jelke in nerešenega vprašanja rastlinojedov (Čater in Diaci, 2017).

Študija rastnih odzivov jelke in bukve na klimatske dejavnike vzdolž Karpatov nam daje pomemben vpogled k boljšemu razumevanju dveh ekološko in gospodarsko pomembnih drevesnih vrst, tudi za slovenske gozdove. Skupaj s študijo, narejeno na Dinaridih, ki sicer ni v strogem okviru naloge, podajamo zaključke, pomembne za ohranjanje trenutnega stanja in napovedi prihodnjega odziva v času podnebnih sprememb.

3.1.2 Prispevek disertacije k razvoju znanosti

Raziskava odzivov jelke in bukve, sestavljena iz treh dopolnjujočih vsebinskih sklopov (gozdne ekofiziologije, dendrokronologije in lesne anatomije), v katero smo vključili še raziskavo dihanja tal in raziskava podnebnih omejitev rasti jelke in bukve, je pokazala enoten odziv v Karpatih, ki kaže na morebitno večjo dovzetnost bukve za prihodnje suše v primerjavi z jelko, ki je bolj prilagojena na prihodnje ekstremne razmere, zlasti na severu.

Ugotovitve predstavljajo izhodišče za gozdnogojitvene smernice jelke in bukve. Vrednotenje predstavlja inovativni pristop pri obravnavi različnih okoljskih dejavnikov, doprinos v skupnem razumevanju odziva proučevanih vrst ter delovanja ekosistema v spremenljivih okoljskih razmerah na večjem geografskem prostoru. Intenzivno vzorčenje v zaporednih letih je zapolnilo obstoječo vrzel med dejanskim in teoretičnim odzivom jelke in bukve na območju Karpatov in predstavlja izhodišče za bodoče raziskave. Enak metodološki pristop v raziskavi Balkana je omogočil primerjavo odziva obeh vrst med obema večjima kompleksoma. Širok nabor meritev je ponudil aktualne zaključke, pomembne za ohranjanje trenutnega stanja in napovedi prihodnjega odziva proučevanih drevesnih vrst v času podnebnih sprememb.

Naloga je bila izdelana v sklopu mednarodnega sodelovanja s tremi tujimi znanstvenoraziskovalnimi institucijami (Češka Akademija znanosti CzechGlobe, Brno, Inštitutom za gozdno ekologijo, Vukoz, Brno in Fakulteto za gozdarstvo in lesarstvo Mendlove Univerze, Brno) in dvema slovenskima (Znanstvenoraziskovalnim centrom SAZU in Gozdarskim inštitutom Slovenije).

3.2 SKLEPI

V okviru projekta smo dobili nove vpoglede v odzive jelke in bukve na večjem geografskem prostoru. Bukovo in jelovo mladje se v Dinaridih in Karpatih na povečevanje padavin odzivata v razmerah različne svetlobne intenzitete podobno; razlike so v največji asimilacijski učinkovitosti jelke, ki je v svetlobnih razmerah pod zastorom, pri bukvi pa na odprtem, kljub optimalnim prehranskim razmeram. Povečevanje temperatur vpliva na bukev v Dinaridih in Karpatih ter na jelko v Karpatih negativno; v Dinaridih ima povečevanje temperatur zaradi zadostne količine padavin na jelko pozitiven učinek, razlike v odzivu med pragozdnimi rezervati in gospodarskimi gozdovi Karpatov so manjše kot v Dinaridih. Na istih lokacijah izmerjeno dihanje tal ni bilo povezano z odprtostjo krošenj, temveč izraziteje z vsebnostjo talnega ogljika, dušika in zemljepisno širino.

Izrazitejši odziv debelinske rasti na podnebne dejavnike (temperaturo in padavine) odraslih dreves smo potrdili v vzhodnih Karpatih, medtem ko je bil odziv na južnejših legah manj izrazit ali pa ga ni bilo. Tako bukev kot jelka kažeta boljšo debelinsko rast z večjimi padavinami v juliju in počasnejšo rastjo z večjimi povprečnimi in največjimi temperaturami v juniju tekočega leta. Jelka izkazuje pozitivno korelacijo med debelinsko rastjo in temperaturo pozimi, bukev pa negativno korelacijo med debelinsko rastjo in temperaturo poleti. V obdobju od leta 1951 do 1960 so bile povprečne širine drevesnih branik pri jelki in bukvi največje na južnih rastiščih v

primerjavi z drugimi rastišči, od leta 2011 so se na južnih rastiščih povečale najmanj, najbolj na severnih. Spremembe v priraščanju jelke od leta 1950 se kažejo s povečevanjem prirastka na severnih rastiščih, počasnim zmanjševanjem na južnih rastiščih in povečevanjem na vzhodnih rastiščih do leta 2010, ko potrjujemo izrazit upad na južnih in vzhodnih lokacijah. Pri bukvi opažamo na vseh treh skupinah rastišč od leta 1950 počasno večanje prirastkov, ki se na severnih in vzhodnih lokacijah po letu 1990 začno zmanjševati, na južnih lokacijah pa stagnirajo. Bukev in jelka se odzivata na podnebne parametre na izbranih lokacijah različno, pri čemer je jelka bolj odporna na sušo kot bukev.

Lesno-anatomski parametri pri jelki in bukvi so različni. Pri jelki smo potrdili statistično negativno korelacijo med relativno prevodno površino in gostoto celic, povprečno površino celic in gostoto celic ter srednjo debelino tangencialnih celičnih sten in relativno prevodno površino. Izmerjene lastnosti trahej pri bukvi so v korelaciji s širino branik. Lesno-anatomski parametri so bili skladni s prirastnimi analizami. Parameteriziran Vaganov-Shashkin model z uporabo projekcij RCP 4.5 je napovedal rast do leta 2050. Opazovanja kažejo na boljšo prilagodljivost jelk v sušnejših razmerah. Na severnih rastiščih omejujejo rast nizke temperature, na južnejših rastiščih povečujoči primanjkljaj vlage, ki se stopnjuje proti vzhodu. Jelka na severnih rastiščih je občutljiva na mraz in se bolj odziva na podnebne razmere kot bukev, ki jo omejuje premalo vlage.

4 POVZETEK (SUMMARY)

4.1 POVZETEK

Za napovedovanje odziva jelke in bukve na podnebne spremembe so potrebne celovite študije, ki omogočajo temeljit vpogled v odziv in rast dreves na večjem geografskem prostoru ter zajemajo meritve odzivov sedanjega stanja in vključujejo napovedi prihodnjih podnebnih razmer. Raziskava je bila osredotočena na bukev (*Fagus sylvatica* L.) in jelko (*Abies alba* Mill.), ključni drevesni vrsti sredo- in visokogorij večine evropskih držav. Evropski gozdovi postajajo zaradi klimatskih sprememb in pogostejših sušnih razmer vse bolj izpostavljeni, vse večja pogostost in intenzivnost ekstremnih vremenskih dogodkov vplivata na fiziološke procese, spremenjeno produktivnost in na sestavo gozdnih ekosistemov zaradi manjše konkurenčnosti. Multidisciplinarna zasnova naloge, ki je sestavljena iz treh vsebinsko dopolnjujočih sklopov omogoča vpogled v realne odzive izbranih drevesnih vrst in oblikovanje gojitvenih usmeritev za gospodarjenje v prihodnje.

Vzdolž gorskega masiva Karpatov od Češke republike do Romunije smo izbrali osem lokacij v odraslih, optimalno razvitih gospodarskih sestojih in pragozdnih rezervatih jelke in bukve nad 800 m nadmorske višine. Na vsaki lokaciji smo z analizo hemisfernih posnetkov krošenj določili tri različne kategorije svetlobne intenzitete in merili asimilacijski odziv mladja v treh zaporednih rastnih obdobjih. Na izbranih 15 odraslih jelovih in bukovih dominantnih drevesih smo izvedli vzorčenje z izvrtki na izbranih lokacijah, iste vzorce smo uporabili tudi za lesno-anatomsko analizo. Klimatske podatke smo dobili iz podatkovnih baz Climate Explorer in E-OBS, primerjave odziva smo izdelali za obdobje po letu 1950 zaradi zanesljivejših klimatskih podatkov.

Bukovo in jelovo mladje se v Dinaridih in Karpatih na povečevanje padavin odzivata v razmerah različne svetlobne intenzitete podobno; razlike so v največji asimilacijski učinkovitosti (Φ) jelke pod zastorom, pri bukvi pa na odprtem, kljub optimalnim prehranskim razmeram (N_{tot} v listju oz. iglicah). Povečevanje temperatur vpliva na bukev v Dinaridih in Karpatih ter na jelko v Karpatih negativno; v Dinaridih ima povečevanje temperatur zaradi zadostne količine padavin na jelko pozitiven učinek, razlike v odzivu med pragozdnimi rezervati in gospodarskimi gozdovi Karpatov so manjše kot v Dinaridih. Na istih lokacijah izmerjena respiracija tal ni bila povezana z odprtostjo krošenj, temveč izraziteje z lastnostmi tal. Morebiten vpliv podnebja na vnos nove organske snovi s produktivnostjo gozda in vrstno sestavo bo imel v prihodnosti pomembno vlogo pri razgradnji in shranjevanju organske snovi v tleh.

Izrazitejši odziv debelinske rasti na podnebne dejavnike (temperaturo in padavine) odraslih dreves smo potrdili v vzhodnih Karpatih, medtem ko je bil odziv na južnejših legah manj izrazit ali ga celo ni bilo. Tako bukev kot jelka kažeta boljšo debelinsko rast z večjimi padavinami v juliju in počasnejšo rast z večjimi povprečnimi in največjimi temperaturami v juniju tekočega leta. Jelka izkazuje pozitivno korelacijo med debelinsko rastjo in temperaturo pozimi, bukev pa negativno korelacijo med debelinsko rastjo in temperaturo poleti. V obdobju od leta 1951 do

1960 so bile povprečne širine drevesnih branik pri jelki in bukvi največje na južnih rastiščih v primerjavi z drugimi rastišči, od leta 2011 so se na južnih rastiščih povečale najmanj, najbolj na severnih. Severna rastišča postajajo za rast obeh vrst ugodnejša, zlasti za jelko. Jelka na severnih rastiščih, je v obdobju 1970 do 1980 slabše priraščala, upad rasti pa bi bil lahko povezan s pojavom prirastne depresije, ki se je začela v 60-ih letih in ji je sledilo izboljšanje prirastka v 80-ih letih. Bukev in jelka se odzivata na podnebne parametre na izbranih lokacijah različno, pri čemer je jelka bolj odporna na sušo kot bukev.

Parametrizirani Vaganov-Shashkin model z uporabo projekcij RCP 4.5 je napovedal rast do leta 2050. Opazovanja kažejo na boljšo prilagodljivost jelk v sušnejših razmerah. Na severnih rastiščih omejujejo rast nizke temperature, na južnejših rastiščih povečujejo primanjkljaj vlage, ki se stopnjuje proti vzhodu. Jelka na severnih rastiščih je občutljiva na mraz in se bolj odziva na podnebne razmere kot bukev, ki jo omejuje premalo vlage. Severna rastišča se po podnebnih omejitvah rasti postopno približujejo jugozahodnim rastiščem.

Lesno-anatomski parametri pri jelki in bukvi so različni. Pri jelki smo potrdili statistično negativno korelacijo med relativno prevodno površino in gostoto celic, povprečno površino celic in gostoto celic ter srednjo debelino tangencialnih celičnih sten in relativno prevodno površino. Izmerjene lastnosti trahej pri bukvi so v korelaciji s širino branik. Bukev in jelka se na izbranih rastiščih odzivata na podnebne parametre različno, kar kaže na prilagojenost lokalnim razmeram. Lesno-anatomskih parametri so bili skladni s prirastnimi analizami.

Kljub prilagoditveni sposobnosti bukovih sestojev je preživetje bukve in drugih drevesnih vrst zmernega pasu v prihodnosti negotovo, saj se hitrost in intenziteta podnebnih sprememb na različnih območjih razlikujeta. Čeprav jelka v Karpatih kaže večjo odpornost na sušo kot bukev, bo njeno ohranjanje v Sloveniji težavno brez zaščite in intenzivnejših vlaganj zaradi povečevanja števila ekstremnih dogodkov, manjše tekmovalne moči in nerešenega vprašanja rastlinojedov.

4.2 SUMMARY

Predicting the response of fir and beech to climate change requires comprehensive studies that provide deeper insights into the response and growth of trees over a wider geographic area, measure current responses and make predictions about future climate conditions. In our research, we focused on European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.), which are likely to be the two most important tree species for a large part of Europe's mid- and high-altitude forests in the future. European forests are under increasing stress from climate change and more frequent droughts, and the increasing frequency and intensity of extreme weather events are affecting the physiological processes, changing productivity and composition of forest ecosystems as some species become less competitive. The multidisciplinary approach of the dissertation, consisting of three complementary parts, provides insights into the actual responses of selected tree species and the formulation of silvicultural guidelines for future management.

Along the Carpathian Mountains, stretching from the Czech Republic to Romania, eight permanent plots were established in optimally developed, managed and old-growth beech and fir forests above 800 metres above sea level. Based on the analysis of hemispherical photographs, three light intensity categories were defined in which the assimilation responses of young trees were measured in three consecutive growing seasons. In each plot, 15 mature fir and beech dominant trees were double cored, and the same samples were then used for wood anatomical analysis. Climate data were taken from the Climate Explorer and E-OBS databases, and responses were compared for the period after 1950, when climate data was more reliable.

In the Dinarides and the Carpathians, young beech and fir trees respond similarly to increasing precipitation under conditions of different light intensity; the differences lie in the maximum assimilation efficiency (Φ) of the fir under the canopy and of the beech in the open despite optimal nutrient conditions (N_{tot} in leaves or needles). Rising temperatures have a negative effect on beech in the Dinarides and Carpathians and on fir in the Carpathians; in the Dinarides, the rise in temperature has a positive effect on fir due to sufficient precipitation. In the Carpathians, the differences in response between old-growth reserves and managed forests are smaller than in the Dinarides. Soil respiration was closely related to soil properties and less to climate or micrometeorological parameters. Therefore, the potential influence of climate on the input of new organic matter through forest productivity and species composition will play an important role in the decomposition and storage of soil organic matter.

A more pronounced response of tree growth to climate (temperature and precipitation) was observed on the eastern side of the Carpathians, while it was less pronounced or even absent in the southern locations. Both beech and fir show better radial growth with higher precipitation in July and slower growth with higher average and maximum temperatures in June of the current year. Fir shows a positive correlation between radial growth and temperature in winter, while beech shows a negative correlation between radial growth and temperature in summer. In the period 1951-1960, the average tree ring widths of fir and beech were largest at southern sites compared to other sites, while since 2011 they have increased the least at southern sites

and the most at northern sites. Northern sites are becoming increasingly favourable for the growth of both species, especially fir. Fir on northern sites grew less well in the period 1970 to 1980, and the decline in growth may be related to the onset of the growth depression in the 1960s, followed by an improvement in growth in the 1980s. Beech and fir respond differently to climatic parameters at the selected sites, with fir being more drought tolerant than beech.

The parameterised Vaganov-Shashkin model, which uses RCP 4.5 projections, predicted growth until 2050. Observations indicate a better adaptability of fir to drier conditions. In northern locations, growth was limited by low temperatures, in southern locations by increasing moisture deficits, which intensify towards the east. At northern sites, fir was more sensitive to cold than beech, which has moisture limitations, confirming fir's better adaptability to drought. There was a gradual convergence of northern sites to climatically limited growth in south-western sites.

For fir, there is a negative correlation between the relative conductive surface and the cell density, the average cell surface area and the cell density, and the mean thickness of tangential cell walls and the relative conductive surface. Measured tracheal properties in beech show correlations with tree ring width. Beech and fir respond differently to climate parameters at the selected sites, which indicates an adaptation to local conditions. Wood-anatomical characteristics corresponded with the increment analyses.

Despite the adaptability of beech stands, the future survival of beech and other temperate tree species is uncertain, as the pace and intensity of climate change varies from area to area. Although fir shows greater drought tolerance than beech, its conservation in Slovenia will be difficult without protection and more intensive investment due to the increasing number of extreme events, lower competitiveness and the unresolved problem of herbivores.

5 VIRI

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PRILOGE

PRILOGA A: Dovoljenje založnika za objavo članka »Effect of temperature, water availability, and soil properties on soil CO₂ efflux in beech-fir forests along the Carpathian Mts« v tiskani in elektronski verziji doktorske disertacije

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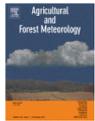
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PRILOGA B: Dovoljenje založnika za objavo članka »Climate growth limitations of European beech and silver fir along the Carpathian arc – the recent state and future prospects« v tiskani in elektronski verziji doktorske disertacije



Climate growth limitations of European beech and silver fir along the Carpathian arc – the recent state and future prospects

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