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Zapis zmian klimatycznych oraz zaburzeń w szerokościach przyrostów rocznych modrzewia (*Larix decidua* Mill.) i limby (*Pinus cembra* L.) w Tatrach

The record of climatic changes and disturbances in tree rings of European larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) in the Tatras

Rozprawa doktorska

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SPIS TREŚCI

STRESZCZENIE

Zmiany klimatyczne zachodzące na przestrzeni ostatnich dekad manifestują się w postaci wzrostu temperatur, zmiany wzorca rozmieszczenia i intensywności opadów oraz wzroście liczby ekstremalnych zdarzeń. Wiedza o dotychczasowym wpływie zmian klimatu na przyrost drzew może być pomocna w przewidywaniu ich reakcji w przyszłości. W przyrostach rocznych oprócz wpływu elementów klimatycznych, zaznaczają się również zaburzenia. Badania rekonstruujące historię zaburzeń oparte są głównie o gatunki cienioznośne (m.in. świerk *Picea abies* (L.) H. Karst), które są w stanie długo trwać w niekorzystnych warunkach świetlnych i bezpośrednio reagować na uwolnienie spod presji konkurencji. Brakuje empirycznych danych o reakcjach gatunków światłożądnych (modrzewia *Larix decidua* Mill.i limby *Pinus cembra* L.) na uwolnienia.

Badania prowadzono w dwóch unikalnych obszarach Tatr Wysokich – powierzchni powiatrowałowej o znanej historii zaburzeń na południowych stokach słowackich Tatr oraz w lasach urwiskowych Tatr polskich. Głównym celem niniejszej rozprawy było określenie dynamiki przyrostu na grubość wybranych gatunków drzew w aspekcie czasowym. Wyniki badań przedstawiono w postaci trzech spójnych tematycznie artykułów naukowych, opublikowanych w międzynarodowych czasopismach o wysokim wskaźniku wpływu. Badania przeprowadzono w oparciu o ciągi przyrostowe 83 modrzewi i 104 limb. Posługując się zarówno miesięcznymi, jak i dobowymi danymi klimatycznymi zbadano wpływ elementów klimatycznych (temperatury powietrza i opadów atmosferycznych) na przyrost drzew w okresie ostatniego stulecia. Ponadto, zidentyfikowano oraz przeanalizowano wpływ zaburzeń na przyrosty roczne badanych gatunków.

Modrzewie wykazały reakcję przyrostową na otwarcie drzewostanu po wiatrowale w wyniku polepszenia warunków świetlnych. Opóźnienie reakcji na zaburzenie (około 4–5 lat) było zależne od pierśnicy, wieku drzewa oraz poprzedniego przyrostu. Reakcje przyrostowe modrzewia na klimat nie były stabilne w czasie. Generalna tendencja, że temperatura lata pozytywnie wpływa na przyrost, zanika po wiatrowale. Ciepły lipiec zaczyna negatywnie wpływać na przyrost, co można wiązać z deficytem wody w otwartym drzewostanie w okresie letnim. Potwierdza to pojawiający się pozytywny wpływ opadów lipca na przyrost modrzewi.

Przyrost radialny sosny limby w lasach urwiskowych Tatr był pozytywnie skorelowany z temperaturą miesięcy letnich (czerwca i lipca) przez cały okres analiz, a opady w tych miesiącach istotnie ograniczały przyrost drzew. Uwolnienia w przyrostach limby nie wykazują ścisłej synchronizacji, co wskazuje, że przeszłe zaburzenia miały charakter lokalny a nie wielkoskalowy. Dzięki zastosowaniu danych o dużej rozdzielczości (dobowych danych klimatycznych) wykazano, że kluczowy okres dla przyrostu sosny limby w lasach urwiskowych Tatr to 15 dni od 21 czerwca do 4 lipca. Warto podkreślić, że w ostatnich dekadach maleje wpływ temperatury powietrza na przyrost, głównie temperatury minimalnej. Tym samym, zmniejsza się znaczenie temperatury, jako czynnika minimum, ograniczającego przyrost drzew przy górnej granicy lasu.

Niniejsze badania są pierwszą próbą połączenia wpływu czynników środowiskowych takich jak zaburzenia i klimat na przyrost światłożądnych gatunków drzew w lasach górskich. Należy podkreślić, że reakcje drzew na zmiany czynników środowiskowych nie są jednorodne i w zależności od gatunku, lokalnych warunków siedliskowych oraz struktury drzewostanu będą one różne. Dlatego badania w różnej skali czasowej i przestrzennej są niezbędne by w pełni zrozumieć dynamikę lasów górskich w obliczu zmian klimatycznych.

ABSTRACT

Climate change over recent decades is manifested in rising temperature, changes in the precipitation pattern, and an increase in the number of extreme disturbances. Knowledge of the impact of current climate changes on tree growth may help predict their response in the future. Tree-ring patterns are determined by climatic factors as well as past disturbances. In this research we studied two light-demanding species: European larch and Swiss stone pine. Reconstruction of disturbance historical disturbances is based mainly on shade-tolerant species (e.g., Norway spruce *Picea abies* (L.) H. Karst), which can survive for a long time in unfavourable light conditions (suppression) and can respond rapidly to canopy opening (reduced competition). There is a lack of empirical evidence about the growth reactions of light-demanding species (e.g. European larch *Larix decidua* Mill., Swiss stone pine *Pinus cembra* L.) to disturbances.

The study areas are located in two unique stands in the High Tatras: a post-windstorm area with a known disturbance history on the southern slopes of the Slovakian Tatras, and a cliff forest on the upper treeline ecotone of the Polish Tatras. The main aim of this dissertation was to determine the dynamics of annual growth of selected tree species over time. The results are presented as three thematically coherent research articles published in international scientific journals with high impact factors. The research was based on 83 synchronized ring width series of larches, and 104 of stone pine. Monthly and daily climate data (air temperature, precipitation) were used to determine how climate change affected the formation of tree rings over the last century, and the growth release patterns were analysed to reconstruct the disturbance regime.

European larch responded with a delay to stand opening after the windstorm (ca. 4–5 years). The lag time was significantly correlated with diameter at breast height, the age of the studied trees, and previous growth. The trees' growth reactions to climate were not stable over time. A positive influence of summer temperature disappeared after the windthrow in 2004. Furthermore, a water deficit changed in the open canopy forest, as confirmed by significant positive correlations between growth and July precipitation.

The radial growth of Swiss stone pine in the cliff forest was positively correlated with summer temperature (June and July) through the entire analysed period. Also, precipitation limited tree growth in these months. The past disturbance does not

show synchronized release patterns. Past disturbances was not associated with synchronized releases. This may suggest that disturbances occurred locally rather than on a large spatial scale. The use of daily climate data gave more detailed results on the climate–growth pattern of Swiss stone pine. Temperature from mid-June to mid-July was the key factor influencing the growth of trees on the cliffs. The study confirmed that summer temperature is a key factor limiting the growth of these trees, but this pattern has been diminishing in the last decades, especially for minimum temperature.

The general result of our study is that temperature has become less important as a growth factor at high elevations in the Carpathians. The results presented in this dissertation may help in predicting the climatic optimum for the studied species and the possible extent of their elevation range in the future. The methodological novelty of this work was its combined study of the influence of both disturbance and climate on annual tree growth in light-demanding species.

WYKAZ PUBLIKACJI WCHODZĄCYCH W SKŁAD ROZPRAWY DOKTORSKIEJ

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Artykuł nr 1: Izworska, K., Muter, E., Fleischer, P., Zielonka, T. 2022. Delay of growth release after a windthrow event and climate response in a light-demanding species (European larch *Larix decidua* Mill.). Trees 36: 427–438.
DOI: https://doi.org/10.1007/s00468-021-02218-4
IF: 2,3; Punkty MEiN: 100

Artykuł nr 2: Izworska, K., Muter, E., Matulewski, P., Zielonka, T. 2023. Tree rings as an ecological indicator of the reaction of Swiss stone pine (*Pinus cembra* L.) to climate change and disturbance regime in the extreme environment of cliff forests. Ecological Indicators 148: 110102.
DOI: https://doi.org/10.1016/j.ecolind.2023.110102
IF: 6,9; Punkty MEiN: 200

Artykuł nr 3: Izworska, K., Zielonka, T., Matulewski, P., Muter, E. 2023. Daily Climatic Data Better Explain the Radial Growth of Swiss Stone Pine (*Pinus cembra* L.) in High-Elevation Cliffs in the Carpathians. Forests 14 (7): 1411.
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1. WSTĘP

Zmiany klimatyczne zachodzące na przestrzeni ostatnich dekad można dostrzec w postaci wzrostu temperatury, zmiany wzorca rozmieszczenia i intensywności opadów oraz wzroście liczby ekstremalnych zdarzeń (Allen i in. 2010; Seidl i in. 2017; Esper i in. 2020; IPCC 2021). Wpływ tych zmian na drzewostany jest zróżnicowany pod względem regionalnym i czasowym (Oberhuber i in. 2008; Popa i Kern 2009; Babst i in. 2013). Prognozuje się, że największy wzrost średniej rocznej temperatury będzie miał miejsce na wschodzie Europy w miesiącach zimowych, zaś latem w zachodniej Europie. Suma opadów letnich zmniejszy się w całej Europie, natomiast opady zimowe wzrosną na północy kontynentu (Lindner i in. 2010). Cieplejsze i bardziej suche warunki szczególnie sprzyjają pożarom, suszom i gradacjom owadów, natomiast cieplejsze i bardziej wilgotne warunki zwiększają zaburzenia powodowane przez wiatr i choroby grzybowe (Seidl i in. 2017). Przewiduje się, że w nadchodzących dziesięcioleciach zmiany klimatyczne silnie wpłyną na skład gatunkowy (Gonzalez i in. 2010, Hanewinkel i in. 2013), strukturę (Elkin i in. 2013) i produktywność (Boisvenue i Running 2006) przyszłych drzewostanów (Huber i in. 2021). Równocześnie, zasięgi występowania gatunków drzew będą się zmieniać wraz z postępującymi zmianami klimatycznymi (Casalegno i in. 2010; Camarrero i in. 2017; Dyderski i in. 2018, Babst i in. 2019). Wiedza o wpływie dotychczasowych zmian klimatu na przyrost drzew może być pomocna w przewidywaniu ich reakcji w przyszłości.

Drzewa w ciągu swojego życia podlegają działaniu wielu czynników wpływających na ich przyrost. Zmiany warunków środowiska wpływają na tempo podziałów komórkowych i w konsekwencji szerokości przyrostów rocznych (Tranquillini 1979; Schweingruber 1996). Słoje roczne, czyli warstwy drewna wtórnego, w warunkach klimatu umiarkowanego tworzone są w każdym roku w okresie aktywności kambium. Różnicowanie się komórek drewna jest ściśle powiązane z parametrami środowiskowymi, które ulegają corocznym zmianom. Odmienne warunki, w pełnym spektrum zmienności, aż do ekstremalnie negatywnych i pozytywnych, mogą hamować lub przyspieszać podziały kambium i dalszy wzrost komórek drewna (Wimmer 2002; Rossi i in. 2006; Bräuning i in. 2016; Carrer i in. 2018). Przyrosty roczne stanowią zatem cenne źródło informacji o różnorodnych zmianach zachodzących w środowisku, a ponieważ drzewa są organizmami długowiecznymi, zmiany te można śledzić na przestrzeni setek, a nawet tysięcy lat. Stąd, długoterminowe informacje o dynamice szerokości słojów rocznych z powodzeniem wykorzystuje się do określenia wpływu elementów klimatycznych na przyrost drzew oraz rekonstrukcji przeszłego klimatu (Fritts i in. 1976; Briffa i in. 2004; Schweingruber i in. 2006; Allen i in. 2010; Esper i in. 2019).

W Alpach, izotermy w ostatnim stuleciu podniosły się w wyniku wzrostu temperatury (Rubel i in. 2017). Również w Tatrach obserwujemy wzrost średniej rocznej temperatury w ciągu ostatniego stuleciu od +0,6 do +2,0°C (Izworska i in. 2023a). Słoje drzew rosnących w ekstremalnych warunkach środowiskowych w górach, mogą być dobrymi wskaźnikami fizjologicznej reakcji roślin na zmiany klimatyczne (Fritts i in. 1976; Körner i Paulsen 2004; Adler i in. 2022). W badaniach dendroklimatycznych analizuje się głównie związki pomiędzy szerokością przyrostu, a temperaturą powietrza i opadami. Dla obszarów wysokogórskich, temperatura jest kluczowym czynnikiem ograniczającym przyrost drzew. Na dużych wysokościach, sezon wegetacyjny jest krótki i ogranicza się do miesięcy letnich, w których fotosynteza jest najbardziej intensywna (Tranquillini 1979; Körner 2004; 2015; Rossi i in. 2016). Jednak, jak pokazują ostatnie badania, ta ogólna zasada uzależniona jest od warunków lokalnych (Büntgen i in. 2007; 2015; Bošeľa i in. 2021; Begović i in. 2023; Unterholzner i in. 2023; Izworska i in. 2023a). Reakcje drzew na poprawę warunków termicznych, szczególnie w lasach górskich, są bardzo zróżnicowane i nie zawsze bezpośrednią konsekwencją wzrostu temperatury jest poprawa przyrostu drzew (D'Arrigo i in. 2008; Harsch i in. 2009; Isaac-Renton i in. 2018). Również temperatura jesieni roku poprzedniego ma wpływ na szerokość przyrostów w roku bieżącym. Jest to okres rozwoju pąków i gromadzenia zapasów na kolejny sezon wegetacyjny oraz ważny etap budowania ochrony przed zimowymi mrozami, wiatrem i suszą (Tranquillini 1982; Mayr i in. 2006). Ze względu na wyższe opady w obszarach górskich, woda zwykle nie stanowi czynnika minimum. Dlatego pojawienie się intensywnych opadów w środku sezonu wegetacyjnego negatywnie wpływa na przyrost drzew z powodu większego zachmurzenia i obniżenia temperatury powietrza (Bednarz 1981; Körner 2012; Izworska i in. 2023a; 2023b). Ważną rolę odgrywa również dostępność wody zmagazynowanej w glebie, która jest okresowo niezależna od opadów atmosferycznych (Tranquillini 1979; Körner i Paulsen 2004; Körner 2012). Wahania grubości pokrywy śnieżnej w Alpach wskazują, że czas jej trwania zmniejszał się w ciągu ostatnich 50 lat o 5% na każdą dekadę. Izolacyjne właściwości pokrywy śnieżnej wpływają na temperaturę gleby, co może mieć znaczenie dla formowania się przyrostów wiosną (Havranek i Tranquillini 1995; Beniston 2012; Carrer i in. 2023).

W przyrostach rocznych oprócz wpływu elementów klimatycznych, zaznaczają się również zaburzenia (zarówno naturalne, jak i antropogeniczne). Naturalne zaburzenia kształtują dynamikę lasu (rozpad drzewostanu, odnowienie) i procesy w nim zachodzące, przez co kontrolują funkcjonowanie całych ekosystemów leśnych. Reżim zależy od intensywności i częstotliwości zaburzeń oraz ich zasięgu przestrzennego. Może on wpływać na różnorodność gatunkową drzewostanów przez selektywne oddziaływanie na niektóre gatunki, strukturę wiekową i długość trwania generacji (Splechtna i in. 2005; Black i in. 2016; Trotsiuk i in. 2018; Altman 2020). Zaburzenia stanowią silny sygnał w przyrostach rocznych, dlatego możliwa jest ich retrospektywna identyfikacja. Warunki świetlne w drzewostanie regulowane są przez konkurencję pomiędzy drzewami. Drzewa przygłuszone (nadmiernie ocienione) mogą nawet przez dziesięciolecia wytwarzać znacznie węższe słoje niż drzewa rosnące w dobrych warunkach świetlnych. Po uwolnieniu spod presji wyeliminowanego sąsiada, drzewa takie reagują gwałtownym zwiększeniem szerokości słojów (Lorimer i Frelich 1989; Fraver i White 2005; Chalupová i in. 2020). Nagłe zmiany przyrostu są powszechnie wykorzystywane do rekonstrukcji wcześniejszych zaburzeń w drzewostanach (Niklasson i in. 2002; Fraver i White 2005; Zielonka i in. 2010; Svoboda i in. 2011; Holeksa i in. 2016; Pyttel i in. 2019). W niniejszej pracy zaburzenie rozumiane jest jako otwarcie pułapu koron drzewostanu. Do takiej sytuacji może doprowadzić wiatrował, wiatrołom, czy lawina, powódź, trzęsienie ziemi, ale pod warunkiem, że doprowadzą do śmierci wielu drzew w drzewostanie, a te, które przetrwają będą miały lepsze warunki świetlne (Lorimer 1980; Lorimer i Frelich 1989, Nowacki i Abrams 1997). Rok zaburzenia może być określony jako początek tego procesu w szeregu słojów, jeśli przyspieszenie przyrostu po zaburzeniu przekracza zadany próg. Datę wystąpienia zaburzenia ustala się wówczas, jako rok przejścia od wąskich przyrostów do pierwszego roku sekwencji szerokich przyrostów po zaburzeniu (Lorimer i Frelich 1989; Nowackiego i Abramsa 1997; Fraver i White 2005; Trotsiuk i in. 2019). Badania rekonstruujące historię zaburzeń oparte są głównie o gatunki cienioznośne (m.in. świerk *Picea abies* (L.) H. Karst), które są w stanie długo trwać w niekorzystnych warunkach świetlnych i bezpośrednio reagować na uwolnienie spod presji konkurencji (Niklasson i in. 2002; Svoboda i in. 2011; Šilhán 2017). W przypadku gatunków światłożądnych (takich jak modrzew *Larix decidua* Mill. i sosna limba *Pinus cembra* L.), reakcja ta nie jest oczywista, ponieważ nie są one w stanie znosić długotrwałego, silnego ocienienia (Klopčič i in 2015; Chalupová i in. 2020). Należy podkreślić, że brakuje empirycznych danych o reakcjach gatunków światłożądnych na uwolnienia. Niektórzy badacze sugerują, że uwolnienie przyrostu może wystąpić kilka lat po zaburzeniu. Może to być efektem opóźnionej reakcji fizjologicznej i regeneracji drzewa po zaburzeniu, a także może wpływać na dokładność datowania zaburzeń (Chalupová i in. 2020; Izworska i in. 2021a).

Zaburzenia w lasach są zależne od klimatu. Nasze rozumienie dynamiki zaburzeń w odpowiedzi na zmiany warunków klimatycznych pozostaje niekompletne. Jest to szczególnie widoczne w odniesieniu do wzorców na dużą skalę, efektów interakcji i sprzężeń zwrotnych (Seidl i in. 2017). W niniejszej pracy analizowana jest dynamika przyrostów rocznych zarówno pod kątem wpływu klimatu jak i zaburzeń w dwóch unikalnych drzewostanach Tatr. Pierwszy z nich to bór *Larici–Piceetum*, położony na południowych stokach słowackich Tatr Wysokich, który cyklicznie nawiedzany jest przez huraganowe wiatry powodujące wielkopowierzchniowe wiatrowały. Taka dynamika lasu, oparta na pojawiających się co kilkadziesiąt lat wiatrowałach, tworzy warunki dla współistnienia dwóch gatunków o różnych wymaganiach ekologicznych: cienioznośnego świerka i światłożądnego modrzewia (Fleischer 2008). Ostatni wiatrował, który wystąpił w 2004 roku, daje doskonałą możliwość śledzenia reakcji przyrostowych modrzewia na to zdarzenie w dobie zachodzących zmian klimatycznych (Artykuł 1). Drugi obszar badań to urwiskowe lasy z reliktową sosną limbą w polskiej części Tatr Wysokich. Ten unikalny ekosystem może być użytecznym modelem do badań dynamiki przyrostów rocznych w obliczu ekstremalnych warunków środowiskowych (Artykuł 2 i 3). Tatrzańskie lasy urwiskowe rosną na szkieletowym podłożu z niską zawartością składników odżywczych (Zięba i in. 2019). Narażone są na zaburzenia powodowane przez silne wiatry oraz grawitację: obrywy skał, osuwiska, lawiny. Procesy geomorfologiczne mogą (ale nie muszą) być zainicjowane przez ekstremalne warunki pogodowe (silne opady deszczu, śniegu) oraz trzęsienia ziemi (Kotarba 2004; Malik i Wistuba 2012; Wistuba i in. 2021). Ten wyjątkowy ekosystem narażony jest na ekstremalne warunki pogodowe, także ze względu na duże amplitudy temperatury w różnych skalach czasoprzestrzennych, które są kontrolowane przez nasłonecznienie, wiatr i wilgotność (Tranquillini 1979; Körner i Paulsen 2004). Wszystkie te cechy wyróżniają lasy urwiskowe na tle lasów górskich, jako wyjątkowe środowisko, w którym słoje drzew mogą odzwierciedlać zmiany środowiskowe z większą wrażliwością.

Należy podkreślić, że reakcje drzew na zmiany czynników środowiskowych nie są jednorodne i w zależności od gatunku, lokalnych warunków siedliskowych (w tym glebowych i klimatycznych) oraz struktury drzewostanu będą one różne (Oberhuber i in. 2008; Popa i Kern 2009; Larysch i in. 2021). Dlatego badania w różnej skali czasowej i przestrzennej są niezbędne by w pełni zrozumieć dynamikę lasów górskich w obliczu zmian klimatycznych. Badania oparte na długich ciągach przyrostowych, podjęte w niniejszej pracy, mogą być niezwykle przydatne w ocenie reakcji ekosystemów położonych na dużych wysokościach nad poziomem morza na zmiany klimatyczne z szerokiej perspektywy ekologicznej. Nowatorski charakter niniejszych badań polega na kompleksowej analizie wpływu elementów klimatycznych i zaburzeń na dynamikę przyrostu radialnego modrzewia i limby. O ile świerk, jako podstawowy gatunek górnoreglowy w Europie środkowej, jest dobrze poznany, znacznie mniej badań dotyczy modrzewia i limby. Ponadto te dwa światłożądne gatunki nie były analizowane pod kątem reakcji przyrostowych na zaburzenia. Klasyczne badania dendroklimatyczne oparte są na poszukiwaniu związków pomiędzy chronologiami a miesięcznymi danymi klimatycznymi. Jednak miesiące są dla roślin sztucznie wyznaczonymi przedziałami czasu, co wpływa ograniczająco na wyniki analiz (Vaganov i in. 2006; Jevšenak 2019; Pearl i in. 2020). Dostępność danych klimatycznych o większej rozdzielczości, takich jak dane dobowe, pozwala na nowatorskie podejście, uściślenie wyników dotychczasowych badań i dostarczenie szerszego spojrzenia na reakcje przyrostowe drzew.

2. CEL BADAŃ

Głównym celem niniejszej rozprawy było określenie dynamiki przyrostu na grubość drzew wybranych gatunków rosnących w Tatrach: modrzewia europejskiego i sosny limby. Reakcje przyrostowe drzew analizowano w aspekcie czasowym. Przyczyn określonych zachowań przyrostowych poszukiwano w oddziaływaniu zmiennych elementów klimatycznych (temperatury powietrza i opadów atmosferycznych) oraz występowaniu zaburzeń.

Cele szczegółowe:

Artykuł nr 1:

- analiza reakcji przyrostowych modrzewia europejskiego 15 lat po wielkoskalowym wiatrowale w listopadzie 2004 roku oraz rekonstrukcja reakcji przyrostowych na inne historyczne zaburzenia;
- określenie wpływu elementów klimatycznych na przyrost radialny modrzewia oraz sprawdzenie, czy relacja klimat-przyrost modrzewia zmienia się po wiatrowale w 2004 roku.

Artykuł nr 2:

- określenie wpływu miesięcznych elementów klimatycznych na przyrost radialny sosny limby w lasach urwiskowych Tatr i analiza zmian tych zależności w czasie;
- określenie reżimu zaburzeń lasów urwiskowych Tatr w oparciu o uwolnienia w przyrostach rocznych limby.

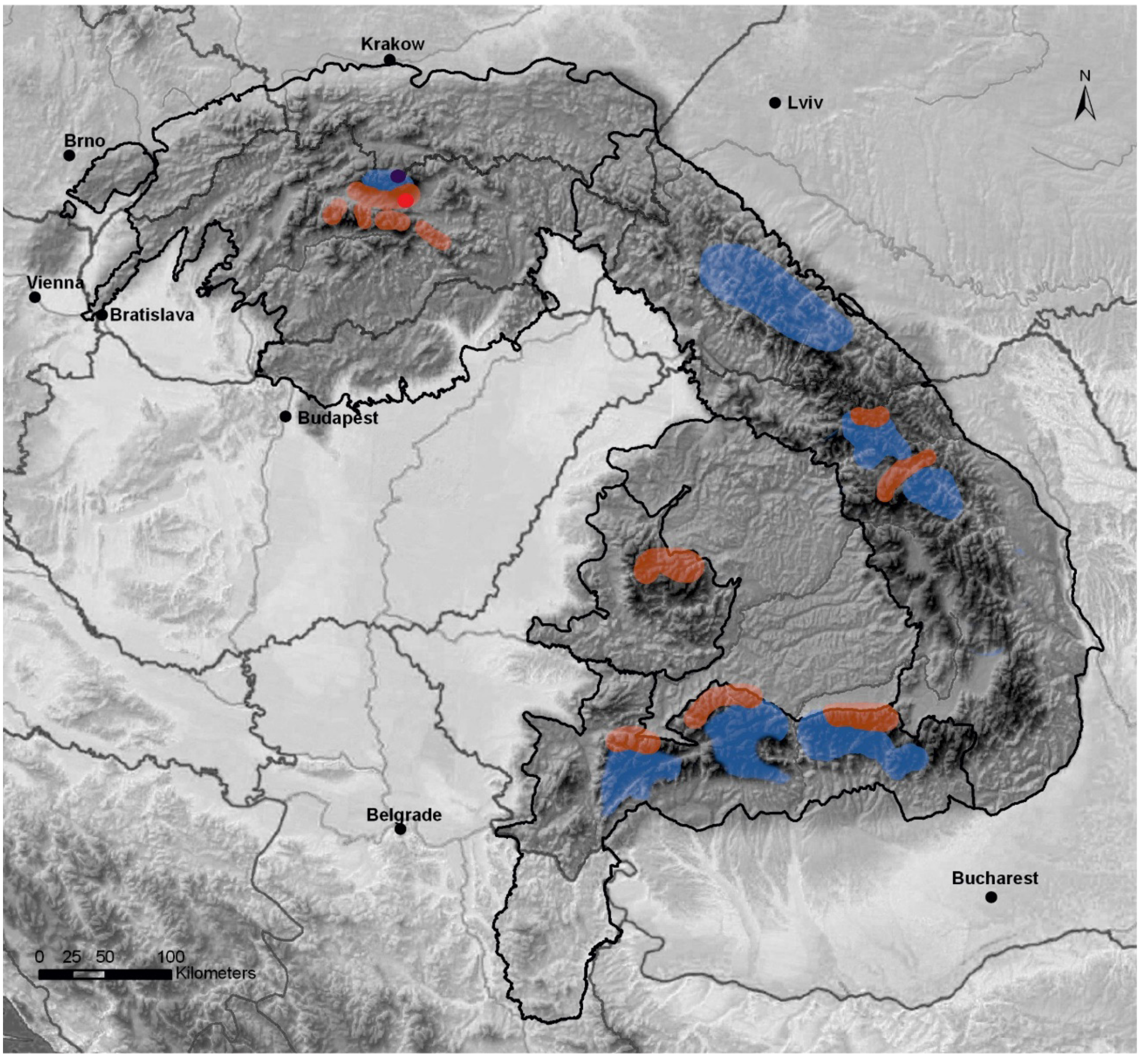
Artykuł nr 3:

- określenie wpływu klimatu w oparciu o dobowe dane klimatyczne na przyrost radialny sosny limby w lasach urwiskowych Tatr;
- określenie zmian reakcji przyrostowych limby w okresie ostatniego stulecia na średnie, minimalne i maksymalne temperatury dobowe oraz dobowe sumy opadów.

3. MATERIAŁY I METODY

3.1. Teren badań

Badania były prowadzone w Tatrach Wysokich (Karpaty Zachodnie) w obrębie TANAP'u (Tatranský Národný Park) na Słowacji (Artykuł nr 1) oraz Tatrzańskiego Parku Narodowego (TPN) w Polsce (Artykuł nr 2, 3) (Ryc. 1.).



Ryc. 1. Lokalizacja terenów badań (Artykuł nr 1 czerwona kropka oraz Artykuł nr 2, 3 fioletowa kropka) oraz zasięgu *Larix decidua* (pomarańczowy obszar) oraz *Pinus cembra* (niebieski obszar) w obszarze górskim Karpat (Caudullo i in. 2017).

Wywierty z modrzewia pobrano na powierzchni o wielkości 100 ha, założonej po wiatrowale, który miał miejsce 19 listopada 2004 roku (Artykuł nr 1). Huraganowy wiatr zniszczył 12000 ha drzewostanu, który przed wiatrowałem stanowił bór *Larici–Piceetum.* W celu prowadzenia wielokierunkowych badań związanych ze zmianami środowiskowymi po wiatrowale, pracownicy Stacji Badawczej TANAP założyli powierzchnie badawcze. Jedna z nich, o nazwie EXT site (skąd usunięto drewno) stanowiła teren badań (Artykuł nr 1, Fleischer 2008). Po zaburzeniu dominującym gatunkiem został modrzew. Obszar badawczy położony jest na łagodnym (ok. 15°) stoku na wysokości 1000–1300 m n.p.m. Dominują gleby bielicowe. Wśród roślin zielnych dominują borówka czarna *Vaccinium myrtillus*, borówka brusznica *Vaccinium vitis-idaea*, trzcinnik owłosiony *Calamagrostis villosa* i podbiałek alpejski *Homogyne alpina* (Fleischer 2008).

Wywierty z limb pobrano w lasach urwiskowych na stokach Czuby Roztockiej (1300–1525 m n.p.m.), Opalonego (1390–1605 m n.p.m.) oraz Żabiej Czuby (1465–1560 m n.p.m.; Artykuł nr 2, 3). Badane drzewa rosły na półkach skalnych o dużym nachyleniu (ok. 70–80°), na glebach ubogich, kwaśnych, wykształconych na granitowym podłożu. Drzewostany te tworzą górną granicę lasu na wysokości 1400–1500 m n.p.m., w których dominuje limba oraz świerk pospolity (*Picea abies* (L.) H. Karst.) wraz z pojedynczymi osobnikami kosodrzewiny (*Pinus mugo* Turra) i jarzębem pospolitym (*Sorbus aucuparia* L.) (Komornicki i Skiba 1996; Zięba i in. 2019).

Tatry Wysokie znajdują się w strefie klimatu umiarkowanego kontynentalnego ze znacznymi różnicami między dobowymi temperaturami maksymalnymi i minimalnymi oraz dużymi opadami (Niedźwiedź 1992). W latach 1926–2019 średnia roczna temperatura wynosiła 5,57°C (Tatranská Lomnica), w latach 1905–2009 5,1°C (Zakopane). Średnie roczne opady w tym okresie wynosiły 805 mm (Tatranská Lomnica), 1136 mm (Zakopane) (Izworska i in. 2023a).

3.2. Charakterystyka gatunków drzew

Modrzew europejski jest reliktowym gatunkiem o silnie pofragmentowanym zasięgu (Ryc. 1). W Alpach i Karpatach rośnie w wysokich partiach gór. W Alpach występuje do 2500 m n.p.m. tworząc wraz z limbą bory modrzewiowo-limbowe (*Larici-Cembretum*). W Tatrach polskich modrzewie rosną na nielicznych stanowiskach, np. u wylotu Doliny Roztoki, pod Czubą Roztocką i na zboczach Wołoszyna (do 1300 m n.p.m.; Myczkowski 1957; Bednarz 1969). Populacja modrzewia w Tatrach słowackich jest liczniejsza, głównie między Doliną Koperszadzką, a Doliną Cichą, gdzie gatunek ten współtworzy laski modrzewiowo-limbowe na południowych stokach Tatr (Holeksa i Szwagrzyk 2004). W odróżnieniu od nich, w niższych położeniach górskich w Tatrach słowackich modrzew jest ważną domieszką w borach świerkowych *Larici–Piceetum* (powyżej 1000 m n.p.m.) (Fleischer 2008). Właśnie z takiego stanowiska pobrany został materiał badawczy do Artykułu nr 1.

Optymalne warunki wzrostu odnajduje na dobrze ustrukturyzowanych i napowietrzonych glebach. Modrzew jest gatunkiem pionierskim, jednak jako gatunek światłolubny przegrywa w konkurencji z innymi drzewami (głównie ze świerkiem). Ze względu na te cechy, naturalnemu występowaniu oraz regeneracji modrzewia europejskiego sprzyjają częste zaburzenia występujące w wysokich górach (tj. osunięcia ziemi, lawiny, wiatrowały), które niszczą gatunki konkurencyjne lub zmieniają warunki siedliskowe. Jest dobrze przystosowany do klimatu kontynentalnego gór środkowej Europy – toleruje bardzo niskie temperatury w okresie zimowym. Przewiduje się, że zmiany klimatu doprowadzą do migracji populacji modrzewia europejskiego na wyższe wysokości, co na niektórych obszarach może poważnie ograniczyć jego występowanie (Fleischer i Homolová 2012; Holeksa i in. 2016; Klippel i in. 2020).

Sosna limba jest długowiecznym gatunkiem występującym w górnej granicy lasu w Alpach i Karpatach (Ryc. 1) (Casalegno i in. 2010; Caudullo i in. 2017; Beloiu i Beierkuhnlein 2019; Zięba i in. 2019). Dzięki silnemu systemowi korzeniowemu kolonizuje bardzo strome zbocza, skaliste półki, szczeliny i inne skrajne nisze, które nie są dostępne dla innych gatunków (głównie świerka) (Myczkowski i Bednarz 1974; Zięba i in. 2019). Zasięg populacji sosny limby jest pofragmentowany (Ryc. 1). Ponadto, działalność człowieka zmieniła ekoton górnej granicy lasu w Alpach i Karpatach z uwagi na historyczne użytkowanie gruntów (wypas owiec, eksploatacja przez drwali i górnictwo, a także obecna turystyka) (Popa i Kern 2009; Popa i in. 2017; Pini i in. 2017; Kučera 2019). Nadmierne pozyskiwanie sosny limby miało miejsce w przeszłości w Karpatach Południowych m.in. w górach Retezat (Beloiu i Beierkuhnlein 2019). Mimo, że populacje karpackie są znacznie mniejsze niż alpejskie, ich różnorodność genetyczna jest większa (Belokon i in. 2005; Höhn i in. 2009; Tóth i in. 2019). Reliktowe populacje sosny limby rosnące w lasach urwiskowych Tatr w niewielkim stopniu były dotknięte bezpośrednim wpływem działalności człowieka i mimo dużego rozdrobnienia charakteryzują się wysoką różnorodnością genetyczną (Dzialuk i in. 2014). Tatrzańskie bory limbowe tworzą dwa odrębne zbiorowiska roślinne. Te występujące na granitowym podłożu, podobne są do alpejskich lasów limbowych i tworzą zespół *Vaccinio-Pinetum cembrae* Oberd. 1962. Natomiast bory limbowe porastające wapienną część Tatr tworzą zbiorowisko *Swertio perennis-Pinetum cembrae* ass. nov. (Zięba i in. 2018). Łącznie zajmują 917 ha, z czego 166,38 ha w Tatrach Polskich. Występują w Tatrach Wysokich, Bielskich i Zachodnich na stromych stokach, położonych w strefie górnej granicy lasu (1300–1650 m n.p.m.) (Zięba i in. 2019).

3.3. Materiał badawczy

Materiał badawczy w postaci wywiertów z modrzewia i sosny limby zebrano w okresie jesiennym – po zakończeniu przyrostu na grubość u drzew. Na powierzchniach badawczych wytypowano drzewa żywe, bez widocznych uszkodzeń. Wywierty pobrano za pomocą świdra przyrostowego Presslera na wysokości pierśnicy (1,3 m). By przeanalizować zmiany w przyroście drzew wywierty z 42 modrzewi zostały pobrane w 2005 roku, a z 41 modrzewi 15 lat po zaburzeniu, czyli w 2019 roku (Artykuł nr 1). Materiał badawczy do Artykułu nr 2 i 3, stanowiły wywierty ze 104 limb rosnących w lasach urwiskowych Tatr.

Pobrany materiał poddano standardowej procedurze dendrochronologicznej: wywierty wysuszono, wyszlifowano oraz zeskanowano w rozdzielczości 2400 DPI (Schweingruberb 1996). Szerokości przyrostów rocznych zmierzono z dokładnością do 0,01 mm za pomocą programu WinDendro (Regent Instruments Canada Inc. 2009), a poprawność datowania pomierzonych słojów sprawdzono w programie COFECHA (Holmes 1983; Grissino-Mayer 2001). Do dalszych analiz wykorzystano zsynchronizowane serie przyrostów rocznych z 83 modrzewi i 104 limb.

3.4. Dane klimatyczne

Miesięczne dane klimatyczne (średnia miesięczna temperatura powietrza oraz miesięczna suma opadów atmosferycznych) pochodzą ze stacji meteorologicznej w Tatrzańskiej Łomnicy (49°9′ N; 20°17′ E, 827 m n.p.m., ok. 10 km od terenu badań, Artykuł nr 1) oraz w Zakopanem (49°17′36.48″ N; 19°57′ 36.97″ E, 846 m n.p.m., ok. 12 km od terenu badań, Artykuł nr 2). W analizach wykorzystano dane z Tatrzańskiej Łomnicy dla okresu: 1926–2019 (Artykuł nr 1) oraz z Zakopanego dla okresu 1905–2009 (Artykuł nr 2). Dobowe dane klimatyczne (średnia, maksymalna i minimalna temperatura oraz suma opadów, Artykuł nr 3) pobrano z bazy danych klimatycznych E-OBS (wersja 25.0e, regularna siatka 0,1 stopnia) dla punktu położonego najbliżej badanych drzew (49°12′54.48″ N; 20°4′34.68″ E) dla okresu 1921–2009 (Cornes i in. 2018).

3.5. Analizy dendrochronologiczne

Na podstawie zsynchronizowanych szerokości słojów rocznych obliczono chronologie rzeczywiste (TRW, Tree-ring width) dla modrzewia oraz limby. W celu wyeliminowania długookresowych trendów, fluktuacji oraz indywidualnych cech drzew dokonano standaryzacji (indeksacji) pomiarów, która jest zalecana przed podjęciem analiz dendroklimatycznych (Cook i in. 1990). W Artykule nr 1 standaryzację przeprowadzono wykorzystując ujemne funkcje wykładnicze, proste regresji o ujemnym albo dodatnim współczynniku nachylenia lub proste poziome przechodzące przez średnią szerokość słoja w programie ARSTAN (Cook i in. 2017). W Artykule 2 i 3 standaryzację przeprowadzono używając funkcji wielomianowej (*spline function)* w pakiecie dplR w R (Bunn 2010; R wersja 4.0.0 R Development Core Team 2020). Obliczając średnią z serii indeksów otrzymano chronologie indeksowane, osobno dla modrzewia i limby (TRWI, *tree-ring-width index*). Dla wszystkich serii pomiarów obliczono standardowe statystyki, w tym EPS (*Expressed Population Signal*) i Rbar (*Interseries correlations*). EPS jest miarą jakości chronologii i wyraża siłę sygnału klimatycznego zawartego w szerokościach słojów. Uznaje się, że EPS powyżej 0,85 daje podstawy do prowadzenia analiz dendroklimatycznych na podstawie danej chronologii. Rbar jest wskaźnikiem, który informuje o jednorodności (homogeniczności) reakcji przyrostowych w grupie badanych drzew (Wigley i in. 1987; McCarroll i Loader 2004).

3.6. Analizy dendroekologiczne

W celu rekonstrukcji zaburzeń analizowano nagłe zmiany szerokości przyrostów rocznych – uwolnienia. Metoda ta zakłada, że drzewa, które przeżyły zaburzenie (wiatrowały, wiatrołomy, lawiny niszczące drzewostany) reagują nagłym zwiększeniem szerokości przyrostów będącym efektem spadku konkurencji (głównie eliminacji sąsiednich drzew, czyli otwarcia stanowiska). Do wykrywania uwolnień wykorzystano najczęściej stosowaną metodę opartą na obliczeniach procentowej zmiany przyrostu (PGC, *percent growth change*) (Nowacki i Abrams 1997). PGC obliczono według wzoru:

$$\%PGC=(M2-M1)/M1x100,$$

gdzie %PGC to procentowa zmiana szerokości przyrostu w danym roku, M1 to średni przyrost z poprzednich 10 lat, a M2 z kolejnych 10 lat (Nowacki i Abrams 1997; Black i Abrams 2003). Dla modrzewia obliczenia wykonano według powyższej formuły, a wartości PGC w przedziale 50–100% przyjęto za zaburzenia o dużej intensywności (Artykuł nr 1, Nowacki i Abrams 1997; Black i Abrams 2003). Dla limby uwolnienia były skalowane według maksymalnego obserwowanego potencjalnego przyrostu, czyli linii granicznej (*boundary line*) i zdefiniowane jako uwolnienie, gdy %PGC ≥ 25% linii granicznej. Obliczenia przeprowadzono w pakiecie TRADER w R (Artykuł nr 2, Black and Abrams 2003; 2004; Altman i in. 2014, R Development Core, wersja 4.0.0).

W większości rekonstrukcji zaburzeń na podstawie przyrostów rocznych moment uwolnienia przyrostu utożsamiany jest z rokiem pojawienia się zaburzenia. Jednak reakcja przyrostowa może być opóźniona w czasie (Chalupová i in. 2020). Ponieważ w niniejszych badaniach znana była dokładna data powstania wiatrowału w 2004 roku, a także wcześniejsze historyczne wiatrowały, można było przeanalizować potencjalne opóźnienie uwolnień przyrostu na otwarcie drzewostanu. Taka sytuacja może być konsekwencją opóźnionej reakcji fizjologicznej i regeneracji drzew po zaburzeniu (Chalupová i in. 2020). W przypadku modrzewia (Artykuł nr 1) obliczono opóźnienie uwolnień przyrostu (*time lag*) po wiatrowale w 2004 roku i historycznych wiatrowałach (1869, 1915 i 1941) (Vadas 1916; Koreň 1994; Zielonka i Malcher 2009). W celu określenia zależności między opóźnieniem uwolnienia, a pierśnicą drzewa (DBH), wiekiem drzewa i poprzednim przyrostem (PG, *previous growth*) dla wymienionych wiatrowałów obliczono współczynniki korelacji.

W celu określenia wpływu historycznych zaburzeń na przyrost radialny sosny limby (Artykuł nr 2) w lasach urwiskowych Tatr, porównano go z udokumentowanymi i zarchiwizowanymi informacjami o trzęsieniach ziemi i intensywnych opadach tj. roczną sumą opadów, sumą opadów letnich od czerwca do sierpnia, oraz sumą opadów jesiennych od września do października (Kotarba 2004).

3.7. Analizy dendroklimatologiczne

Analizy wpływu miesięcznych elementów klimatycznych (średnich miesięcznych temperatur i miesięcznych sum opadów) oraz ich zmian, na szerokości słojów modrzewia i sosny limby przeprowadzono w programie DendroClim2002 (Artykuł nr 1 i 2; Biondi i Waikul 2004). Obliczono współczynniki korelacji prostej i regresji wielokrotnej pomiędzy chronologiami indeksowanymi TRWI, a danymi klimatycznymi, wykorzystując metody bootstrapowe. Polegają one na losowaniu liczb ze zbiorów danych do wielkości próby N = 1000 i na tej podstawie testowaniu istotności współczynników korelacji i regresji na poziomie $p \leq 0,05$ (Biondi i Waikul 2004). Wpływ klimatu na przyrosty modrzewia (Artykuł nr 1) określono dla całego okresu dostępnych danych (1926–2019) oraz dla dwóch 15-letnich podokresów przed wiatrowałem (1990–2004) i po wiatrowale (2005–2019). Analizy obejmowały okno czasowe od października roku poprzedniego do września roku bieżącego (Artykuł nr 1). Dla limby (Artykuł nr 2) określono wpływ klimatu dla trzech 35-letnich podokresów (1905–1939, 1940–1974, 1975–2009), aby sprawdzić, czy zmienił się wzorzec zależności przyrost-klimat. Analizy obejmowały okno czasowe od sierpnia roku poprzedniego do września roku bieżącego (Artykuł nr 2).

Ponadto, w celu określenia zmian wpływu średnich miesięcznych temperatur oraz miesięcznych sum opadów na przyrost badanych modrzewi i limb, przeprowadzono analizy metodą *moving intervals* w programie DendroClim2002 (Biondi i Waikul 2004). Dla modrzewia obliczenia wykonano w 30-letnich okresach, przesuwanych rok po roku od 1926–1955 do 1990–2019 (Artykuł nr 1). W przypadku sosny limby obliczenia wykonano od w 30-letnich okresach od 1905–1934 do 1980–2009 (Artykuł nr 2). W ten sposób uzyskano informacje na temat charakteru zmian zależności (słabnąca lub coraz silniejsza), pomiędzy poszczególnymi elementami klimatu, a przyrostami badanych gatunków drzew.

Zależności pomiędzy przyrostem sosny limby na grubość, a dobowymi temperaturami (średnią, maksymalną i minimalną) oraz sumami opadów zostały przeprowadzone dla okresu 1921–2009 oraz dla dwóch podokresów (1921–1965 i 1966–2009), by wykazać ewentualne zmiany we wzorcu związków klimat-przyrost w ostatnich dziesięcioleciachmi (Artykuł nr 3). W tym celu wykorzystano funkcję 'daily_response()' z pakietu 'dendroTools' w R (Jevšenak i Levanič 2018; Jevšenak 2019). Przy jej pomocy obliczono współczynniki korelacji pomiędzy chronologią indeksowaną TRWI, a zagregowanymi danymi dobowymi, uśrednionymi w oknie czasowym od 7 do 210 dni, czyli dla okresów od jednego tygodnia do 7 miesięcy, potencjalnie ważnymi dla przyrostu limby. Analizy obejmowały miesiące od lipca poprzedniego roku do września bieżącego roku (Artykuł nr 3).

4. WYNIKI

Artykuł nr 1

Skonstruowana chronologia rzeczywista (TRW) modrzewia europejskiego w Tatrach Słowackich obejmuje 239 lat w okresie 1781–2019. Obliczony wskaźnik EPS dla okresu analiz dendroklimatycznych 1926–2019 wynosi 0,96 i wskazuje na bardzo silny sygnał klimatyczny zawarty w słojach tej populacji drzew. Wskaźnik Rbar wynosi 0,41, co świadczy o wysokiej homogeniczności reakcji przyrostowych badanych modrzewi.

Wykazano, że okesie po wiatrowale (2004–2014) 78% drzew zareagowało reakcją przyrostową powyżej 50% PGC, a 34% bardzo silną reakcją powyżej 100% PGC. Najwięcej drzew wykazało reakcje przyrostowe w 2007 roku. Reakcje przyrostowe obserwowano w okresie 10 lat po historycznych wiatrowałach (1869, 1915, 1941). Od 38% do 67% drzew wykazało reakcje powyżej 50% PGC. Uwolnienia w przyrostach rocznych nie następowały bezpośrednio po zaburzeniach. Średnie opóźnienie w reakcjach przyrostowych na wiatrowały wynosiło 3,4 do 5,5 lat (mediana 4). Wykazano, ujemną korelację między opóźnieniem reakcji, a pierśnicą ($r = -0.27$) i wiekiem drzewa ($r = -0,27$) dla historycznych zaburzeń ($p < 0.01$). W przypadku wiatrowału z 2004 roku opóźnienie było zależne od poprzedniego przyrostu (PG; $r = -0,47$). PGC było zależne od szerokości pierśnicy dla historycznych wiatrowałów ($r = - 0,38$) oraz dla wiatrowału z 2004 roku ($r = -0,48$) i poprzedniego przyrostu ($r = -0,39$) dla zaburzeń z lat 1869, 1915 i 1941.

Analiza dendroklimatyczna wykazała, że w całym analizowanym okresie (1926–2019) modrzewie reagowały szerokimi przyrostami na wysokie temperatury w marcu i czerwcu roku tworzenia słoja oraz obfite opady w listopadzie ubiegłego roku i niskie opady we wrześniu roku bieżącego. Ponadto wykazano, że reakcje badanych drzew na klimat zmieniały się w ciągu ostatnich stu lat. W ciągu ostatnich lat po zaburzeniu, zanika istotny pozytywny wpływ wysokiej temperatury maja i czerwca, a ujawnia się istotny negatywny wpływ wysokiej temperatury lipca. Ze względu na wykorzystanie 30-letnich okien czasowych, współczynniki korelacji nie oddają wyraźnie reakcji przyrostu na klimat przed i po wiatrowale w 2004 roku i są trudne do interpretacji. Dlatego zbadano różnice w reakcjach przyrostu na klimat obliczone dla 15 lat przed i po wiatrowale (1990–2004, 2005–2019). Stwierdzono istotny pozytywny wpływ obfitych opadów w lipcu roku tworzenia słoja (r = 0,52, N = 15, p = 0,045) po wiatrowale, natomiast we wcześniejszym okresie wartość ta była bliska 0. Wyniki tych analiz wskazują, że pozytywny wpływ wysokiej temperatury w lipcu kończy się w latach 80. XX wieku. Odwrotna zależność pojawia się po wiatrowale w 2004 roku, czyli ciepły lipiec wpływa negatywnie na przyrost radialny modrzewia. Jest to najprawdopodobniej związane z deficytem wody, co potwierdza wysoka i istotna korelacja z opadami w lipcu w okresie ostatnich 15 lat. Jest to prawdopodobnie połączony efekt ocieplenia klimatu i otwarcia drzewostanu po wiatrowale.

Artykuł nr 2

Skonstruowana chronologia rzeczywista (TRW) sosny limby w lasach urwiskowych Tatr obejmuje 449 lat w okresie 1561–2009. Obliczony dla okresu analiz dendroklimatycznych 1905–2009 wskaźnik EPS wynosi 0,955 i wskazuje na bardzo silny sygnał klimatyczny zawarty w słojach tej populacji drzew. Wskaźnik Rbar wynosi 0,178, co może wynikać z faktu, że badane drzewa rosną w trudnych warunkach lasów urwiskowych i charakteryzują się silnymi, indywidualnymi fluktuacjami i trendami przyrostu radialnego, różny jest także ich wiek. Wartości Rbar generalnie są wyższe w bardziej jednorodnych drzewostanach/obszarach.

Analiza dendroklimatyczna wykazała, że we wszystkich analizowanych podokresach (1905–1939, 1940–1974, 1975–2009) limby reagowały szerokimi przyrostami na wysokie temperatury w czerwcu i lipcu roku tworzenia słoja, co zgadza się z obserwacjami innych autorów i jest stabilne w czasie. Jednak porównanie wyników analiz dendroklimatycznych dla innych miesięcy pokazuje, że zmienił się wzorzec relacji przyrost-klimat. O ile w dwóch pierwszych podokresach wysokie temperatury jesienią poprzedniego roku wpływały pozytywnie na przyrost limby, w ostatnim okresie brak jest takiej zależności. W pierwszym podokresie zaznaczyła się istotna ujemna korelacja z temperaturą marca, która w następnych dwóch podokresach nie wystąpiła. Można to powiązać z faktem, że w trakcie długich, surowych zim, wczesnowiosenne ocieplenie prowadziło do suszy mrozowej. Od kilku dekad temperatura w styczniu, lutym i marcu systematycznie rośnie, co może tłumaczyć brak tej zależności w ostatnich dwóch podokresach. W dwóch pierwszych podokresach opady w czerwcu i/lub lipcu wpływały negatywnie na przyrost limby. W ostatnim 35-leciu zależności te nie są istotne statystycznie, natomiast zaznacza się istotna pozytywna zależność od opadów w styczniu. Zjawisko to stwierdzono również w Alpach, co tłumaczy się faktem, że gruba pokrywa śnieżna stanowi warstwę izolacyjną i chroni glebę przed głębokim zamarzaniem.

Przeprowadzono rekonstrukcję uwolnień w przyrostach rocznych limby w lasach urwiskowych w okresie 1753–1999 (dla N ≥10 drzew). Najstarsze uwolnienie odnotowano w 1770 roku. W okresie 1820–1826, 63% drzew wykazało uwolnienia. Kolejne istotne epizody przypadają na koniec XVIII wieku (1787–1795), gdy 46% drzew zareagowało silnym uwolnieniem oraz połowa XIX wieku (1850–1857), gdzie u 24% drzew wykazano reakcje przyrostowe. Jednak nie wykazano silnej synchronizacji uwolnień w czasie, co sugeruje, że w ciągu ostatnich 250-u lat pojedyncze drzewa były eliminowane w sposób lokalny. Liczba drzew wykazujących uwolnienia nie była istotnie skorelowana z: roczną sumą opadów ($r = 0,06$, $p = 0,553$), sumą opadów miesięcy letnich ($r = 0,10$, $p = 0,322$) oraz sumą opadów miesięcy jesiennych ($r = 0,01$, $p = 0,921$). Tym samym, reżimu zaburzeń nie można powiązać bezpośrednio z występowaniem ekstremów opadowych, które potencjalnie mogły być odpowiedzialne zainicjowanie zaburzeń o charakterze geomorfologicznym w Tatrach. Na podstawie historycznych danych stwierdzono, że uwolnienia przyrostu nasiliły się po powodziach w latach 1960 i 1980. Mimo, że w analizowanym okresie odnotowano dziewięć trzęsień ziemi, nie znaleziono żadnego związku z uwolnieniami.

Artykuł nr 3

Dostępne dobowe dane klimatyczne obejmują lata 1921–2009. Ten przedział czasu chronologii TRWI sosny limby z lasów urwiskowych Tatr został wykorzystany do analiz dendroklimatycznych. Analizowano maksymalną, minimalną i średnią temperaturę dobową oraz dobowe sumy opadów i stwierdzono, że reakcje drzew na klimat nie były stabilne w czasie. Wykazano, że przyrost radialny sosny limby był najsilniej skorelowany ze średnią temperaturą w okresie od połowy czerwca (21.06) do początku lipca (04.07) ($r = 0,44$) i jest to zależność stabilna w czasie. Natomiast najbardziej wyraźne są zmiany wpływu temperatury minimalnej na przyrost limby. W pierwszym podokresie analiz (1921–1965), temperatura minimalna od końca sierpnia do połowy listopada poprzedniego roku oraz okresu letniego roku tworzenia słoja pozytywnie i istotnie wpływała na przyrost badanych drzew. Zależności te nie wystąpiły w drugim podokresie (1966–2009). Stwierdzono także negatywny wpływ opadów od połowy czerwca do początku lipca (co pokrywa się w czasie z pozytywnym wpływem temperatury lata) na przyrost radialny limby ($r = -0{,}35$) w okresie ostatnich 35 lat. Wysokie opady w okresie letnim oraz zachmurzenie z nimi związane, obniżają temperaturę i usłonecznienie, wpływając negatywnie na przyrost światłożądnej limby. Ponadto, w okresie 1921–1965 wykazano istotny negatywny wpływ opadów zimowych (od 25 grudnia poprzedniego roku do 2 lutego roku tworzenia słoja ($r = -0{,}38$) na przyrost limby. Trend ten odwrócił się w drugim analizowanym okresie (1966–2009) i obecnie wpływ obfitych opadów w zimie jest istotny i pozytywny ($r > 0.40$). Tym samym potwierdzono wyniki analiz prowadzonych w oparciu o miesięczne sumy opadów.

5. WNIOSKI

Artykuł nr 1

Modrzewie wykazały pozytywną reakcję przyrostową na otwarcie drzewostanu po wiatrowale w 2004 roku oraz wcześniejszych, historycznych wiatrowałach, jednak z opóźnieniem o około 4–5 lat. Drzewa grubsze, starsze i z większym wcześniejszym przyrostem reagują szybciej niż młode, cienkie i zdominowane, które reagują do 10 lat po zaburzeniu. Oznacza to, że w drzewostanie mieszanym ze świerkiem, modrzewie które mają dostęp do światła w koronach i stosunkowo dobry wzrost promieniowy, mogą nadal korzystać z gwałtownego otwarcia i reagować zwiększonym przyrostem.

Badane modrzewie reagowały szerokimi przyrostami na wysokie temperatury w marcu i czerwcu roku tworzenia słoja oraz obfite opady w listopadzie ubiegłego roku i niskie opady we wrześniu roku bieżącego. Reakcje przyrostowe modrzewia na klimat nie są stabilne w czasie. Po wiatrowale 2004 roku pojawia się negatywny wpływ wysokiej temperatury oraz pozytywny wpływ obfitych opadów w lipcu roku tworzenia słoja. Oznacza to, że wielkoskalowe zaburzenia, eliminujące okap drzewostanu na dużej powierzchni, mogą istotnie zmieniać wpływ elementów klimatu na przyrost światłożądnego gatunku. Tego typu zaburzenia wzmacniają efekt obecnych zmian klimatycznych, w których wysokie temperatury w środku lata i deficyt wody są kluczowymi czynnikami ograniczającymi przyrost drzew na południowych, cieplejszych skłonach Tatr.

Artykuł nr 2

Relatywnie długi, ponad stuletni okres analiz pozwala stwierdzić, że reakcje przyrostowe limby na klimat nie są stabilne w czasie. Chociaż wysoka temperatura w lecie (czerwiec-lipiec) w całym okresie analiz pozytywnie wpływa na przyrost radialny sosny limby w lasach urwiskowych Tatr, to zależności przyrostu od temperatury poprzedniej jesieni, zimy i wczesnej wiosny, które w przeszłości były istotne, obecnie straciły na znaczeniu. W ostatnich dekadach, negatywny wpływ obfitych opadów w lecie również zanika, co można wiązać z coraz cieplejszym latem. Obecne warunki klimatyczne w Tatrach wydają się promować wzrost limby i przesuwanie jej zasięgu w górę.

Uwolnienia w przyrostach sosny limby w lasach urwiskowych nie wykazują ścisłej synchronizacji, co wskazuje, że przeszłe zaburzenia miały charakter lokalny, a nie wielkoskalowy. Katastrofalne zdarzenia, takie jak ekstremalnie wysokie opady i trzęsienia ziemi, które mogłyby inicjować zaburzenia o charakterze geomorfologicznym, nie tłumaczą pojawiających się uwolnień. Reżimu zaburzeń nie można powiązać bezpośrednio z występowaniem określonych ekstremów klimatycznych w Tatrach. Dynamika lasów urwiskowych wydaje się być determinowana przez wydzielanie się pojedynczych drzew, uszkadzanych lub eliminowanych przez losowe czynniki.

Artykuł nr 3

Badania dendroklimatyczne na podstawie danych dobowych pozwalają znacznie dokładniej określić przedziały czasu (dni kalendarzowe), które determinują radialny przyrost drzew. Tak przeprowadzone analizy, z jednej strony potwierdzają wyniki uzyskane dla miesięcznych danych klimatycznych, ale dają znacznie bardziej precyzyjny obraz relacji przyrost-klimat. Pozwalają także uniknąć uogólnień formułowanych na temat wzrostu roślin w oparciu o sztucznie wyznaczone granice miesięcy. Jest to szczególnie istotne przy analizie przyrostu drzew na dużych wysokościach nad poziomem morza, na których okres wegetacyjny jest krótki, a elementy klimatyczne silnie ograniczają przyrost radialny.

W literaturze dendroklimatycznej dotyczącej limby, dotychczas wskazywano silny, pozytywny wpływ wysokich temperatur w czerwcu i w lipcu, natomiast w niniejszym badaniu uściślono ten kluczowy okres do 15 dni od 21 czerwca do 4 lipca. Reakcje drzew na klimat nie są stabilne w czasie. Najbardziej wyraźne są zmiany zależności przyrostu od minimalnej temperatury dobowej. W ostatnich dekadach zanika jej wpływ jako elementu ograniczającego przyrost drzew, co można wiązać z ocieplającym się klimatem w Tatrach. Analiza danych dobowych wskazuje ponadto, że opady w miesiącach zimowych obecnie pozytywnie wpływają na przyrost, prawdopodobnie zabezpieczając glebę przed głębokim zamarzaniem i stanowiąc rezerwę wody na wiosnę.

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7. ZAŁĄCZNIKI – PUBLIKACJE WCHODZĄCE W SKŁAD ROZPRAWY DOKTORSKIEJ

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ORIGINAL ARTICLE

Delay of growth release after a windthrow event and climate response in a light-demanding species (European larch *Larix decidua* Mill.)

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Abstract

Key message **Larch trees respond to stand opening with an approximately 4-year delay of growth, and low precipitation in July limits radial growth after a windthrow event.**

Abstract Precise cross-dating of disturbance events is crucial to understanding the functioning of forest stands, and may help explain ongoing ecological processes in a forest. Tree rings are very often used to reconstruct the history of disturbances and to study the response of trees to climatic factors. This study analyzed how quickly European larch can benefit from an abrupt change after catastrophic windthrow events and the extent of trees' sensitivity to climate. The study is based on cores from 83 larch trees collected in a post-disturbance 100 ha plot established after a catastrophic windstorm in 2004 in the Slovakian High Tatras. Growth release was calculated from the percentage of growth change (PGC) measured in tree rings. The time lag between the disturbance event and release was related to tree diameter at breast height, tree age, and tree's previous growth. The time lag between the year of the event and the year of growth reaction was 4.6 years on average (median 4 years) in a multi-aged group of trees. The climate analyses employed residual chronology. The new environmental conditions in the post-disturbance area have altered the trees' growth reaction to climate; in particular, they show sensitivity to water deficit in July.

Keywords Climate · Dendroecology · Disturbances · Growth release · *Larix decidua* · Tree rings

Introduction

An increase of annual temperature and changes in the distribution of precipitation due to climate change have recently been recorded across the world (Carrer and Urbinati 2006; Esper et al. 2020; IPCC 2021). In addition, noted is a rise in the number of extreme events such as windthrows, persistent drought, or spring frosts. A better understanding of those changes is needed for assessment of forest diversity, vegetation dynamics, and future forest productivity (Büntgen et al. 2007; Mihai et al. 2021; Larysch et al. 2021).

Natural disturbances are an important element of forest ecosystems. They significantly influence the dynamics of forest stands. Depending on the type, severity, spatial scale, and interval of disturbance events, they shape the structure of a forest stand. A knowledge of precisely cross-dated disturbance events is crucial to understating the functioning of a forest stands, and may help explain ongoing ecological processes in forests (Altman et al. 2013; Svoboda et al. 2011; Vaganov et al. 2006). Tree rings are very often used to reconstruct the history of disturbance events. An ever-increasing number of research papers use various dendrochronological

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techniques to determine the moment of a past disturbance (Svoboda et al. 2011; Trotsiuk et al. 2018; Zielonka et al. 2010; Zielonka and Malcher 2009).

One type of reconstructions is based on cross-dating direct injuries left by the disturbance factor. Dating of scars allows researchers to determine the exact year of a disturbance, because scars form as a result of direct damage to the cambium (Chen et al. 2020; Niklasson et al. 2002; Stambaugh et al. 2011). Another kind of study examines abrupt increases in radial growth following a disturbance. This method is based on the assumption that trees surviving a disturbance respond with the formation of wider rings. Such a reaction is a result of increased resource availability due to decrease competition. The year of the disturbance can be detected in a tree-ring series when an increase of growth due to a disturbance exceeds a given threshold (Fraver and White 2005; Lorimer and Frelich 1989; Nowacki and Abrams 1997; Payette et al. 1990; Stambaugh et al. 2011). Many techniques are used to identify and describe a growth release (Altman et al. 2016; Rubino and McCarthy 2004; Trotsiuk et al. 2018). The following methods are used most often: the radial growth averaging criteria developed by Nowacki and Abrams (1997), the boundary-line method (Black and Abrams, 2003), the absolute-increase method (Fraver and White, 2005), and a combination of radial growth averaging and boundary-line techniques (Splechtna et al., 2005). Most methodological papers focus on setting radial growth thresholds to ascertain whether we are really dealing with a release caused by a disturbance (Altman et al. 2016; Rubino and McCarthy 2004; Trotsiuk et al. 2018). The year of occurrence of a disturbance is determined as the first year before the transition from narrow rings in an undisturbed stand and the first wide ring in the stand after a disturbance. However, it may be wrong to assume that a disturbance occurred 1 year before the formation of the first of a series of wide rings within a release. Growth release may be shifted some years after the year of the event. This shift does not depend on the method of calculating a release, but rather seems to be an effect of a tree's lagged physiological reaction and recovery after a disturbance (Chalupová et al. 2020).

On the other hand, case studies describing stand histories concentrate mostly on shade-tolerant species in a situation in which sub-canopy trees are released from suppression by former canopy trees, because light-demanding species would not endure the period of suppression before the disturbance (Fraver and White 2005; Pyttel et al. 2019). In the case of shade-tolerant species, boundary-line release criteria allow us to identify the growth reactions based on the previous growth (PG) dynamic (Black and Abrams 2003, 2004). This method is based on the fact that suppressed, slow-growing trees can react more intensely to an abrupt improvement of habitat conditions (Lorimer and Frelich 1989). Thus, the method can detect whether a tree is strongly suppressed or not. Still, this procedure does not account for a possible physiological time lag in the trees' growth reaction. In this paper, we analyze growth releases after windthrows in the European temperate montane zone.

The study was conducted in the Slovakian High Tatras. On 19 November 2004, a swathe of forest was flattened by a catastrophic windstorm, which destroyed over 12,000 ha of the stand. As much as 2,500,000 m^3 of timber was uprooted or broken. Prior to the windstorm, the stand composed of spruce (ca. 80%), larch (ca. 20%), and single pines. Mortality was highest among the spruces. Most of the larches survived due to having small leafless crowns and a stronger root system (Holeksa et al. 2016; Zielonka and Malcher 2009; Zielonka et al. 2010). Currently, larch is the dominant tree species in the sparse-canopy stand. Local people believe that the 2004 event was unprecedented, but similar events from the past have been documented. The following "catastrophic windstorms" are mentioned in historical sources: 18 November 1915, 287,000 m^3 timber volume (Koreň 1994; Vadas 1916); 1 May 1919, 52,000 m^3; 1–3 September 1941, ca. 60% (420,000 m^3); 23 October 1971, 94,000 m^3; and 1981, 295,000 m^3 (Vadas 1916). These dates were partly confirmed by dendroecological reconstructions. Tree rings analyses allowed us to detect strong and synchronized growth releases after 1941, in 1915–1919 and at the end of the 1860s (Zielonka and Malcher 2009; Zielonka et al. 2010). A disturbance regime based on the repeated occurrence of windthrows seems to be responsible for the coexistence of spruce and larch within the stand.

In this paper, we ask how light-demanding European larch responds to a very severe disturbance event. The aim of this study was to analyze growth reactions in larch trees 15 years after a severe windthrow in a mixed spruce–larch stand. How quickly can larch benefit from the abrupt change of environment from a closed-canopy forest to an open stand in a post-disturbance plot? How do the biometric characteristics of a tree influence the potential time lag between a disturbance event and growth release? Our study was designed to pinpoint the potential bias inherent in detection of disturbance events based on releases found in tree-ring series.

In analyzing the changes in ring width caused by a disturbance, we cannot neglect the influence of climatic factors, because the formation of tree rings also strongly depends on climate (Fritts 1976; Schweingruber 1996). Trees may respond differently to seasonally distributed temperatures and precipitation in different geographical areas. A substantial number of papers deal with the growth–climate relationship in European larch (Carrer and Urbinati 2006; Büntgen et al. 2007; Koprowski 2012; Oberhuber et al. 2020; Oleksyn and Fritts 1991; Saulnier et al. 2019), but such studies rarely relate the tree response to both climate and disturbances. Widening the focus might prove especially important in large post-disturbance areas, where elimination of the canopy may lead to substantial changes in insolation, temperature amplitude, water accessibility, anemometric factors, humidity, etc.; it is highly probable that the response of trees to climatic elements will be altered. We might also expect such changes to overlap with the biosocial interactions of survival trees (decrease of competition). Hence, other questions should be addressed. Does the occurrence of a disturbance change the growth response to climatic factors? Does the sensitivity of larch to climatic factors change over time—before and after the occurrence of a disturbance?

Materials and methods

Study area and climate

The study area is in the Slovakian Tatra (the Western Carpathians). Cores were collected in a 100 ha plot established after the windstorm for multidisciplinary studies, the so-called EX-SITE (Fleischer 2008). The soils consist of rocky podzolic cambisols. The plot is on a gentle (15% grade) south-facing slope. Plot elevation ranges from 1000 to 1300 m a.s.l. The ground vegetation composed mostly of *Vaccinium myrtillus*, *V. vitis-idaea*, *Calamagrostis villosa*, and *Homogyne alpina*.

Climatic data were collected in the meteorological station in Tatranská Lomnica (49°9´ N; 20°17´ E, 827 m a.s.l.) located ca. 10 km from the study site. For the period 1926–2019, mean annual precipitation was 805 mm and mean annual temperature was 5.57 °C (January minimum − 4.8 °C, July maximum 15.4 °C). Figure 1 presents climate diagrams of the 15-year periods before the event (1990–2004) and after it (2005–2019). For all months except January and February, mean annual temperature in the second period was 1.0 °C higher than in the first one. Data from the meteorological station in Zakopane also shows an increase of mean annual temperature in respective periods, though a weaker one (0.68 °C). Total annual precipitation after 2004 was only slightly higher than before 2004 (by 18.8 mm/year), but the seasonal distribution changed more markedly (Fig. 1).

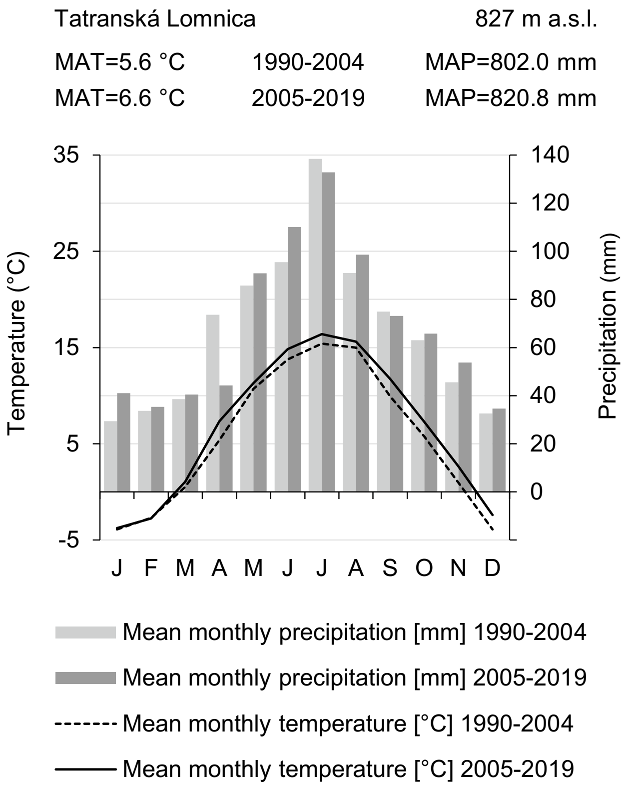

Fig. 1 Climate diagrams for the meteorological station in Tatranská Lomnica for 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow); monthly mean temperatures (lines) and total monthly precipitation (bars); *MAT* mean annual temperatures [°C], *MAP* mean annual precipitation [mm]

Tree-ring data

The locations of the larch trees selected for study were spaced evenly over the whole plot. They were observed to be healthy, without visible stem injury or branch loss. Tree sampling followed the standard dendrochronological protocol (Schweingruber 1996). Two cores were extracted from each tree perpendicularly at ca. 1.3 m height above the ground. The cores were dried, sanded and scanned (2400 DPI resolution). Ring width was measured with WinDendro software (https://www.regentinstruments.com/assets/windendro_about.html). During these measurements, we verified the sequences of pointer years (Schweingruber et al. 1990; Yamaguchi 1991). The validity of cross-dating was checked with COFECHA (Grissino-Mayer 2001; Holmes 1983). Time series that did not correlate with others were excluded due to possible errors in cross-dating. The tree-ring width series were averaged between the two cores of each tree. In total, we used 83 cross-dated ring width series for further analyses. In 2019, 15 years after the disturbance, 41 trees were cored. To increase the number of samples, we used 42 cores extracted just after the disturbance in 2005. All series were also used to study the growth response to earlier events in the nineteenth and twentieth centuries.

Growth release

We analyzed the growth response after the disturbance in 2004, as the exact date of stand opening was known, and in 10 years, after the most probable disturbance episodes in 1941, 1915, and 1869, known from historical data and dendroecological reconstructions (Koreň 1994; Zielonka and Malcher 2009; Vadas 1916). For detection of release, we applied the most commonly used method, based on calculation of percent growth change (PGC) (Nowacki and Abrams 1997). For our purposes, PGC was calculated for each ring according to the formula:

$$\mathrm{PGC} = \left(M_2 - M_1\right)/M_1 \times 100, \tag{1}$$

where PGC is the percent growth change for a single year, M_1 is the preceding 10-year mean growth, and M_2 the subsequent 10-year mean growth. Since in this procedure, the last 10 years from the time series must be excluded, for the 2004 event, we additionally used shorter (5-year) windows for M_1 and M_2 (Nowacki and Abrams 1997; Black and Abrams 2003). This allowed us to extend our calculations of releases to 2014.

In most cases, a PGC threshold of 25% is regarded as a disturbance (Lorimer and Frelich 1989; Nowacki and Abrams 1997, but we decided to set a PGC threshold of 50% to avoid "false releases". Values exceeding 100% were treated as strong releases. If a local maximum of PGC exceeded 50% during the 10-year period after the disturbance event, we treated such a signal as a response to a previous event and then calculated the delay of the response. We used regression to relate the time lag to tree diameter, tree age, and previous growth (mean of the 10 ring widths preceding the year of the disturbance event). Tree age and diameter at the moment of disturbance was calculated from the ring width series. The intensity of the release (value of PGC peak) was calculated in the same way.

Climate analysis

As releases were calculated from raw tree-ring series, for the climate study, we used ARSTAN software for standardization. A negative exponential curve or a linear regression line or a horizontal line through the mean ring widths was fitted to all tree-ring series and then the measurement values were divided by the values of the fitted lines (Holmes 1994). Autoregressive modeling was performed for the indexed series to remove autocorrelation and to enhance the common signal. The residual chronology was used for calculating the growth response to climatic conditions in Tatranská Lomnica (mean monthly air temperature and monthly sums of precipitation). Analyses of the correlation and response function between tree growth and climate values employed DendroClim2002 (Biondi and Waikul 2004). Bootstrapping process was applied to assess the statistical significance of the correlations. In the program, we analyzed changes in the relationship between tree growth and the same climatic factors in period 1926–2019 over 30-year intervals. The correlations were calculated for moving intervals shifted progressively by 1 year in the analyzed period. The climate data covered periods from October of the previous year to September of the current year. This procedure aimed to find all changes in growth response of trees to climate in the whole analyzed period (1926–2019). Mean monthly temperature and sums of monthly precipitation were calculated for periods 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow). Pearson's correlations were used to determine the climate–growth relationships in these two periods. In addition, the climate data from the meteorological station in Zakopane (49°17′ N; 19°57′ E, 846 m a.s.l.) were compared with data from Tatranská Lomnica, an undisturbed site located in the same mountain range. Zakopane is located on the other side of the Tatra range at approximately the same elevation.

Results

Chronology characteristics

The chronology contained 239 years in the period of 1781–2019 (Fig. 2). From 1815, the chronology was based on at least 11 trees. Mean tree-ring width was 1.34 mm (±0.85 SD) and the mean index value was 1.0 (±0.3 SD). Mean sensitivity to tree-ring widths was 0.287, and for the index value it was 0.4, values suitable for dendroclimatic research. The mean value of the first-order autocorrelation was 0.77 computed for tree-ring widths and 0.0 for index value. The expressed population signal (EPS) for 1926–2019 was 0.96, and the mean inter-series correlation value (Rbar) was 0.412.

Releases

Over the 2004–2009 period, 18% of trees responded with growth release; most of the trees showed a reaction in 2007 (PGC calculated using 10-year windows). Using shorter (5-year) intervals for PGC calculation made it possible to extend the period of observation to 2014. During this time (2004–2014), 78% of trees responded with growth release of over 50% of PGC, and 34% with reactions over 100% PGC. There was no immediate growth reaction. No release indicated the correct year of disturbance in 2004. The highest number of trees (29%) showed peak PGC in 2007, 3 years

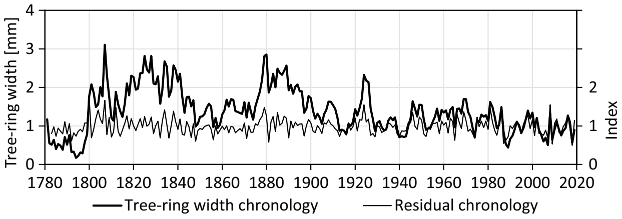

Fig. 2 Chronologies based on raw measurements and indexed series

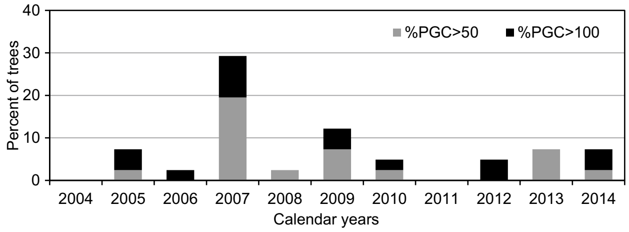

Fig. 3 Percentage of trees showing growth reaction after the 2004 windthrow. PGC values over 50% and 100% indicated. Calculation of PGC based on 5-year intervals of preceding and subsequent mean growth

after the event. Single trees continued the response to the following years until 2014 (Fig. 3).

The time lag between the year of event (2004) and the year of growth reaction was 4.9 years on average (median 3.5 years). This lag for individual trees extended to even 10 years (Table 1).

In linear regression the time lag between 2004 and the growth reaction (as the dependent variable) was not significantly related to diameter ($R^2 = 0.0442$) or tree age ($R^2 = 0.0159$) (Fig. 1a, b in Supplementary Material). The time lag significantly depended on previous growth (PG) [Fig. 1c (Supplementary Material) and Table 2]. Trees having smaller average previous ring width responded later than those with larger average width of previous rings [Fig. 1c (Supplementary Material)].

The intensity of the growth reaction, measured as the PGC peaks value (dependent variable), depended significantly on tree diameter ($R^2 = 0.2328$) (Table 2). Higher diameter trees responded with lower PGC, while thinner ones reacted with higher PGC [Fig. 2a (Supplementary Material)]. A similar inverse relationship was found for, age and previous growth, but these relationships were not significant for the 2004 event [Fig. 2b, c (Supplementary Material) and Table 2].

Table 1 Time lag between the calendar year of disturbance event and occurrence of release, calculated for the 2004 windthrow event and for probable events in 1941, 1915 and 1869

Year	Mean ± SD	Median
2004	49. ± 2.8	3.5
1941	3.4 ± 2.6	2
1915	4.7 ± 1.5	4
1869	5.5 ± 2.7	5.5
All	4.6 ± 2.5	4

In the period prior to 2004, episodes of synchronized releases overlap with historically known windthrows (Fig. 4). The oldest one, reflected in a higher percentages of trees showing release, began in 1869. The next two release episodes began after 1915 and 1941. Low-intensity releases were observed in the 1990s, but as we had no information about intensive wind damage in the area, we excluded them from further analyses. In the 10-year period after 1869, 67% of the trees responded with growth reactions and a third of the trees exhibited a reaction over 100%. After the windthrow in 1915, 43% of the trees responded with growth reactions and 29% had reactions higher than 100% PGC. After 1941, 38% of the trees reacted with growth release and 14% had PGC greater than 100%.

The time lag between year of event and year of growth reaction calculated for events in 1869, 1915, and 1941 (taken together) shows a slightly negative, but significant relation to tree diameter ($R^2 = 0.072$) [Fig. 3a (Supplementary Material)] and tree age ($R^2 = 0.0717$) [Fig. 3b (Supplementary Material) and Table 2]. Older and thicker trees seem to have reacted faster than younger and thinner ones. The time lag was not related to previous growth ($R^2 = 0.0046$) (Table 2). For those dates, the time lag between a disturbance year and release varied from 3.4 to 5.5 years on average (median 2–5.5) (Table 1).

The intensity of release (PGC of local maximum) was negatively correlated with tree diameter ($R^2 = 0.1423$) [Fig. 4a (Supplementary Material)] and previous growth ($R^2 = 0.1485$) [Fig. 4b (Supplementary Material) and Table 2]. The reactions of larger trees and those with greater previous growth were smaller than those of young and suppressed trees.

Climate

Over the whole analyzed period (1926–2019), the trees responded positively to high February, March, May and June temperature, but the correlations were significant only

Table 2 Correlation coefficients for the relationship between time lag of growth release and tree DBH, tree age, and previous growth (PG) for the windthrow in 2004, and for the disturbance events of 1941, 1915, and 1869 taken together

Year		DBH	AGE	PG
2004	Time lag	0.21	0.13	**−0.47**
	Max PGC	**−0.48**	−0.17	−0.21
1941	Time lag	**−0.27**	**−0.27**	−0.07
1915				
1869	Max PGC	**−0.38**	−0.18	**−0.39**

Significant values with $p < 0.01$ are in bold

Bold values are significant

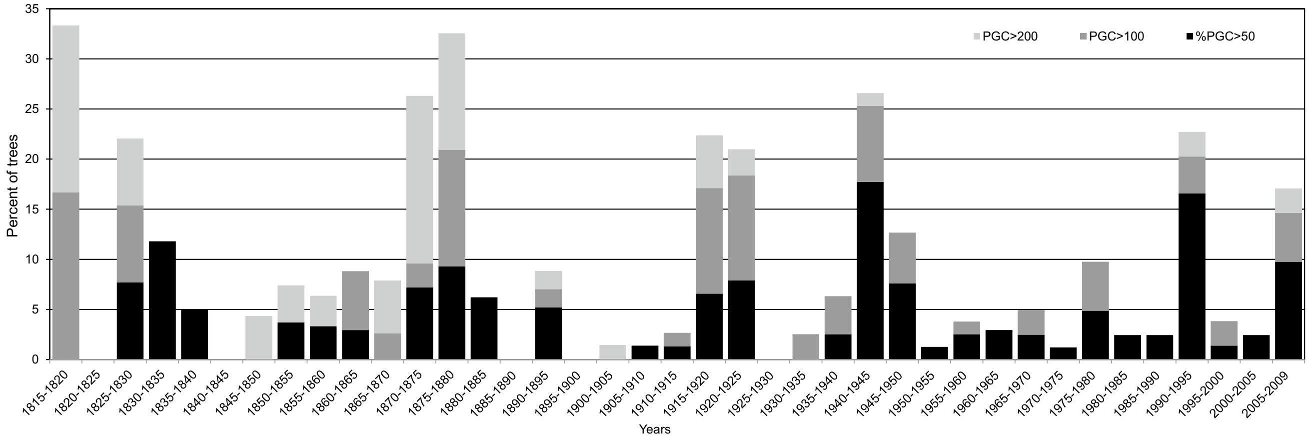

Fig. 4 Distribution of release signals in trees. PGC calculations employed 10-year intervals for preceding and subsequent mean growth. These PGC values were used to determine the disturbance pattern after the events in 1869, 1915, and 1941

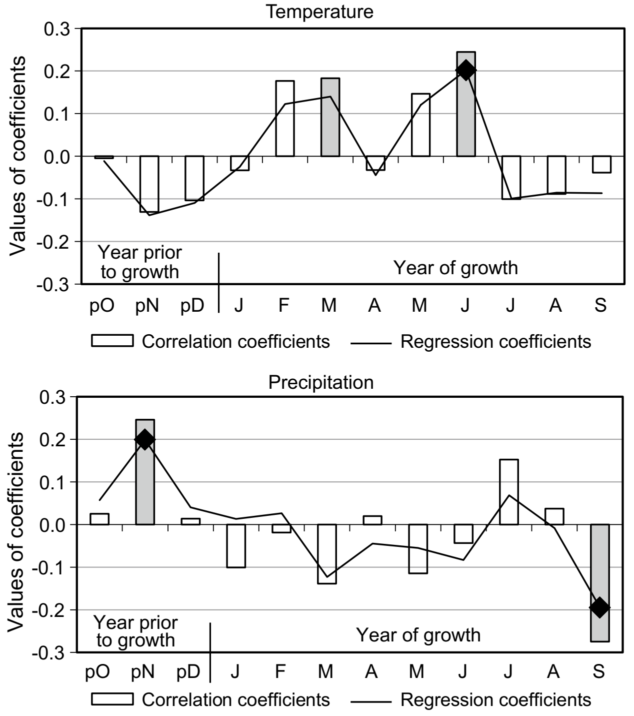

Fig. 5 Bootstrapped correlation coefficients (bars) and response function coefficients (lines) between residual chronology and mean monthly air temperature and total monthly precipitation for 1926–2019 period. Grey bars and markers denote significance p ≤ 0.05

for March and June. Temperature of the previous autumn as well as the second half of the current vegetation season (July, August, and September) seems to have had a negative influence on growth, but none of those correlations was significant (Fig. 5).

Larch responded positively to precipitation in the November of the previous year and negatively to the current September, both of those correlations being significant. The growth response to precipitation in the other months was highly variable and not significant: slightly negative in January, March, and May, and weakly positive in July (Fig. 5).

Time-dependent analysis showed that the response of trees to climate has varied during the last hundred years. The most striking change in the reaction to temperature is observed during the last ca. 15 years, during which the positive influence of May and June temperature disappears and a significantly negative influence of July temperature becomes evident (Fig. 6). This stands in contrast to 1965–1987, when trees positively responded to July temperature. The 1970s and 1980s show a negative influence of January temperature. During recent years, the trees seemed to have reacted positively to February temperature (Fig. 6). It should be noted that the mentioned decades are considered here as ends of 30-year windows. Precipitation in the previous November had a positive influence on growth for the studied period as a whole (Fig. 5), but this pattern does not hold for the intervals that end before 1987 (Fig. 7). The strongest negative influence of September precipitation ended before 2000. Over the last few years, July rainfall has had a positive influence on growth (Fig. 7).

Due to our use of 30-year windows for the time-dependent series, the correlation coefficients for the years in 1990–2019 do not clearly separate the growth reactions to climate before and after the 2004 windthrow. The differences in growth reactions to climate calculated for 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow) are presented in Fig. 8. Since 15-year period since the windthrow is too short for response function analyses, we used Pearson's correlations. The only significant positive correlation between growth and climate appearing after the windthrow is for July precipitation ($r = 0.52$, $N = 15$, $p = 0.045$). In the period before the windthrow, this correlation was slightly

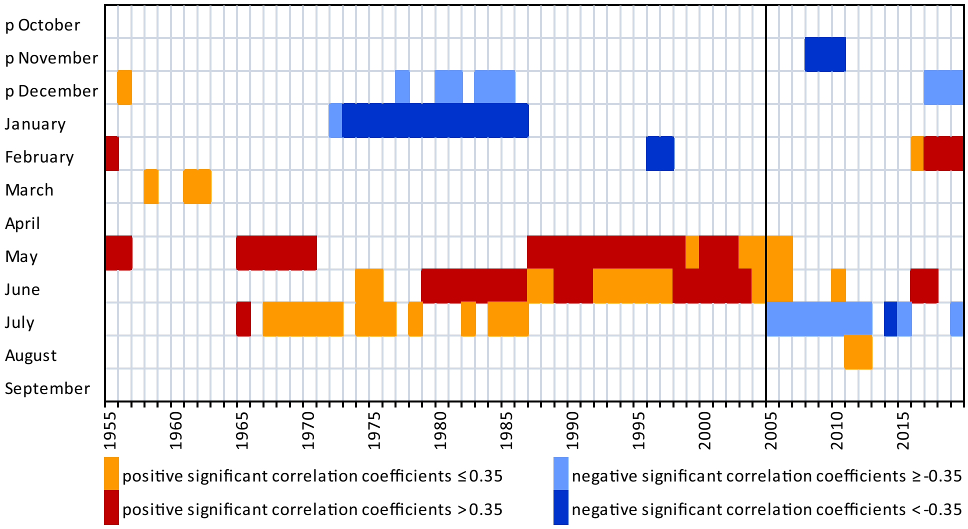

Fig. 6 Moving-interval correlation computed using DendroClim2002 for residual chronology and mean monthly air temperature. The 30-year window was progressively shifted through the total available years from 1926–1955 to 1990–2019. The window starts with the October of the previous year and ends with the September of the current year

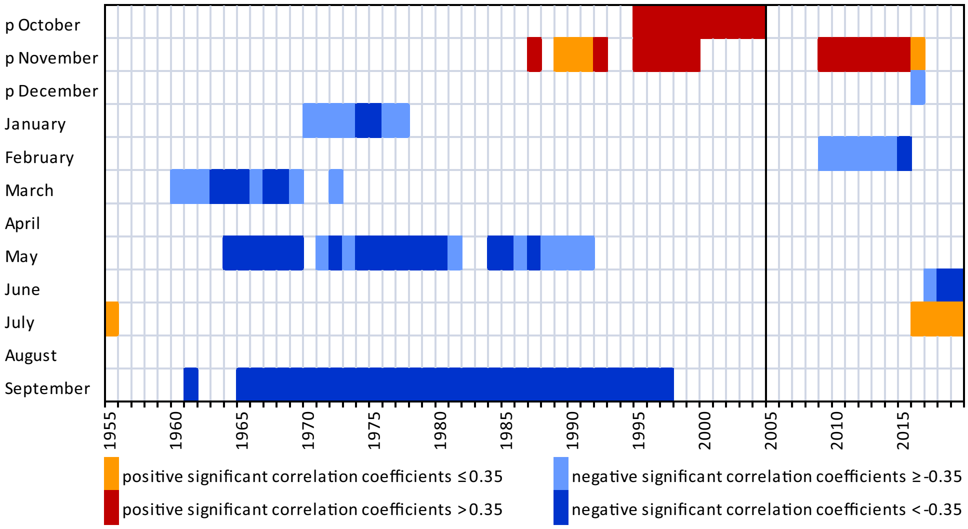

Fig. 7 Moving-interval correlation computed using DendroClim2002 for residual chronology and total monthly precipitation. The 30-year window was progressively shifted through the total available years from 1926–1955 to 1990–2019. The window starts with the October of the previous year and ends with the September of the current year

negative. Changes in the correlation values can be seen in Fig. 8 but none of them is statistically significant.

Discussion

Growth release

Growth releases are commonly used for reconstruction of disturbances event, and very often are the only source of information on the history of forest disturbances. Most of those studies focus on shade-tolerant species, because suppressed trees can react abruptly and immediately to a forest-opening event (Hanson and Lorimer 2007; Kuosmanen et al. 2020). There are far fewer dendroecological reconstructions based on the growth reactions of light-demanding tree species, because such trees are not able to survive periods of suppression. Moreover, most methodological questions about growth release involve setting the criteria for establishing threshold values of growth increase, aimed at separating real disturbance-induced releases from “false negative” and “false positive” releases (Trotsiuk et al. 2018). Less attention is usually given to the temporal precision of disturbance dating, because such calibration requires long-term experiments. However, it has been observed that a growth response can be shifted away from the actual year of the event (Chalupová et al. 2020). The temporal precision of disturbance dating is critical to the reliability of forest history reconstructions (Altman 2020), but it is rarely addressed.

The windstorm on 19 November 2004 is very well documented. In our sampling plot, the EX-SITE, most of the trees were knocked down, broken and uprooted. The only surviving trees were the larches. After the storm

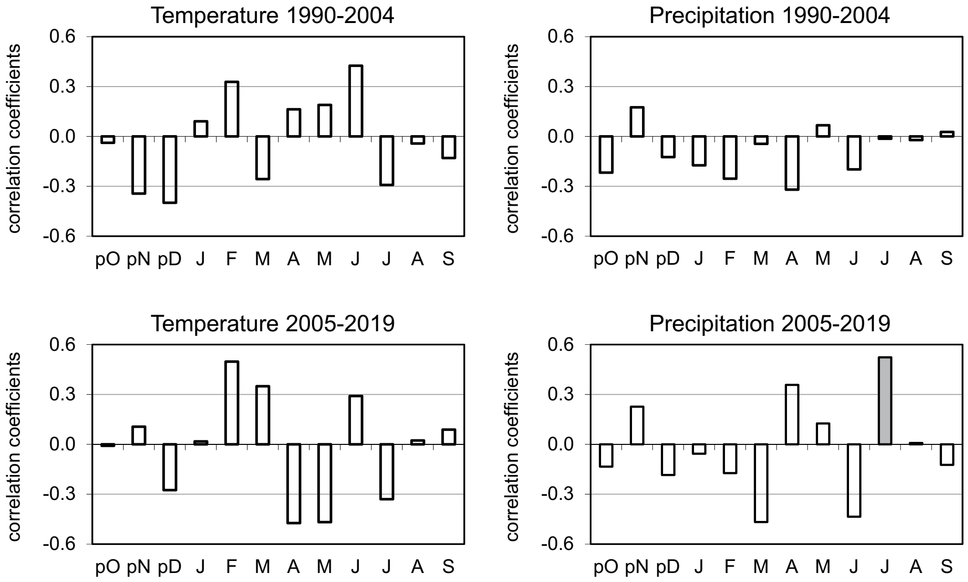

Fig. 8 Correlation between residual chronology and mean monthly air temperature and total monthly precipitation for 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow). Grey shading denotes significance ($p \leq 0.05$)

in the winter of 2004/2005, the site was cleared. The logs were cut and salvaged. The heavily damaged trees were removed, including individual spruces because of the threat of a bark beetle (*Ips typographus*) outbreak (Fleischer et al. 2016, 2017). The stand was transformed from closed-canopy forest with dominant spruce to an open stand composed of sparsely distributed single larch trees; whole trees, including crowns and stems, were now newly exposed to sunlight. We expected that this light-demanding species would immediately benefit from such conditions and that this would be reflected in increased radial growth already in 2005. According to Nowacki and Abrams (1997), a local PGC peak indicates a disturbance year, which will be followed by an increase in the width of the next tree ring. None of the trees we studied responded with increase growth in 2005; in the greater number of trees the response came 3 years later, and single trees kept responding over the following 10 years. A similar pattern of delayed response was observed for the events of 1869, 1915, and 1941. Judging from our historical and recent data, on average the release of growth was shifted away from the actual disturbance year by about 4–5 (Table 1). Such time lags have been observed in other species as well (Altman et al. 2013; Pyttel et al. 2019; Rentch et al. 2002; Samonil et al. 2009). Our results generally seem to show that thinner and younger trees need more years to respond with release after a disturbance, up to even 10 years, while larger and older trees may react in 2–3 years, but this trend did not hold 2004 event. The reason may be that tree rings examined to study the 2004 event represented older, thicker classes, unlike the earlier rings of the same trees used to assess the response to previous disturbances. In addition, those relationships were statistically significant but not strongly so, and can be treated only as a general trend. On the other hand, the time lag in response significantly depended on previous growth: more suppressed trees reacted later than those with wider rings. This correlation was stronger for the 2004 windthrow.

Larches growing in close-canopy forests, especially those mixed with spruce, tend to produce small crowns. The suppression of their previous growth was related to limited access to sunlight. As a consequence, suppressed trees were more likely to have smaller crowns which could not suddenly spread out to take advantage of easy access to light. The first reaction to opening is investment in production of foliage and branches rather than in radial growth of the stem. This period may last 7 years or more before a suppressed tree responds with stem growth release. It is worth noting that the dynamics of previous growth are not necessarily related to tree diameter. A similar mechanism may explain the late response of the oldest generation of trees after 2004. Although they dominated in the stand, their previous growth was limited due to aging.

We observe a stronger reaction to disturbance (higher release) in thinner and suppressed trees, supporting well-known observations (Lorimer and Frelich 1989; Nowacki and Abrams 1997). The percent growth change values strongly depended on previous growth. The highest PGC values are observed only in the most suppressed trees, because PGC expresses the growth increase over previous growth. Trees that have formed wide rings before a disturbance (most likely the dominant trees) cannot increase ring widths very much: they have already occupied a favorable place in the canopy and cannot benefit from canopy opening as much as suppressed ones can (Black and Abrams 2003, 2004; Lorimer and Frelich 1989; Nowacki and Abrams 1997).

The trees we chose for sampling were free of visible damage of the crown and stem, but damage such as windstorm-caused injury of the root system cannot be ruled out. A heavy mechanical impact on the stem may cause unseen damage to the root system, which can be reflected in a decreased radial growth (Gärtner 2007).

Climate

Our dendroclimatic analysis seems to show a change in reaction of larch to climatic factors after the 2004 windthrow. In the period before it, May and June temperature positively influenced radial growth, but this relationship became weaker after the windthrow. In subsequent years, higher February and March temperature seems to have started the vegetation season earlier.

After the windthrow, high April temperature negatively influenced radial growth. Most likely this can be related to the significant decrease of precipitation in 2005–2019 during that month (Fig.1, Fig.8), when foliage develops and flowering occurs (Bednářová et al. 2013). Similarly, after the windthrow the positive effect of June temperature on growth decreased, while for July temperature it changed from positive to negative (Fig. 7). More distinct differences in climate–growth relationships are seen between the 15-year periods before and after 2004 (Fig. 6); however, these analyses are based on very short time series and must be considered with caution.

These climate–growth relationships can be interpreted in two ways. First, after the windthrow, the stand became fully open, and surviving scattered trees received direct access to sunlight not only on the crowns but also along stems. This may have decreased their requirement for warmth. On the other hand, the lower sensitivity to summer temperature might be an effect of the previously mentioned putative mechanical damage to surviving, impeding regular growth. The negative reaction to July temperature that began to appear after the windthrow, as well as the positive influence of precipitation observed over the last few years, speak in favor of the first explanation.

In interpreting time-dependent growth–climate analyses, however, we must bear in mind that we are dealing with 30-year intervals, and briefly, lasting significant correlation might be due to temporary climate variability. In July, the trees apparently suffered from high temperature and water deficit. The observed change in the response to climatic factors might be a result of environmental stress after the windthrow. Increased mean annual temperature was observed at the other meteorological station in the Tatras in Zakopane, used as an example of an undisturbed site, but this rise was not so strong. This may suggest that the post-disturbance opening after 2004 may have additionally boosted the general increase of temperature locally. Indeed, the 2004 windthrow most likely influenced the meteorological observation in Tatranská Lomnica as the station is located in the vicinity of 12,000 ha destroyed forest. In the Alps at the higher elevations (1600–2200 m a.s.l.), larch growth positively depends on the June and July temperatures (Büntgen et al. 2007; Carrer and Urbinati 2006; Saulnier et al. 2019), perhaps attributable to the cooler climate of that zone. In our study, the positive influence of high July temperature ends in the 1980s. After the 2004 windstorm, the opposite trend appears, whereby a warm July negatively affects the radial growth of larch. This is most likely linked to water deficit, as confirmed by high and significant correlations with July precipitation in the last period. A similar pattern was reported from lower elevations of the Alps (1200–1450 m a.s.l.), where mid-summer drought is a limiting factor for larch growth (Saulnier et al. 2019). In the Alps, high February and March temperatures have been found to influence larch growth negatively (Büntgen et al. 2007; Carrer and Urbinati 2006; Saulnier et al. 2019), contrary to our results. This may be explained by the earlier occurrence of the vegetation season in the Tatras, so that trees benefit from the higher temperatures at winter's end. In our plot, we observed a positive reaction to high precipitation in July only in the last period after 2004. There the tree response to climate after the windthrow shows the same effect as lowering of elevation in the Alps. In lowland Poland, the most important factor limiting larch growth is precipitation in May–July, especially June (Koprowski 2012; Oleksyn and Fritts 1991). In our opinion, the altered growth reaction of trees in the post-disturbance period can be related directly to the windthrow event of 2004, through not only via decrease competition with surviving trees but also via the change in local climate due to post-disturbance opening (IPCC 2014, 2018, 2021). In other regions, increased temperature was not accompanied by increased tree growth (Oberhuber et al. 2020).

Conclusions

The European larch responds to severe windthrows with growth release, but the releases occur several years after the event (ca. 4–5 years). For thinner, younger or suppressed trees up to 10 years. Larger, older trees and those with better average growth before the event may react much faster. This means that in a mixed stand with spruce, larch trees that have access to light in the canopy and relatively good radial growth may still benefit from an abrupt opening and respond with a relatively rapid growth release.

Intense, large-scale disturbances like the 2004 windthrow are responsible for at least strengthening the general trend of climate change, and may influence the trees' sensitivity to climatic factors. The main change after the windthrow can be related to the water deficit in open canopy stand in the summertime. This is confirmed by significant positive correlations between growth and July precipitation.

The growth reaction of surviving larches after a windthrow can be compared to a similar reaction correlated with a shift towards a lower elevation in the mountains or with a shift toward more continental climate, where midsummer high temperatures and a water deficit are factors limiting of growth.

Author contribution statement KI, EM, and TZ designed the research and methodology. KI and PF conducted fieldwork. KI was responsible for preparation of samples and for tree-ring measurements. KI and EM conducted data analysis. KI, EM, and TZ led the writing of the manuscript. All the authors gave final approval of the manuscript.

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Declarations

Conflict of interest The authors declare no conflict of interests.

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SUPPLEMENTARY MATERIALS

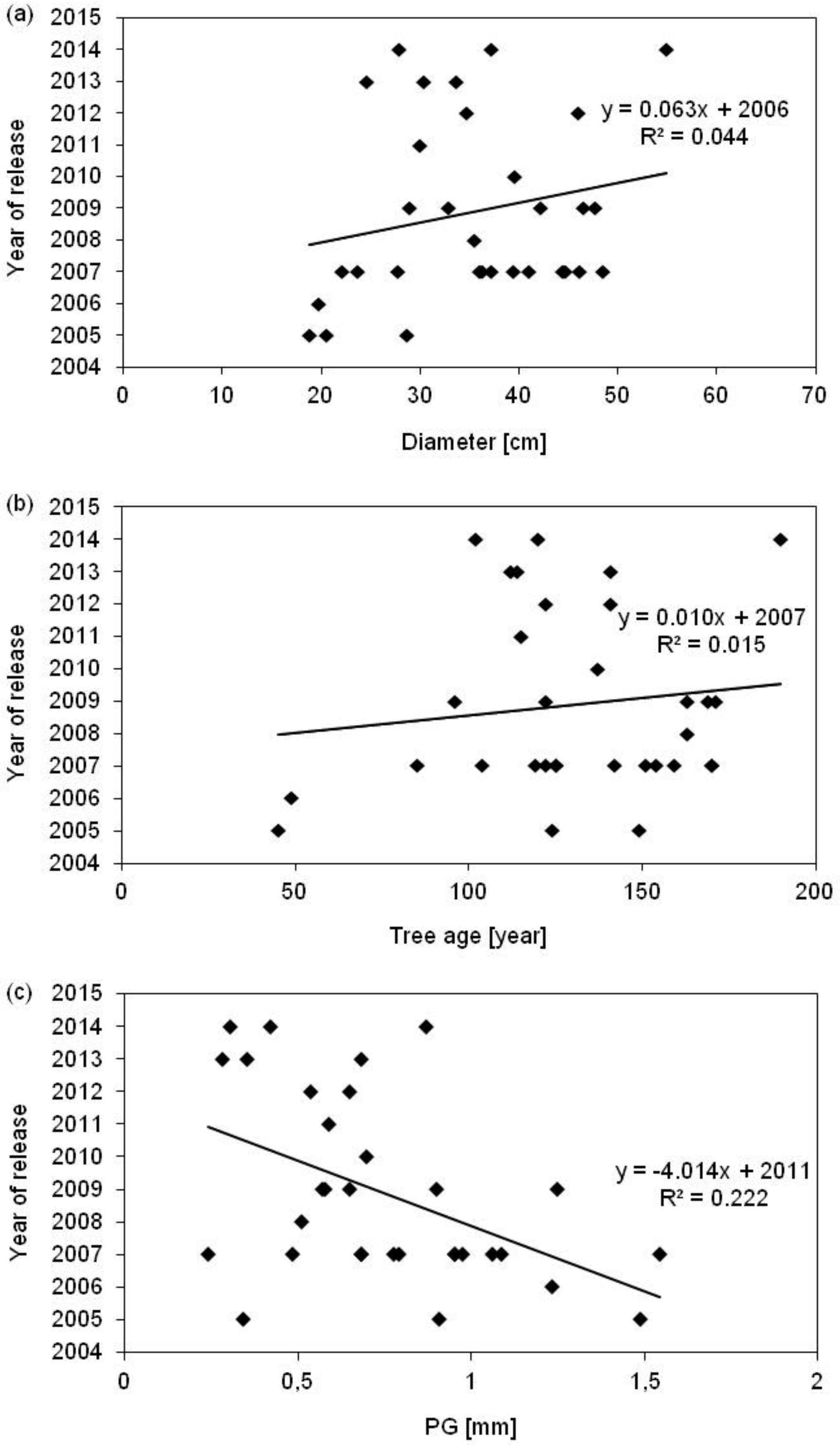

Fig. 1. Relationship between time lag (in calendar years) after the 2004 windthrow and tree growth reaction, by dbh (1a), tree age (1b) and previous growth (PG; 1c)

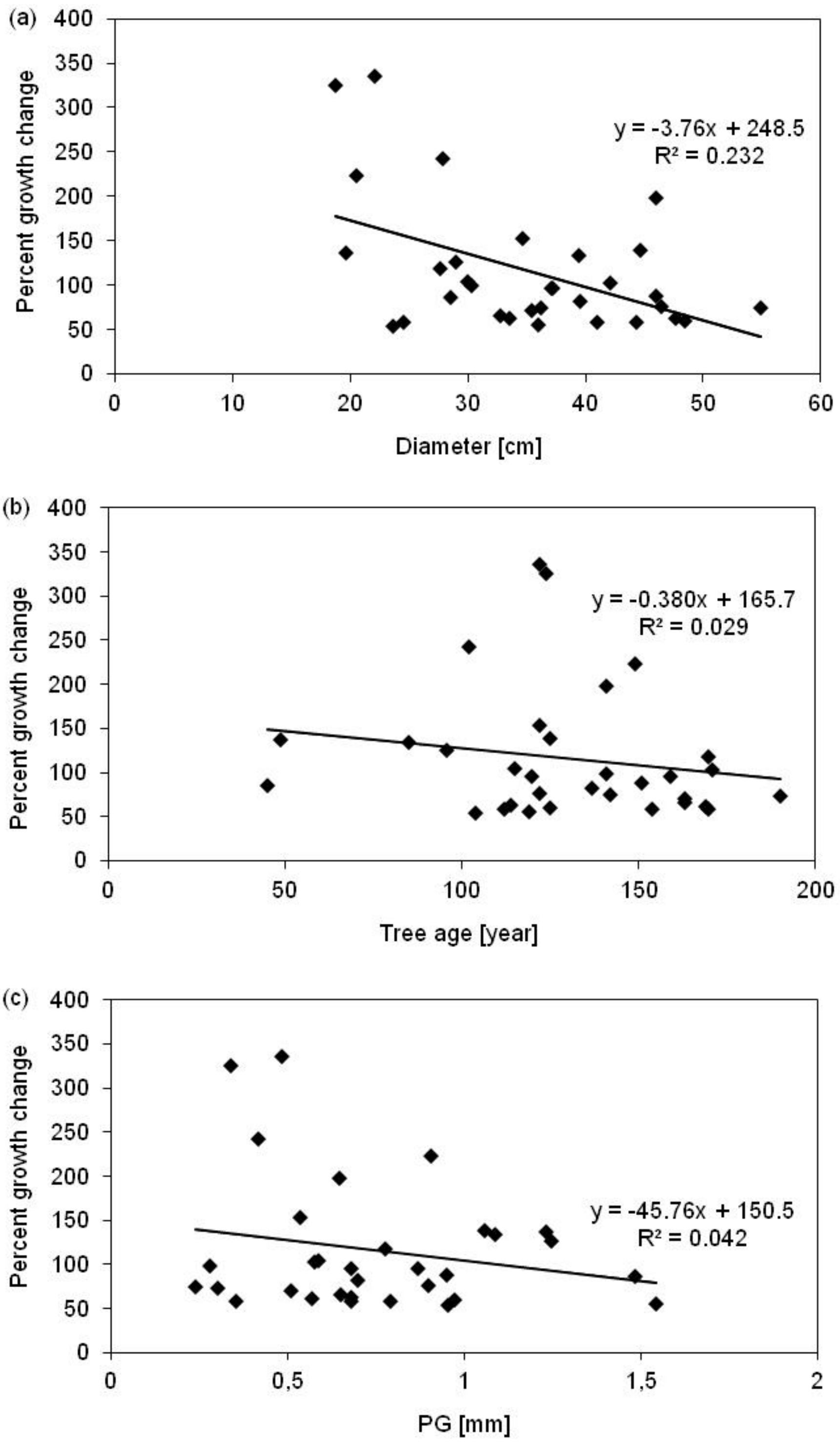

Fig. 2. Relationship between growth reaction intensity (measured as percent growth change) after the 2004 windthrow and tree dbh (2a), tree age (2b) and previous growth (PG; 2c)

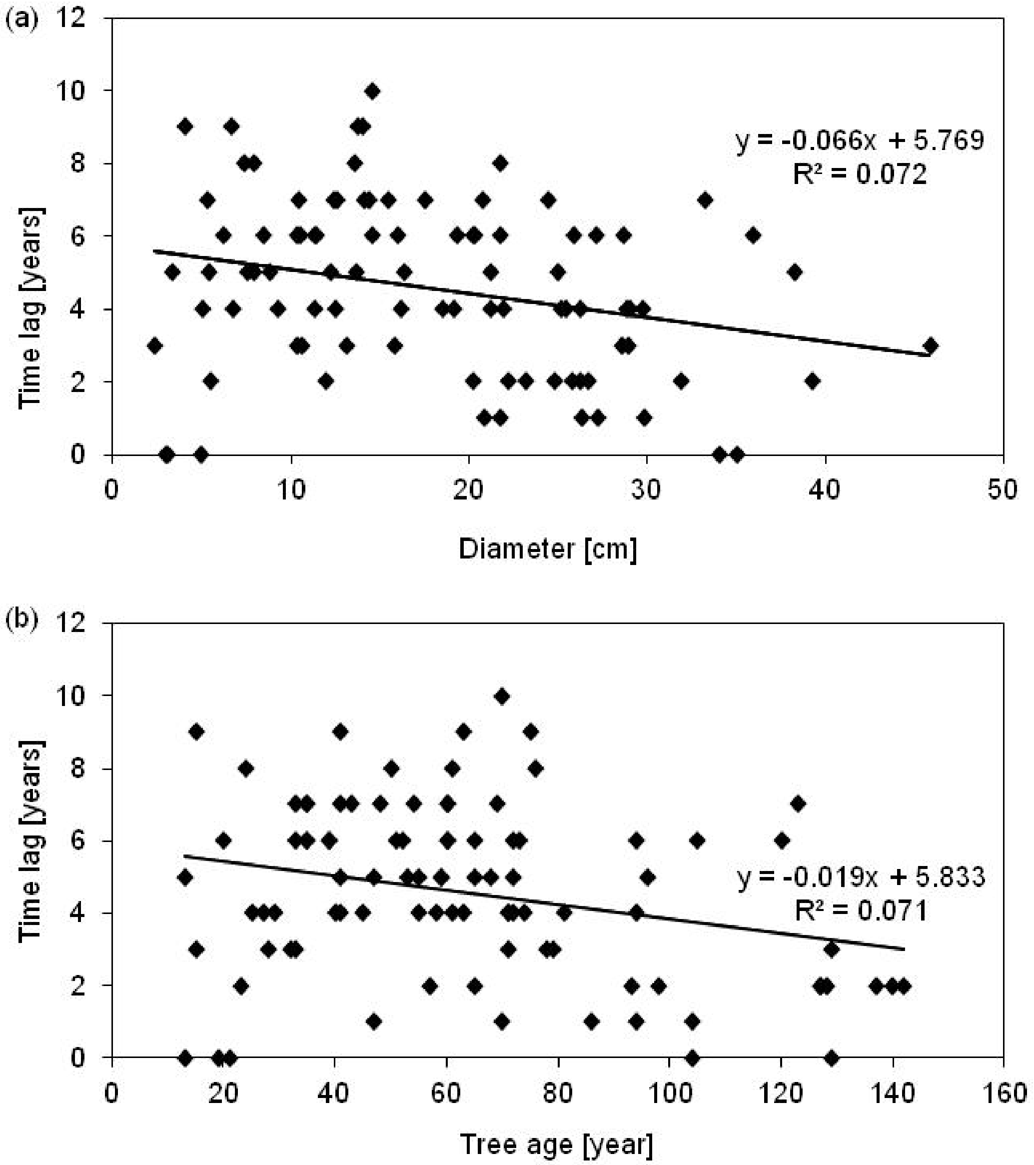

Fig. 3. Relationship between time lag in the 10-years periods after the disturbance events in 1869, 1915, and 1941 (taken together), tree dbh (3a) and tree age (3b)

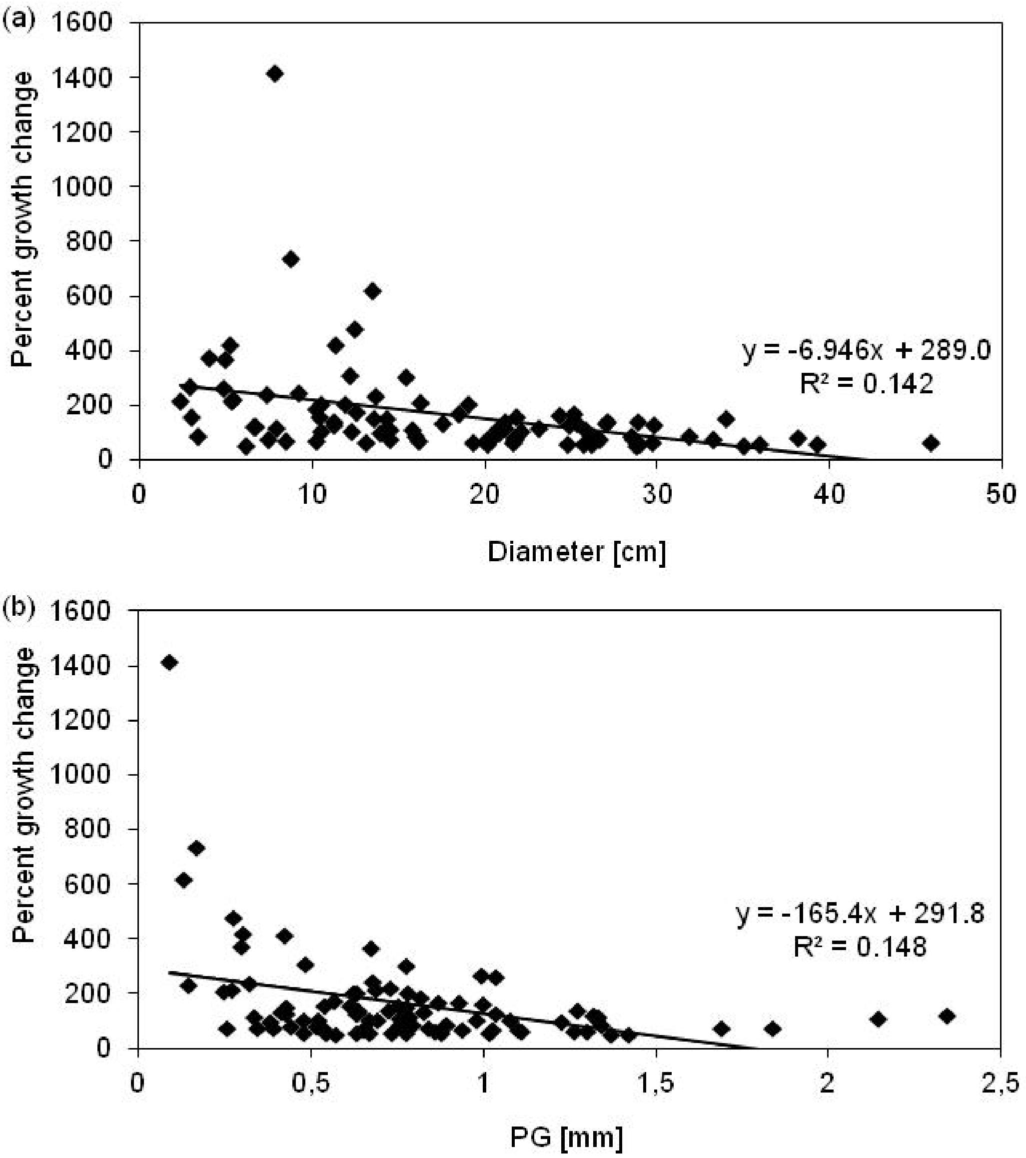

Fig. 4. Relationship between growth reaction intensity (measured as PGC), tree dbh (4a) and previous growth (PG; 4b) for the 1869, 1915 and 1941 events (taken together)

Kraków, 01/10/2021

Oświadczenie współautorów publikacji

Statement of authors' contribution

Niniejszym potwierdzamy, że jesteśmy autorami publikacji pt.:

We hereby confirm that we are the authors of the manuscript:

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The participation of authors in the creation of the text has been duly acknowledged as indicated below:

Autor	Koncepcja badan Conceptualization	Prace terenowe Fieldwork	Przygotowanie materiału i pomiary Preparation of samples and measurements	Analiza danych Data analyzys	Pisanie manuskryptu Writing of the manuscript	Autor korespondencyjny Corresponding author
Katarzyna Izworska	√	√	√	√	√	√
Elżbieta Muter	√			√	√	
Peter Fleischer		√				
Tomasz Zielonka		√			√	

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My total contribution to this work:

65 % Katarzyna Izworska ………………… Data/Date 1.10.21

20 % Elżbieta Muter ………………… Data/Date 1.10.21

5 % Peter Fleischer ………………… Data/Date 1.10.2021

10 % Tomasz Zielonka ………………… Data/Date 1.10.2021

Artykuł nr 2

Izworska, K., Muter, E., Matulewski, P., Zielonka, T. 2023. Tree rings as an ecological indicator of the reaction of Swiss stone pine (*Pinus cembra* L.) to climate change and disturbance regime in the extreme environment of cliff forests. Ecological Indicators 148: 110102.

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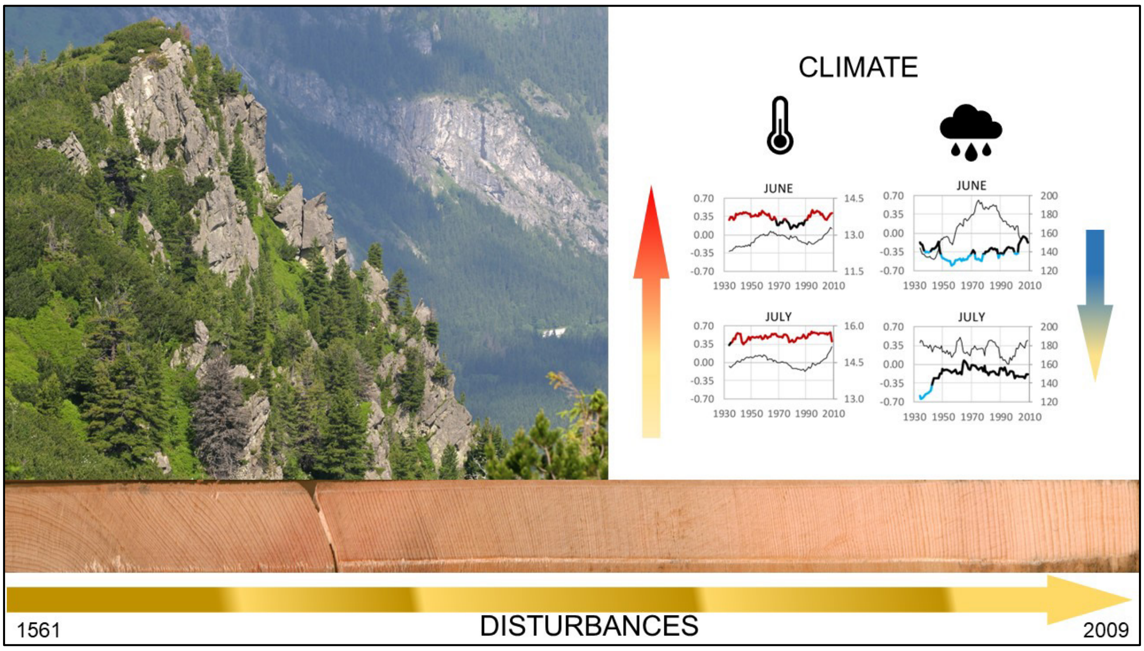
GRAPHICAL ABSTRACT



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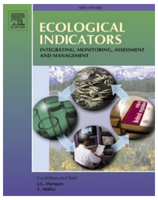

Tree rings as an ecological indicator of the reaction of Swiss stone pine (*Pinus cembra* L.) to climate change and disturbance regime in the extreme environment of cliff forests

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ABSTRACT

Tree rings are an ecological indicator, useful for studying the adaptation of trees in a changing environment, especially in the unique habitat of high-elevation cliff forests. The main aim of this study was to characterize tree-ring changes in Stone pine (*Pinus cembra* L.) growing in the extreme conditions of cliff forests of the Western Carpathians (at elevation 1300–1600 m a.s.l.), in order to reconstruct the growth release pattern and to better understand the influence of climate. The study was based on 104 tree ring series covering a 449-year-long chronology (1561–2009). In the last century, mean annual temperature has increased by +2.0 °C and precipitation has decreased slightly in the Tatras. The growth of stone pine was strongly related to summer temperature of June and July. In the last decades, the negative influence of summer precipitation on tree growth has abated; this may be related to warmer summers and decreasing precipitation. Temperature of the previous autumn, winter, and early spring, which had a significant influence on stone pine growth in the past, is not an important factor now. In the extreme environment of mountain cliffs, the influence of temperature and precipitation on tree growth is not stable over time under changing climate. The current changes in climate seem to promote stone pine and its potential upward elevational shift. The numerous past disturbance events have affected a limited number of trees, suggesting that single individuals have been randomly eliminated from the cliff stands during the last three centuries. Our results highlight the complex pattern of the reaction of stone pine on cliffs to changes in the environment. Swiss stone pine, a long-lived tree species, shows high adaptability for colonization of mountain cliffs and is an excellent object for studying the response of plants to changing climate. Understanding the effect of interactions between climate, disturbances, and the radial growth of trees in extreme environments of cliff forests on different temporal scales (monthly, seasonal, yearly) should increase our knowledge of such ecologically valuable areas.

1. Introduction

Tree rings have been widely applied as an ecological indicator in studies of environmental and climatic changes (Zhang, 2015; Bollati et al., 2018). Tree-ring width, density and wood anatomy allow us to retrospectively reconstruct the influence of environmental factors such as climate or disturbances (Altman, 2020; Pearl et al., 2020). As trees are exposed to environmental factors, their growth rings reflect changes in their habitat (Schweingruber, 1996; Speer, 2010).

For this type of study, high-elevation cliff forest ecosystems offer a useful model in which trees are exposed to multiple site-specific environmental factors. These unique ecosystems usually experience extreme weather conditions due to the high amplitude of day/night as well as seasonal temperature. Rock and soil temperature is controlled by insolation, wind and moisture. In regard to insolation, a key factor is the angle of the sun's rays, which depends on latitude, the day of the year,

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time of day, as well as slope and aspect (Tranquillini, 1979; Körner and Paulsen, 2004). The harsh environment of cliffs is related to low nutrient supply in skeletal soils and to severe disturbances abetted by gravity (rockfalls, landslides), snow accumulation and snowfall, and strong winds. Skeletal substrate that contains a small amount of mineral soil has low water-holding capacity; due to their high elevation, mountains usually receive more precipitation and have higher air humidity (Körner and Paulsen, 2004). Among the disturbance on cliffs, the most important seem to be geomorphological or tectonic. Geomorphological processes can be initiated by extreme weather conditions (heavy rainfall) and earthquakes (Kotarba, 2004; Malik and Wistuba, 2012; Wistuba et al., 2021). All these features clearly distinguish cliff forests as an unique environment, where tree rings should reflect the changes with higher sensitivity.

Under climate change, the increase in annual temperature and changes in the precipitation pattern are expected to impact the entire distribution ranges of tree species (Esper et al., 2020; IPCC, 2021), including on cliffs. The severity of these changes will be manifested across regional and seasonal differences (Oberhuber et al., 2008; Popa and Kern, 2009; Larysch et al., 2021; Izworska et al., 2022). In Europe the largest increases in average temperature are predicted to be in the east of the continent in winter and in the west in summer, while rainfall will increase mainly in the north and during winter, decreasing in the south and east in summer. The effects of such climate changes on forest productivity are assessed both as positive (in Northern and Western Europe) and as negative (especially in Southern Europe, threatened by catastrophic drought) (Lindner et al., 2010). The climate changes will be pronounced on various scales (temporal, spatial, interspecific), will affect productivity and species competitiveness, and will have a direct impact on forest management (Babst et al., 2013). These processes can also be observed on the edge of species distributions in the treeline ecotone, where temperature is known to be a key limiting factor (Körner, 2003). According to some studies, higher temperature and lower precipitation may make rear-edge tree populations of temperate or mountain species vulnerable to drought, causing reduction of radial growth (Camarero et al., 2017; Debel et al., 2021).

Swiss stone pine (*Pinus cembra* L.) is a long-lived tree species highly adapted for colonization and growth on mountain cliffs. It is an endemic coniferous species growing in upper-treeline ecotones of high elevations in the Alps and Carpathians (Fig. 1) (Casalegno et al., 2010; Beloiu and Beierkuhnlein, 2019; Zięba et al., 2019). With its strong root system and resistance to that harsh climate, stone pine can occur above the regular timberline, colonizing very steep slopes, rocky shelves, crevices, and other extreme niches, locations not accessible to its main competitor, Norway spruce (*Picea abies* (L.) H. Karst) (Myczkowski and Bednarz, 1974; Zięba et al., 2019). Due to its potentially long lifespan and the extreme environment of its habitat, this species is very useful for tree-ring studies. In recent decades a number of single-factor studies of *Pinus cembra* tree rings have been conducted in the Alps and Carpathians (Bednarz, 1981; Carrer and Urbinati, 2004; Oberhuber et al., 2008; Popa and Kern, 2009; Saulnier et al., 2011; Büntgen et al., 2015; Popa et al., 2017; Carrer et al., 2018; Oberhuber et al., 2020); usually the studied factor is climate.

The population ranges of Swiss stone pine vary depending on historical land use. Human activities have altered most of the alpine timberline ecotone. Sheep grazing, later exploitation by loggers and miners, and also current tourism have changed the mountain forest cover in the Alps (Pini et al., 2017; Kučera, 2019). On the other hand, Didier (2001) found that the stone pine in the French Alps has been regenerating in young larch woods which grew immediately after the abandonment of pastures 50 years ago. Overharvesting of Swiss stone pine occurred in the past in the Southern Carpathians, for example in Retezat (Beloiu and Beierkuhnlein, 2019). Although the Carpathian population of Swiss stone pine is much smaller and is divided into

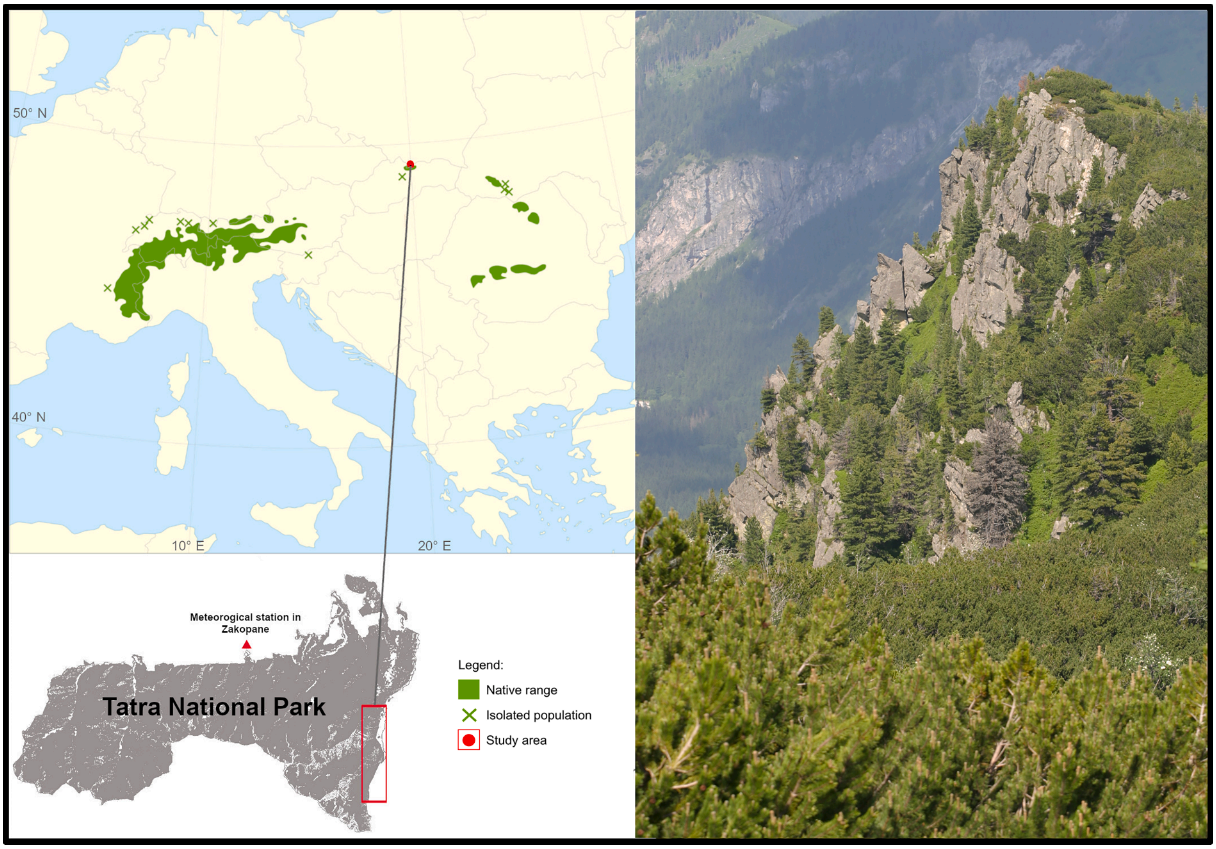


Fig. 1. Map showing the distribution of *Pinus cembra* and the location of the study area (distribution map courtesy of EUFORGEN, 2009).

isolated islands, its genetic diversity is higher than the much larger population in the Alps (Belokon et al., 2005; Höhn et al., 2009; Tóth et al., 2019). Recent genetic research also shows high genetic diversity of Swiss stone pine in the Tatras, despite high fragmentation and small population size (Dzialuk et al., 2014). In view of this genetic background, the Swiss stone pines that grow on cliffs in the Tatras seem to be relicts of primeval forest. The very isolated populations and barely accessible stands are assumed to be untouched by direct human impacts (Zięba et al., 2018). The old-growth stone pines on cliffs in the Tatras offered us a unique platform for studying the influence of climate and disturbance regime.

Natural disturbances are a crucial component of forest ecosystems, exerting a considerable impact on forest stand dynamics (Altman, 2020), including on cliffs. The forest structure and species composition respond slowly to changes in climate, but the abrupt changes induced by agents such as bark beetles, fire, snow, wind, drought, or extremal rainfall may alter them swiftly and profoundly. Though they generally cannot be predicted, alternations of disturbance regimes are one way climate change can manifest itself in forests. Climate-sensitive disturbances have already worsened in recent decades (Thom et al., 2013, 2017; Seidl et al., 2014).

In our work we link the influence of climate and the disturbances regime on tree growth on different temporal scales; this is a novel, comprehensive approach. An increase in annual temperature promotes tree expansion into alpine areas, but such stands can be limited by topography and the absence of suitable soils. Most studies have focused on the altitudinal pattern of the climate-growth relationship (e.g. Oberhuber, 2004; Oberhuber et al., 2020; Vittoz et al., 2008). Not many papers have focused on another important aspect besides climate: the growth response to disturbances (Izworska et al., 2022). The effects of disturbances most often have been overlooked (Ojima et al., 1991; Camarero et al., 2017; Altman 2020).

The main aim of this study was to characterize the tree-ring changes of the Stone pine (*Pinus cembra* L.) growing in extreme conditions of cliff forests, in order to reconstruct the growth release pattern and to better understand the influence of climate. We hypothesized that the climate-growth relationship is changing over the time due to climate change. We also expected to find that disturbance events affected the growth of stone pine in cliff forests. This study was intended to (i) determined how the changes in climate affected the formation of tree rings, (ii) look for possible disturbances in the past that could affect the radial growth and dynamics of stone pine forest growing on cliffs, and (iii) examine the interactions between climate and disturbances. The application of this approach seemed likely to show a distinct response by these trees to the particular factors operating in the unique environment of high-elevation cliff forests, a special case of response to the climate changes that have been observed worldwide.

2. Material and methods

2.1. Study area and climate

The study area is in the Polish Tatras (Western Carpathians), specifically the upper treeline ecotone. The three cliff forests are located ca. 4 km apart: the north-facing slopes of Czuba Roztocka (1300–1525 m a.s.l.) and Opalone (1390–1605 m a.s.l.), and the west-facing slopes of Żabia Czuba (1465–1560 m a.s.l.) (Fig. 1). The stands are on very steep slopes (ca. 70–80°) and the timberline is located at ca. 1550 m a.s.l. in Tatra National Park (Zięba et al., 2019); most likely the stands have not been affected by human activity due to their difficult access (49°12′54.48″N; 20°4′34.68″E). The soils are skeletal and acidic, formed on granite bedrock (Komornicki and Skiba, 1996). The studied stone pines grow in cliff forest on the timberline, between the upper montane zone and subalpine dwarf pine (*Pinus mugo* Turra) scrub at 1300–1600 m a.s.l., the height of sampled trees was ca. 15–20 m, and their diameter at breast height (DBH) ranged from 38 cm to 78 cm. The forest covering the whole slope area is dominated by Norway spruce, with individual stone pines, dwarf pines and rowans (*Sorbus aucuparia* L.).

Climate data were collected from the meteorological station in Zakopane (49°17′36.48″N; 19°57′36.97″E, 846 m a.s.l., ca. 12 km from the sampling site), providing the longest monthly records in the region (1905–2009) and being nearest to the sampling sites. For the period 1905–2009, mean annual temperature was 5.1 °C and mean annual precipitation was 1136 mm. Fig. 2a presents climate diagrams for the analyzed intervals: 1905–1939, 1940–1974 and 1975–2009. Data from the meteorological station in Zakopane indicate that the last period (1975–2009) was distinctly warmer than the earlier ones (Fig. 2a, b); precipitation does not show a clear trend but fluctuations appear (Fig. 2c). Additionally we calculated the mean annual and summer temperature and precipitation for the first and last five-year periods of records used in the analysis (1905–1909; 2005–2009) (Fig. 2d).

2.2. Tree-ring data and chronology development

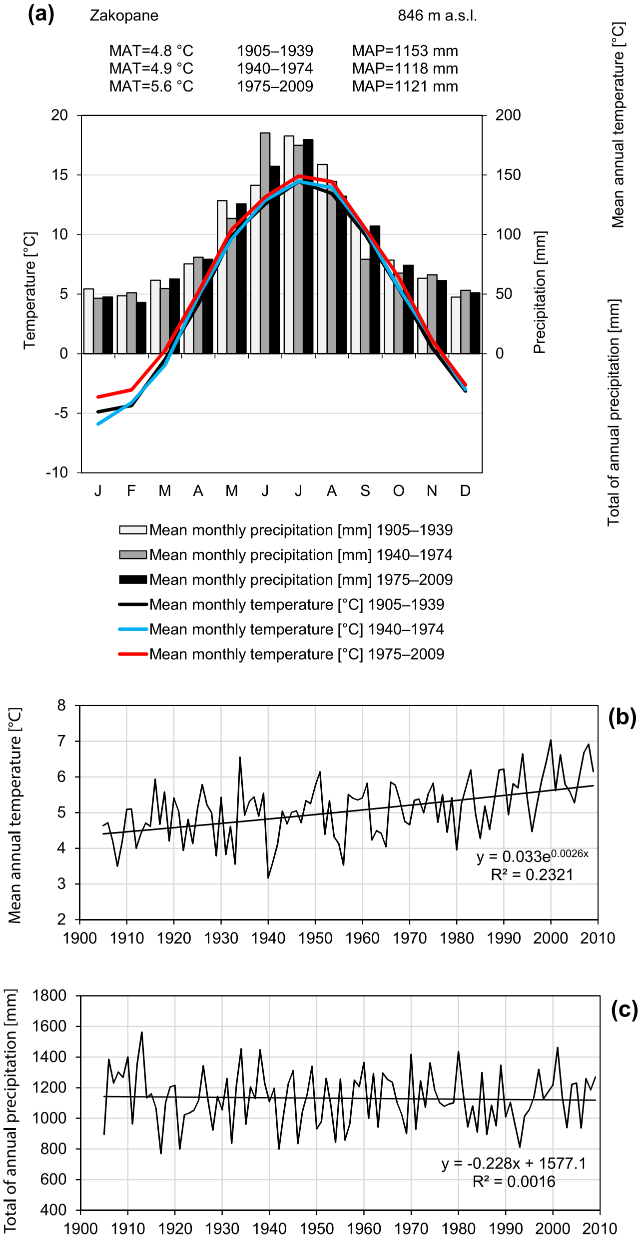
Tree sampling followed the standard dendrochronological protocol (Schweingruber, 1996). Two increment cores were extracted perpendicularly at breast height (~1.3 m height above the ground) with a Pressler borer from undamaged trees. The cores were dried, sanded and scanned at 2400 DPI resolution. Ring widths were measured with WinDendro software (https://www.regentinstruments.com/assets/windendro_about.html). The quality of cross-dating was checked with COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Time series that did not correlate with others were excluded due to possible errors in cross-dating. In total, we used 104 synchronized ring width series (Supplementary Materials Fig. A.1) to construct a tree-ring width (TRW) chronology (Fig. 3).

We conducted standardization by a single-step detrending using a spline function (frequency response of 0.50 cut off at 0.67 series length). For the comparison, we used a two-stage detrending by negative exponential curve, linear regression or horizontal line through the mean growth. The spline method was characterized by a lower variability than the second method (Supplementary Materials Fig. A.2a). The climate-growth relationships calculated with TRWI chronology detrended by the spline method are slightly stronger than the other methods of standardization (Supplementary Materials Fig. A.2b). Detrending was done using the dplR package (Bunn, 2010) in R version 4.0.0 (R Development Core Team, 2020).

Descriptive statistics of the detrended *Pinus cembra* chronology for the time range with a minimum sample depth of 10 trees (1753–2009) and the period selected for climate analyses (1905–2009) were calculated, including: inter-series correlation (Rbar), subsample signal strength (SSS), expressed population signal (EPS) (McCarroll and Loader, 2004), and mean sensitivity (MS) (Fritts, 1976) using the dplR package with the ‘rwl.stats’ and ‘rwi.stats’ functions (Bunn, 2008).

2.3. Climate analysis

For climate-growth analyses we used a residual chronology obtained by fitting a spline function. Our analysis of the correlation and response function between tree growth and climate elements employed DendroClim2002 (Biondi and Waikul, 2004). Bootstrapping was applied to compute coefficients and assess their statistical significance at $p \leq 0.05$. In the program, we analyzed the relationship between tree growth, mean monthly air temperature and monthly total precipitation in the three periods 1905–1939, 1940–1974 and 1975–2009. These subperiods were chosen as equal-lengths (35-years) series of the 105-year climatic data. The results of these analyses were compared to determine whether the pattern of the climate-growth relation of Swiss stone pine in the Tatras has changed. Furthermore, to assess the stability of the climate-growth relationship over time we computed bootstrap correlation coefficients between the TRWI chronology and temperature and precipitation for 30-year windows progressively shifted by one year through



(d)

First and last five-year periods

Period	MAT	MAP	MST	MSP
1905–1909	4.2	1215.8	13.4	177.3
2005–2009	6.2	1176.6	15.1	163.8
difference	2.0	-39.2	1.7	-13.5

Fig. 2. **(a)** Climate diagrams for the meteorological station in Zakopane for the periods 1905–1939, 1940–1974 and 1975–2009, with monthly mean temperature (lines) and mean monthly precipitation (bars); (**b**) Mean annual temperature and (**c**) Total of annual precipitation for the meteorological station in Zakopane, with trend lines (exponential and linear regression, respectively) for the period 1905–2009; (**d**) First and last five-year periods. MAT – mean annual (January–December) temperature [°C], MAP – mean annual precipitation [mm]; MST – mean summer (June–August) temperature [°C], MSP – mean summer precipitation [mm].

the total number of available years from the period 1905–1934 to the period 1980–2009 (moving intervals). The analyzed climate data covered periods from August of the previous year to September of the year of the current vegetation season. Additionally, we added the values of mean monthly temperature and sums of monthly precipitation calculated for all 30-year periods. This helps to understand the change of correlation coefficients over time, which is related to the upward and downward trends of climatic elements.

2.4. *Disturbance analysis*

To characterize the tree-ring changes of the stone pine growing in extreme conditions of cliff forests we reconstruct the growth release pattern, identifying release events in the tree-ring series by applying the boundary line (BL) method (Black and Abrams, 2003). This approach is commonly used to indicate past disturbances by detecting abrupt changes in radial growth – a growth release (Zielonka et al., 2010; Šamonil et al., 2013; Altman et al., 2013; Trotsiuk et al., 2018; Kašpar et al., 2020). The method assumes that trees surviving the disturbance

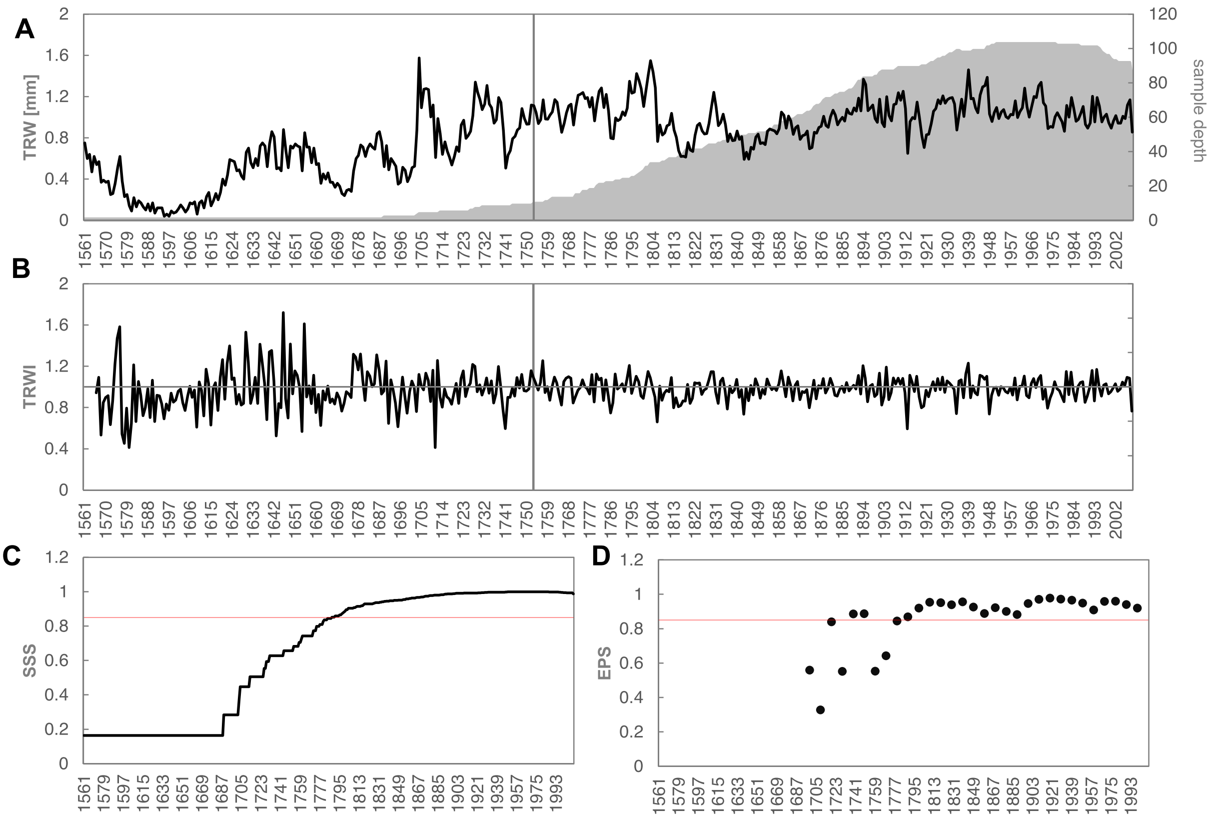


Fig. 3. TRW chronology and sample depth (**a**); TRWI chronology (**b**) of *Pinus cembra* L., grey vertical lines indicate the starting year (1753) with more than 10 trees. Statistical parameters: SSS (**c**) and EPS (**d**), solid red lines represent the value of SSS and EPS equal to 0.85. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(heavy rainfalls, earthquakes etc.) react with growth releases, due decrease of competition. The boundary line release criterion permits researchers to detect release pulses across the range of different values of prior growth (Black and Abrams, 2003). For this purpose, the percentage of growth change (PGC) is calculated according to the formula.

$$\%PGC = (M2 - M1)/M1 \times 100$$

where %PGC is percent growth change for a single year, M1 the preceding 10-year mean growth, and M2 the subsequent 10-year mean growth (Nowacki and Abrams, 1997). The releases are then scaled by their maximum potential observed growth (boundary line), and defined as a release when %PGC ≥ 25% of the boundary line (Black and Abrams, 2003; 2004). The boundary line analyses employed the TRADER package (Altman et al., 2014) in R version 4.0.0 (R Development Core Team, 2020).

Table 1
Descriptive statistics of the detrended *Pinus cembra* chronology for the time range with minimum sample depth of 10 trees (1753–2009) and for the period selected for climate analyses (1905–2009). The selected descriptive statistics for the raw chronology are given in parentheses.

Parameter	For total chronology 1753–2009	For climate study 1905–2009
Number of years [yrs]	257	105
Number of trees	104	104
Interseries correlation [Rbar]	0.167	0.178
Expressed population signal [EPS]	0.925	0.955
Standard deviation [SD] of mean ring width/index	0.300 (0.454)	0.270 (0.393)
Skewness [SKEW]	0.730 (0.922)	0.521 (0.732)
Signal-to-noise ratio [SNR]	12.26	21.06
First-order autocorrelation [AC1]	0.610 (0.763)	0.542 (0.715)

We collected documented and archived records of heavy rainfalls and earthquakes (Kotarba, 2004) to determine potential disturbance agents responsible for stone pine growth releases in the past (Fig. 6). Earthquakes, which have been recorded in the Carpathians, can trigger geomorphological disturbances (Kotarba, 2004). On the timeline, the percentage of trees showing releases was compared with records of extreme events (heavy rainfalls, and earthquakes), and precipitation variability (i.e., total annual precipitation, total summer precipitation from June to August, total autumn precipitation from September to October) (Fig. 6).

3. Results

3.1. Chronology characteristics

The tree-ring width (TRW) chronology of *Pinus cembra* in the Tatras was developed for the period 1561–2009 (449 years) (Fig. 3), and the sample depth of 10 trees covers 257 years (1753–2009). The tree-ring widths ranged from 0.03 mm to 5.65 mm (mean 1.01 mm) for the period 1561–2009 (Supplementary Materials Fig. A.1). For the climate analyses we constructed a residual chronology (tree-ring width index, TRWI). The high values of EPS (0.878 for the whole period 1561–2009, 0.925 for 1753–2009, 0.955 for 1905–2009) allowed us to conduct further climate analyses. Descriptive statistics for the detrended chronology are given in Table 1. Regarding the detrended ring-width series, the SSS value has continuously exceeded the suggested threshold of 0.85 (Buras, 2017; Wigley et al., 1984) since 1788 (Fig. 3).

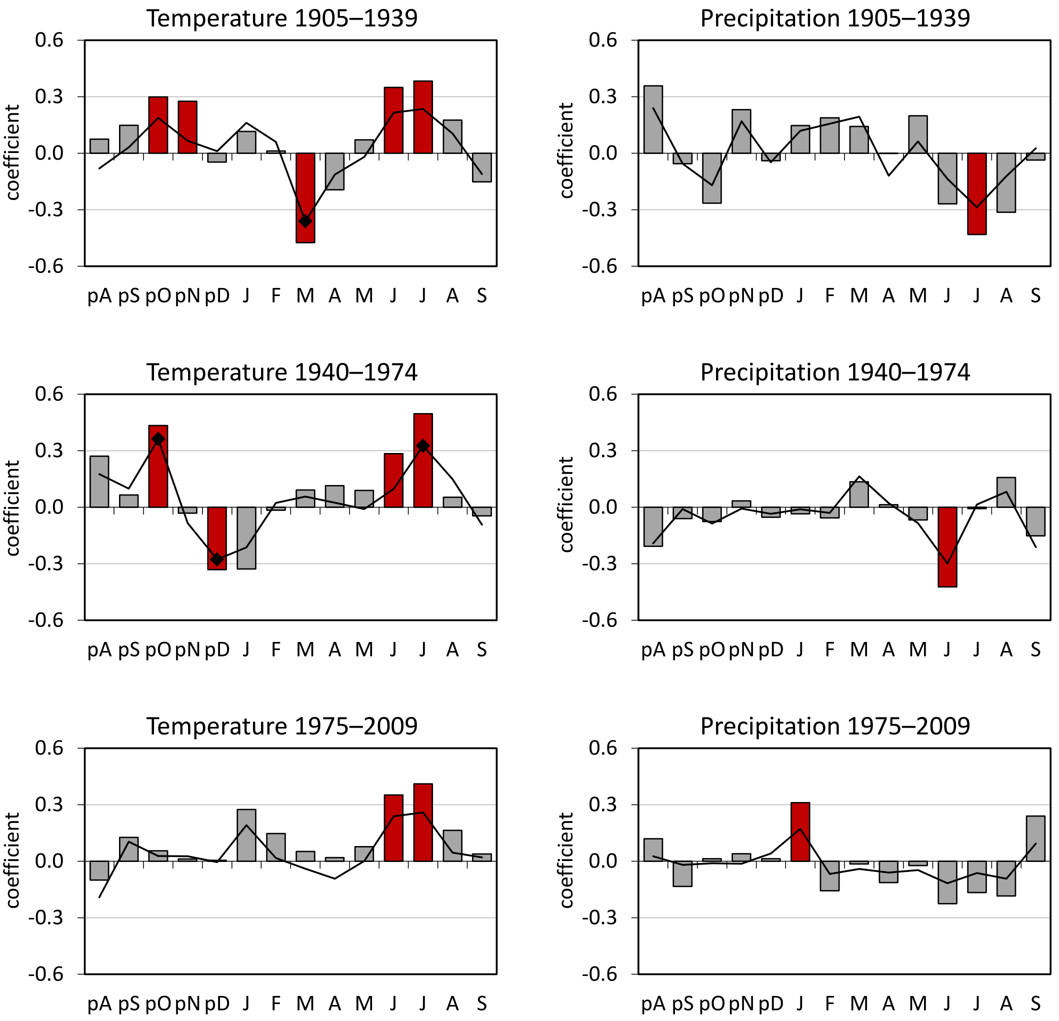


Fig. 4. Bootstrap correlation (bars) and response function (lines) coefficients computed between TRWI chronology and mean monthly air temperature (left) and total monthly precipitation (right) for three periods: 1905–1939, 1940–1974 and 1975–2009. Coefficients were calculated from August of the previous year to September of the current year. Significant ($p \leq 0.05$) coefficients are indicated with red bars (correlation) and black markers (regression). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Climate

In the three analyzed periods (1905–1939, 1940–1974, 1975–2009) the radial growth of Swiss stone pine was strongly related to July and June temperature, the correlations for June being always slightly lower (Fig. 4). In the first period (1905–1939), tree growth was negatively correlated with July precipitation and March temperature. Tree growth was positively influenced by the temperature of the previous October and November. In the second period (1940–1974), stone pine growth was negatively correlated with June precipitation and December temperature. The positive influence of temperature in October of the previous year was higher than in the first analyzed period. In the third period (1975–2009), besides the positive correlation of growth with June and July temperature, January precipitation had a positive effect. A comparison of the response function coefficients of the three 35-year periods shows that the climate-growth pattern changed (Fig. 4).

The correlation coefficients between growth and climate elements (temperature and precipitation) have changed over the analyzed period (Fig. 5). Average temperature has increased and precipitation has slightly decreased during the last century (Fig. 2). These changes are visible over the course of monthly values (Fig. 5). For instance, the temperature increase was highest during recent decades in January and February, but for most of the remaining months the rising temperature trend is seen in the last few years. The strongest (and temporally constant) correlation was between growth and July temperature, regardless of the temperature variation of that month across the whole century. Similarly, there was a positive correlation between growth and June temperature, but in years when June temperature was higher (the 1960 s–1980 s) the correlation became weaker and nonsignificant (Fig. 5). The significant positive correlation between growth and temperature of the previous October disappeared at the end of the 20th century, when October became warmer (Fig. 5). A similar phenomenon was observed for temperature of the previous November: a positive correlation at the beginning of the 20th century, declining when that temperature started to rise at the end of the 1940 s. A positive correlation between growth and temperature of the previous August can be seen in the middle of the 20th century, but this relationship is weak in the earlier period, when average temperature was lower, and at the end of the 20th century when temperature increased. Monthly precipitation did not exhibit a distinct trend during the analyzed period. The highest July precipitation at the

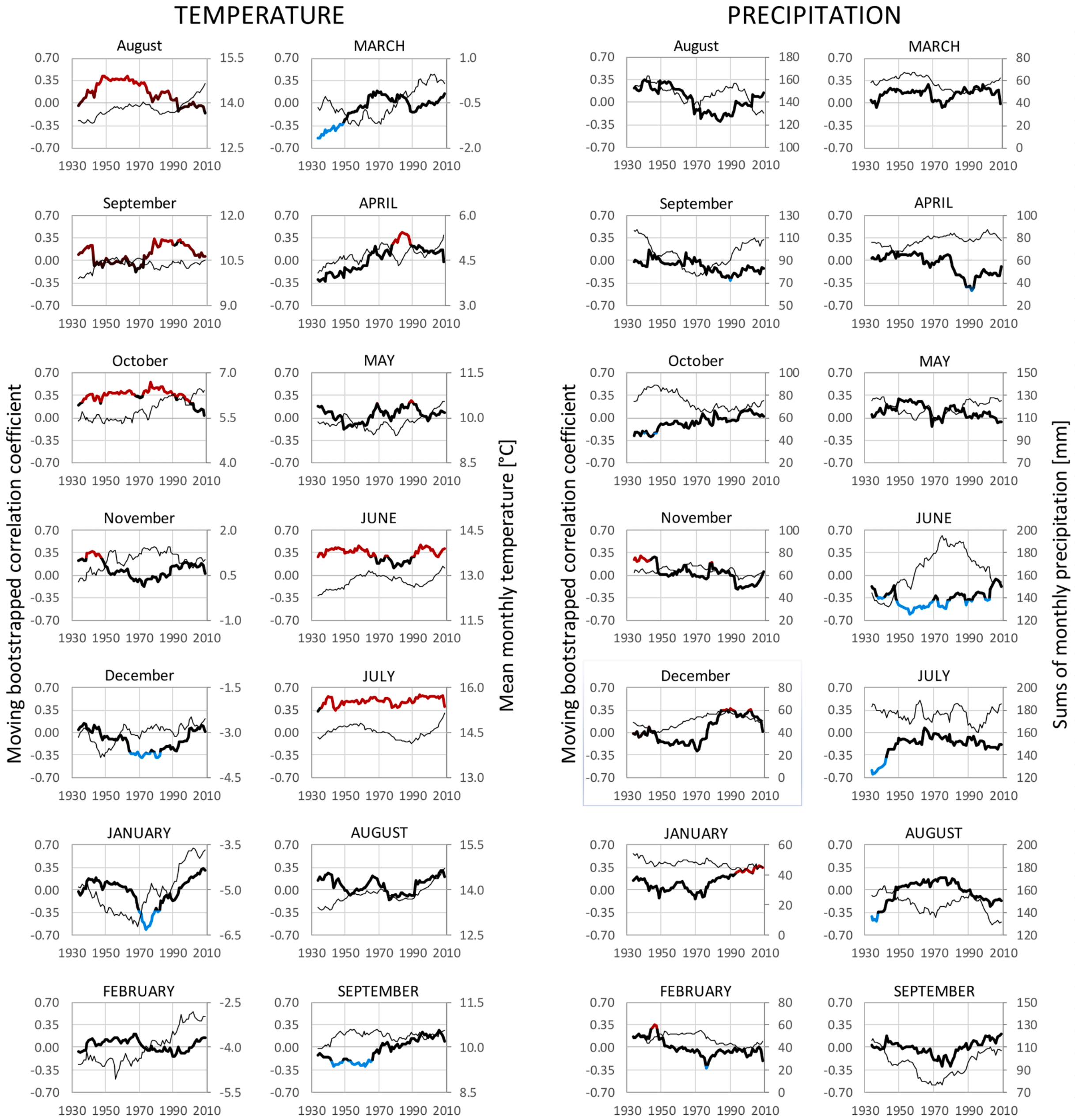


Fig. 5. Bootstrap correlation coefficients (bold line) computed using moving intervals, between the TRWI chronology and mean monthly air temperature (left) and total monthly precipitation (right). A 30-year window was progressively shifted through the total number of available years from the 1905–1934 period to the 1980–2009 period. The last year of the 30-year window is given on the horizontal axis. Correlation coefficients were calculated from August of the previous year (lowercase letters) to September of the current year (uppercase letters). Statistically significant ($p \leq 0.05$) positive correlation coefficients are shown in red, and negative ones in blue. Mean monthly air temperatures (left) and sums of monthly precipitation (right) calculated for each 30-year period are represented by fine lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

beginning of the 20th century corresponds with a significantly negative correlation with radial growth in this period (Fig. 5). The increase of June precipitation after 1950 corresponds with a significant negative correlation in this period. After 1980, June precipitation decreased; this overlaps with the absence of a significant correlation between growth and precipitation. Interestingly, the last decades show a positive correlation between growth and January precipitation (Fig. 5).

3.3. Disturbance analysis

The reconstructed growth releases pattern was obtained from 1753 (minimum of 10 trees) to 1999 (see the formula in the Material and methods). The oldest releases were recorded in 1770 (Fig. 6d). The distribution of releases did not indicate synchronized signals. The episode with the highest number of releases was during 1820–1826, when 63% of the trees exhibited release. Another substantial pulse was at the end of the 18th century (1787–1795), when releases were detected in 46% of trees. The next highest reactions were recorded in the middle of the 19th century (1850–1857), when 24% of trees showed a reaction. Since the end of the 19th century the releases have occurred frequently in single trees (Fig. 6d).

The percentage of trees showing releases (Fig. 6d) was not significantly correlated with total: annual ($r = 0.06$, $p = 0.553$; Fig. 6a), summer ($r = 0.10$, $p = 0.322$; Fig. 6b) and autumn ($r = -0.01$, $p =$

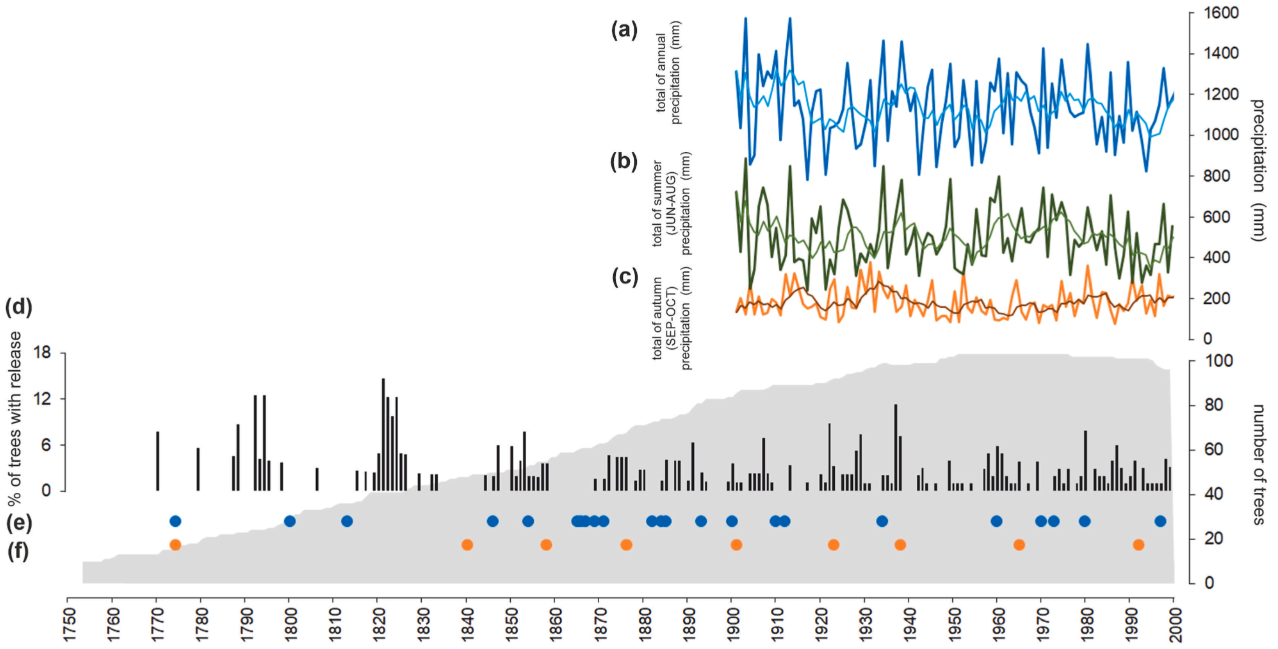


Fig. 6. Comparison of: (**a**) total of annual precipitation with 5-year moving average (blue lines), (**b**) total of summer precipitation (June-August) with 5-year moving average (green lines), (**c**) total of autumn precipitation (September-October) with 5-year moving average (orange lines), (**d**) growth releases and disturbances, i.e., (**e**) heavy rainfalls (blue dots), (**f**) earthquake (orange dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.921; Fig. 6c) precipitation. According to the historical records, frequency of heavy rainfall in the Tatras was highest in the second half of the 19th century. The most catastrophic rainfall occurred in 1813, 1882, 1934, and 1973 (Kotarba, 2004) (Fig. 6 e). We found that the growth releases intensified after floods in 1960, and 1980 (Fig. 6d, e). Although nine earthquakes were noted in the analyzed period, we found no relation with growth release (Fig. 6d, f).

4. Discussion

Our data show that tree rings can be a valuable indicator of the changing environment. Both climate and growth releases determine the variability of radial growth of stone pine on cliffs. In interpreting our results we must take into consideration the unique habitat of high elevation cliffs reaching the upper tree line limit. Swiss stone pine is physiologically well adapted to such extreme conditions (Tranquillini, 1979; Saulnier et al., 2011), however, so our results do more generally shed light on the complex pattern of the reaction of living trees to changes in the environment (climate versus growth release).

4.1. Climate

The mean annual temperature in the Tatras has risen over the last 100 years, but the increase is lower than that observed in the Alps. For the Central European Alps, Oberhuber et al. (2020) reported a +2.5 °C increase of annual temperature between two five-year periods (1915–1919, 2011–2015). In the Tatras, mean annual temperature increased by only +2.0 °C between two roughly similar periods (1905–1909, 2005–2009). The difference in temperature increase between the Tatras and the Alps is even clearer for the summer months (June–August). Between those five-year periods, mean summer temperature increased by +3.1 °C in the Alps (Oberhuber et al., 2020) but by only +1.7 °C in the Tatras. Other authors confirm the high increase of temperature in the Alps: for example, +2.1 ± 0.77 °C from 1900 to 2003 (Housset et al., 2021); and +1.9 °C (winter) and +2.4 °C (summer) from 1966 to 2000 (Vittoz et al., 2008).

Our study shows that the growth of stone pine is controlled mostly by summer (June and July) temperature, a key factor that usually determines the growth of tree species at high elevations (Bednarz, 1981; Carrer and Urbinati, 2004; Carrer et al., 2007; Oberhuber et al., 2008; Vittoz et al., 2008; Saulnier et al., 2011; Housset et al., 2021). This effect can be explained by the short vegetation season, which is limited to those months when photosynthesis is most intensive at high elevations. According to current knowledge, “the carbon can only be converted into biomass to the extent chemical elements other than carbon, temperature or cell turgor permit” (Körner, 2015). A few areas in the Alps have not confirmed the positive influence of increase in summer temperature on stone pine growth. Oberhuber et al. (2020) found that stone pine did not exhibit a positive growth reaction to the increase in summer temperature in the Central European Alps, and explained this by suggesting that the growth of stone pine is more limited by the supply of nutrients, light and water than it is benefited by an increase in temperature. D’Arrigo et al. (2008) found that an increase in summer temperature may have a negative influence on trees growing at high elevations, due to increased late-summer drought stress, coincident with recent warming trends. We suppose that these results may be due to differences in water availability on regional/local scales.

A positive influence of temperature of the previous October and November on radial growth has been reported (Bednarz, 1981; Carrer et al., 2007; Oberhuber et al., 2008; Vittoz et al., 2008; Housset et al., 2021), but in our study this was confirmed only for the period 1905–1974; for the last decades this relationship was not observed. Probably this is related to an increase in winter temperature (Fig. 2). Autumn is the period for needle cuticle development and accumulation of reserves for the next season; it is an important stage for building up good protection against winter frost, drought or wind (Tranquillini, 1979; Oberhuber, 2004; Mayr et al., 2006).

The negative relation between growth and March temperature in the beginning of the 20th century can be explained by winter desiccation, which can occur in late winter when transpiration cannot be compensated because the soil is still deeply frozen (Saulnier et al., 2011 Havranek and Tranquillini 1995; Tranquillini 1979; 1982). This pattern disappears in further years when winters become warmer, leading to faster defrosting of soil. Such an inverse relationship between growth and March temperatures also appears in studies from the Alps (Pfeifer et al., 2005; Carrer et al., 2007; Oberhuber et al., 2008; Vittoz et al., 2008; Housset et al., 2021).

The first two periods of our analyses (1905–1939, 1940–1974) clearly show summertime precipitation to be a limiting factor on radial growth (Fig. 4). In the last decades (1975–2009) these negative relationships became weaker and nonsignificant. Similar results come from different parts of the Alps, where summer precipitation was seen to have no negative influence on growth (Oberhuber et al., 2008; Saulnier et al., 2011). What is more, some locations in the Alps showed a positive correlation with summer precipitation (Vittoz et al., 2008; Carrer et al., 2007).

Another interesting observation from our study is the positive influence of January precipitation in the last decades (1975–2009) (Fig. 4). A similar pattern was observed in the Alps (Carrer et al., 2007; Saulnier et al., 2011). High snow depth prevents deep soil frost and reduces the risk of damage due to frost drought (Körner, 2012).

Understanding the effect of interactions between temperature, precipitation and the radial growth of trees in extreme environments (i.e., above timberline) and on different temporal scales (monthly, seasonal, yearly) should add to our knowledge of such ecologically valuable areas.

4.2. Disturbances

The tree-ring series we studied show frequent release signals in individual trees over the centuries. We conclude that there is no single significant common driver responsible for the growth releases of stone pine in the Tatras cliff forests. The abrupt increases in ring width identified as releases can be explained only by substantial improvement of growth conditions, brought on by a decrease in competition. Such an improvement in growth conditions is most likely due to the elimination of, or serious damage to, neighboring trees, caused by various agents (e.g., soil erosions, lighting, snow or wind breakage). Most often the releases result from a disturbance event in the calendar year preceding the increase of ring width (Lorimer and Frelich, 1989; Altman, 2020). The lack of distinct peaks of release rather excludes the occurrence of large-scale disturbances affecting the whole studied area. In such a case we would see single release pulses in a higher percentage of trees (Zielonka et al., 2010; Holeksa et al., 2016; Izworska et al., 2022). The only such episode, when 63% of the stone pines reacted synchronously was in the early 19th century. Releases occurred over the whole studied period (17th to 20th centuries), suggesting that the mortality or damage of trees in cliff forests is rather random and involves single individuals at different times. Most of the oldest stone pines grew solitary or at low density. Their releases indicate that in the past these trees must have been part of a denser stand. Our results suggest, that the disturbance regime in cliff forests is most likely related to the local events caused by orographic conditions.

Climate events such as extraordinary rainfalls may set off landslides, rockfalls or other disturbances of the terrain (Kotarba. 2004; Zielonka and Dubaj, 2009). It is worth noting that the Little Ice Age, which in the Tatras ended at the beginning of the 20th century, was characterized by significantly higher precipitation (Kotarba, 2004); this may explain the mortality of aging trees growing in locally less stable conditions (Larson et al., 2005), hence the interest to study cliff populations. The stone pine forests in the Tatras, like other examples of cliff forests all over the world, are regarded as the most primeval ecosystems, occurring locally in inaccessible places (Zięba et al., 2018; 2019). Felling of single trees on cliffs would have thinned the stand, leading to growth release in trees that were left intact, but we note that releases still occurred in the second half of the 20th century, when the study area was protected as a strict reserve in Tatra National Park and human activity was significantly restricted. This suggests that stone pine mortality in the past should be attributed primarily to natural factors.

Swiss stone pine in the Tatras constitutes a relatively small and highly fragmented population which, however, shows high genetic variability (Dzialuk et al., 2014). The presence of numerous seedlings and saplings observed during our fieldwork, confirmed by other authors (Zwijacz-Kozica and Żywiec, 2007; Zięba et al., 2019), indicates that this population is stable. The limited space of rocky shelves, crevices and layers of organic matter accumulated on rocks and boulders can provide conditions sufficient for germination and juvenile growth of more individuals (Zięba et al., 2019). Moreover, the upward spread of *Pinus cembra* is supported by a fruit-dispersal bird, the nutcracker *Nucifraga caryocatactes*, which can promote pine recruitment in new areas above the tree line (Tomback et al., 1993). Casalegno et al. (2010) predicted that in the more distant future stone pine in the Alps may decline due to increasing competition from co-dominant species (i.e., Norway spruce), following scenario predicting the upward shift of the treeline due to warming.

The high-elevation cliffs in the Tatras seem to provide a suitable habitat for the persistence of the relict stone pine population in the future. Uniquely, our study linked climate changes and disturbance regimes in a consideration of the future of Swiss stone pine in such extreme cliff forest ecosystems.

5. Conclusions

Tree rings are widely used as an ecological indicator in studies of environmental and climatic changes. Dendroecological analyses are highly useful for understanding the growth of trees, especially in the harsh mountain conditions. Such a tool is important, since observed and predicted changes of climate and disturbance regimes may substantially influence the growth of trees in the nearest future.

Summer temperature (June and July) positively influenced the radial growth of stone pine in high-elevation cliff forests in the Tatras over the last century. The temperature of the previous autumn, winter and early spring, which had a significant influence on stone pine growth in the past, has declined in importance now. On the other hand, in recent decades the negative influence of summer precipitation on tree growth has declined; this may be related to warmer summers and decreasing precipitation. We showed that the influence of temperature and precipitation on tree growth on cliffs is not stable over time under climate change. The current climatic conditions in the Tatras seem to promote stone pine growth and its potential upward shift. The numerous past disturbance events have affected a limited number of trees. This may suggest that single individuals have been randomly eliminated from the cliff stand during the last three centuries. We found that the disturbance regime cannot be linked directly to the occurrence of specific climatic extremes in the Tatras. Our study, conducted in the unique environment of high-elevation cliff forests, shows a change in the pattern of the climate-growth relationships along with changing temperature and precipitation in the last century.

Further observation of the stone pine population in the Tatras under changing climate and possibly changing disturbance intensity will help us to better protect and preserve this valuable species as an integral element of the primeval high-elevation environment. Future work using higher-resolution data (e.g., daily climatic data, detection of blue rings) should more precisely characterize the climate-growth relationships and the disturbance regime along the timberline.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110102.

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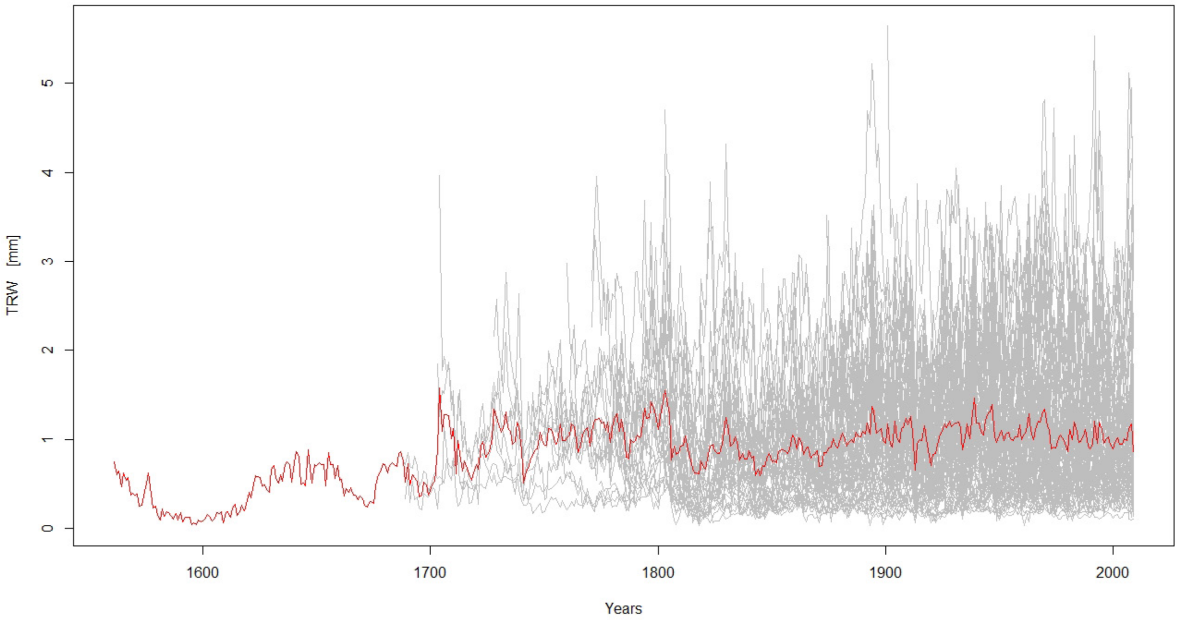
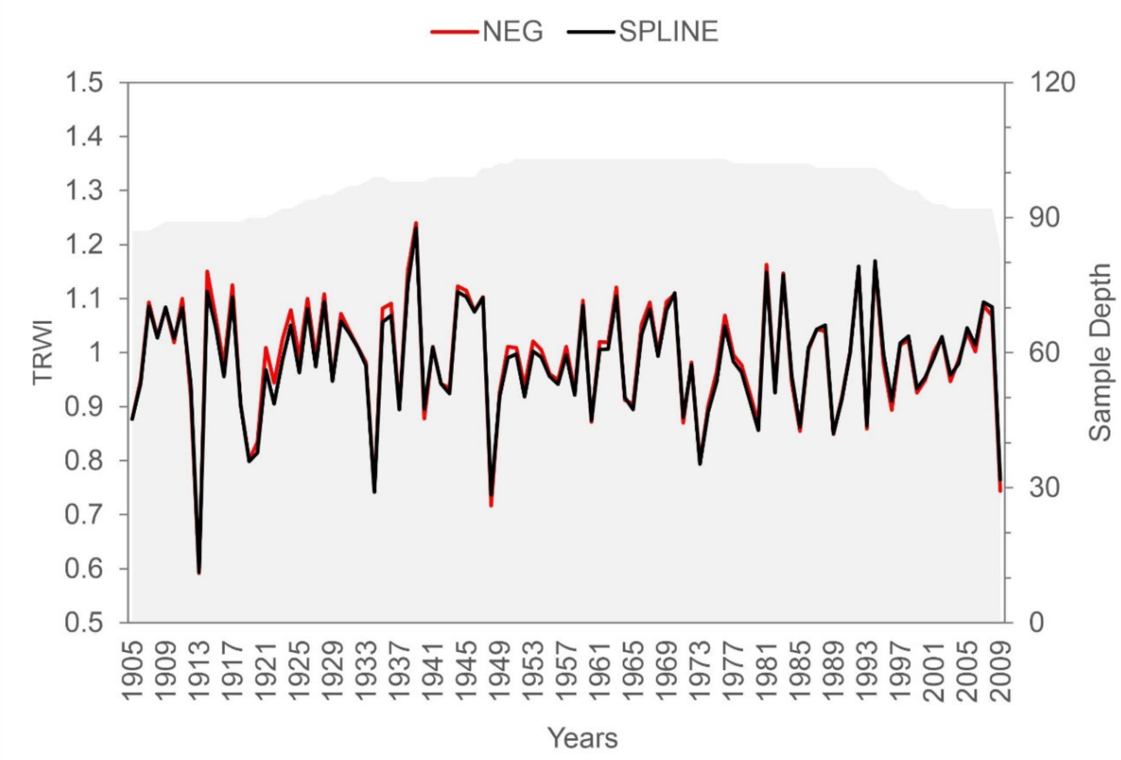
SUPPLEMENTARY MATERIALS

Supplementary materials Fig. A.1 The 104 synchronized tree-ring width series and TRW chronology (red line) of *Pinus cembra* in the Tatras

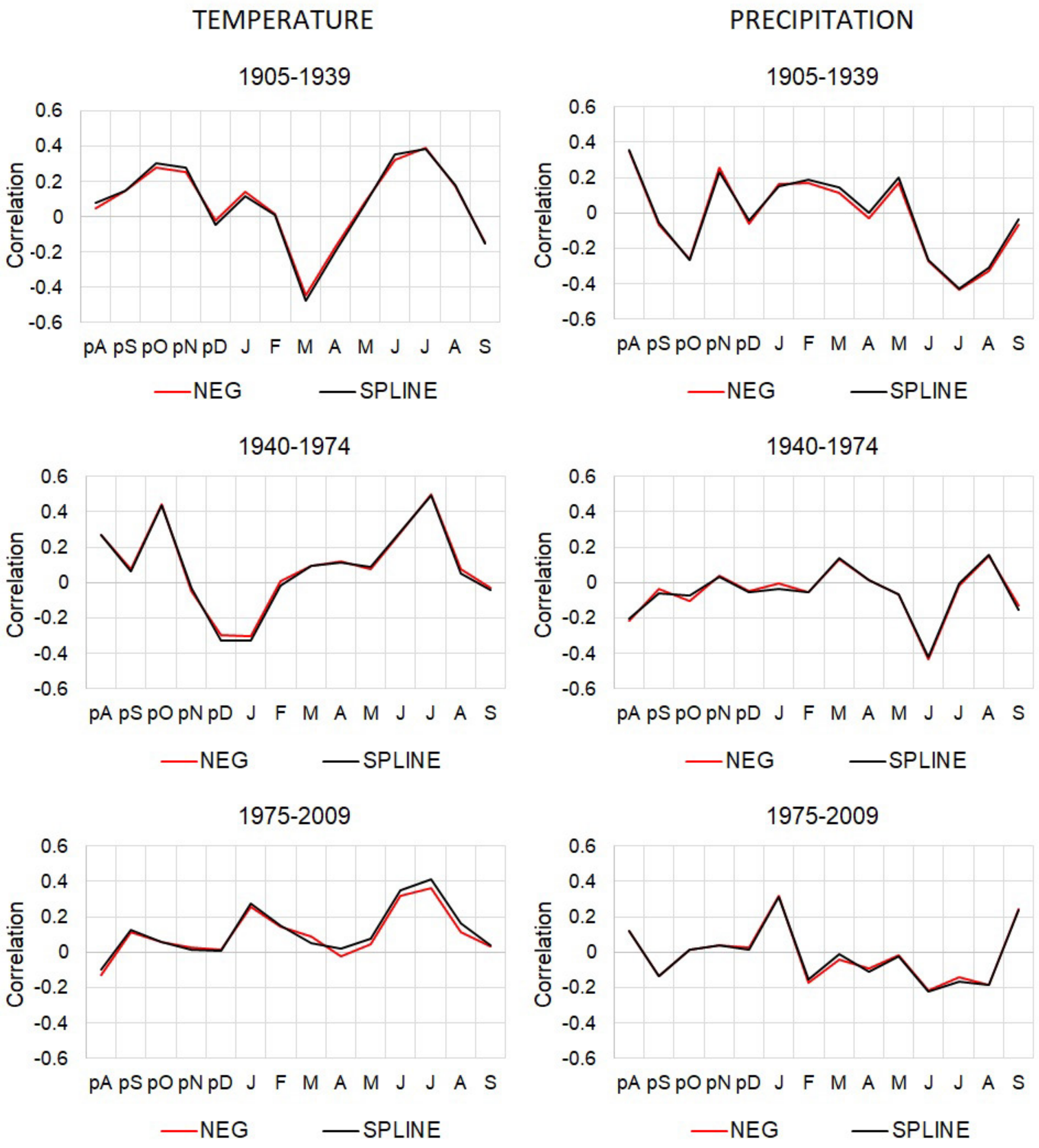


Supplementary materials Fig. A.2 (a) Comparison of chronologies used different standardization methods (spline function (frequency response of 0.50 cut of at 0.67 series length), and two-step detrending by negative exponential curve, linear regression or horizontal line through the mean growth). **(b)** Bootstrap correlation coefficients computed between TRWI chronologies produced by different methods of standardization and mean monthly air temperature (left) and total monthly precipitation (right) for three periods: 1905–1939, 1940–1974 and 1975–2009.

(a)



(b)


TEMPERATURE
PRECIPITATION
1905-1939
1940-1974
1975-2009
Correlation
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
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Artykuł nr 3

Izworska, K., Zielonka, T., Matulewski, P., Muter, E. 2023. Daily Climatic Data Better Explain the Radial Growth of Swiss Stone Pine (*Pinus cembra* L.) in High-Elevation Cliffs in the Carpathians. Forests 14 (7): 1411.

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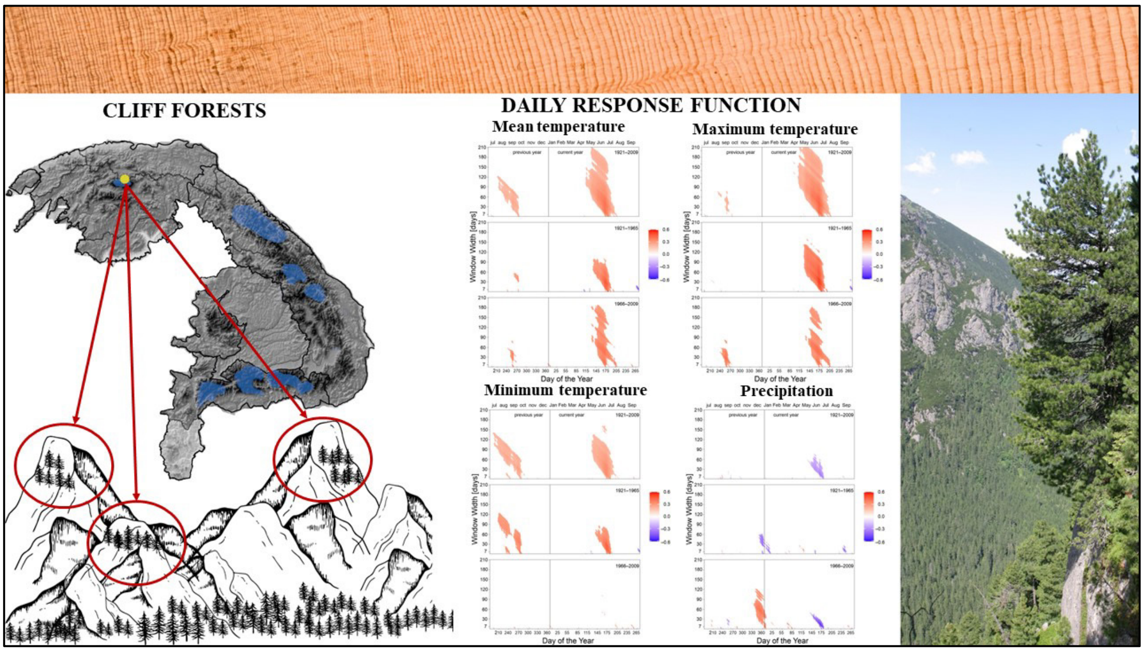
GRAPHICAL ABSTRACT



forests

Article

Daily Climatic Data Better Explain the Radial Growth of Swiss Stone Pine (*Pinus cembra* L.) in High-Elevation Cliffs in the Carpathians

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Abstract: Information about climate–growth relationships is crucial for predicting the potential climatic impact on tree species, especially those growing on the edges of their distribution range, for instance, in high-elevation forests. This study aimed to determine changes in the relationships between tree-ring widths and daily climatic data in high-elevation forests in the Western Carpathians over time. Climate–growth relationships were calculated to obtain the TRWI (tree-ring-width index) chronology (based on 104 trees) and day-wise aggregated data for temperature (mean, minimum, and maximum) and sums of precipitation. The radial growth of stone pine was mostly determined by the mean temperature in the period between mid-June (21st) and the beginning of July (4th) for the critical 14-day window width (r = 0.44). The negative influence of precipitation on the radial growth occurred in summer (r = −0.35) and overlapped with the period of the positive influence of temperature. Dendroclimatic studies based on daily data may define the exact periods (expressed in calendar days) that influence the radial growth of trees much better than the commonly used monthly means. This is particularly important in analysing the growth of trees at high elevations, where the climatic factor strongly limits radial growth.

Keywords: climate change; cliff forest; daily climatic data; dendrochronology; *Pinus cembra*; tree rings

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1. Introduction

Climate change is a phenomenon observed worldwide in recent times. It is related to increases in annual temperature and the distribution of precipitation [1–3]. Although we are still far from the Holocene climatic optimum, recent models predict further progress towards higher temperature and lower precipitation [4–6].

Thus, it is predicted that the distribution range of tree species will be changing parallel to climate change. The possible delays in tree responses will be minor or the range changes will be unable to keep up with climate change; therefore, the adaptation of species in accordance with environmental conditions will significantly worsen [7–11]. The frequency and intensity of extreme climatically induced events are also expected to change [4,12,13]. Climate change is widespread, affecting forests within a variety of geographical regions where warmth (e.g., in mountain or boreal ranges) or water availability (e.g., in arid and Mediterranean areas) are limiting environmental factors [13]. Trees on the edge of their distribution range are subjected to environmental stress, and their growth response to climate can reveal ecological thresholds beyond which they may not be able to persist. This information is critical for predicting the potential impacts of climate change on the distribution of tree species and the vitality of species populations.

Moreover, climate impacts on forests range from single extreme events with a difficult-to-predict time and location, to more obvious gradual changes. Therefore, it is necessary to conduct research on different spatial scales, from local to global, with the use of data of varying resolutions and species. Retrospective tree-ring-based studies are a useful tool for investigating how trees may adapt to forecasted changes [5,14–16]. A long-living organisms exposed to environmental variability, trees seem to be the best indicators of the reactions of living organisms to climate change [14,15]. This is especially important for trees growing on the edge of their distribution range, such as the north and upper timberlines.

High-elevation forests are the sentinels of change due to their location at the edges of their distribution range. They react quickly and strongly to environmental changes, including climate [17]. Extreme weather conditions are common in high-elevation ecosystems, due to the large amplitude of day–night and seasonal temperatures [17–19]. A low nutrient supply, as well as significant disruptions produced by gravity—rock and avalanche, snowfall and snow accumulation, and winds—contribute to the harsh environment of cliffs [17]. The Swiss stone pine (*Pinus cembra* L.) is a taxon with scattered populations (the Alps and Carpathian Mountains), exhibiting the finest adaptations for colonisation and growth in high-elevation cliffs [9,20–24]. Previous studies from the Alps [9,24–26] and Carpathian Mountains [20,27,28] have shown that the response of this species to climate changes is not stable over time.

The analysis of the relationship between radial growth and climate has typically been carried out using monthly meteorological data, e.g., [25,26,29,30]. Such data can provide a broader perspective on the long-term relationship between growth and climate, as it captures seasonal and annual fluctuations in environmental conditions. It is useful to identify general patterns and trends in growth responses to climate variables over time. However, it is important to consider the limitations of monthly data and its disadvantage to miss short-term climatic effects. Nevertheless, most of these studies have used the mean monthly climatic data when the months are artificially time-compressed [31–33]. Methodological improvements, access to gridded climate datasets and computing power to manage big databases have allowed for conducting more comprehensive studies with high-resolution data sets [16]. Daily climatic data offer a more detailed view of environmental conditions, which can help identify subtle effects of climate on tree growth that may be missed with monthly data. The daily resolution of climatic data detects the exact days of the year when temperature and precipitation significantly influence the radial growth of trees [32,33]. Overall, the use of daily climatic data can be valuable in analysing climate–growth relationships, but it requires careful consideration of advantages and disadvantages and the research question addressed.

This study aimed to enhance the precision and temporal resolution of the climate–growth correlation for Swiss stone pine in an extreme environment of highly elevated cliff forests. Specifically, we aimed to (1) examine climate–growth relationships using a daily response function, (2) determine the exact days of the year in which climatic parameters significantly affect growth, and (3) explore how the growth response to climate changes over time (throughout the last 90 years). It was hypothesised that the strength of the climate–growth relationship decreased in the warming climate over the last decades.

2. Materials and Methods

2.1. Study Area and Climate

The study site was located in the upper treeline ecotone in the Tatras (the Western Carpathian Mountains) (49°12′54.48″ N; 20°4′34.68″ E) (Figure 1). The Tatra Mountains, having classic alpine terrain and elevations of over 2600 m a.s.l., represent the highest and most rugged Carpathian mountain range [22,34]. The studied stone pines grow in high-elevation cliff forests on steep, granite slopes (ca. 70–80°) between the subalpine zone and dwarf pine scrub (*Pinus mugo* Turra) (ca. 1480 m a.s.l.). The study area was described in detail in the previous paper analysing the same tree samples [20]. It is a protected area of the Tatra National Park under a temperate-continental climate zone with significant differences between the daily maximum and minimum temperature and large amounts of precipitation [34]. The annual mean temperature of the sample site was 3.32 °C covering the period of 1921–2009, and the sum of annual precipitation was 1212 mm (Figure 2a,b).

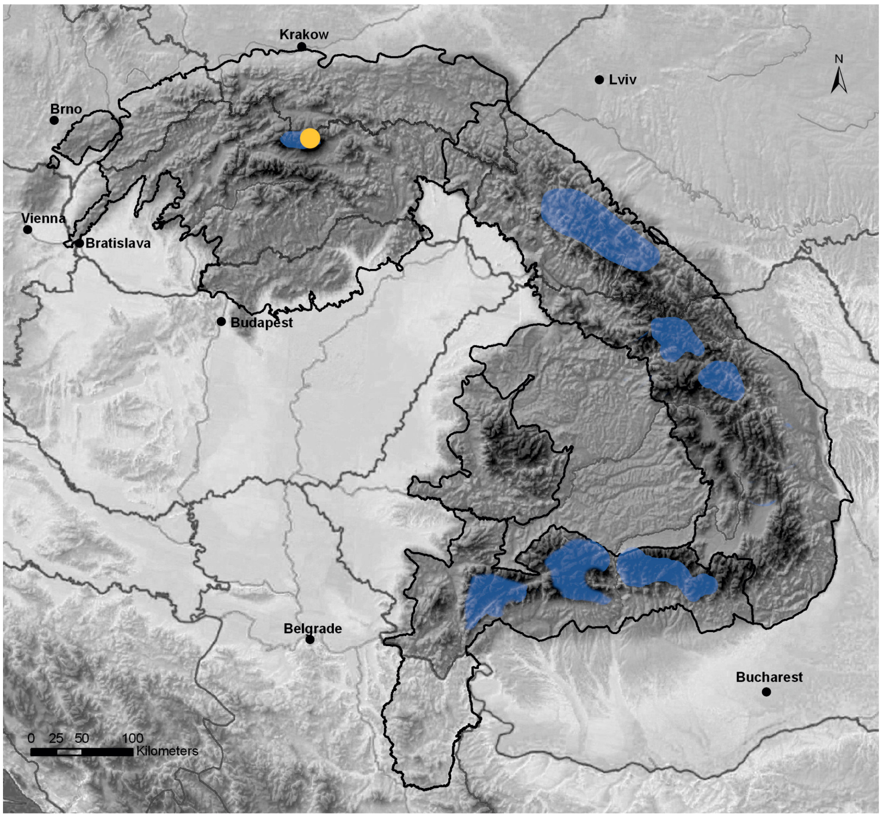
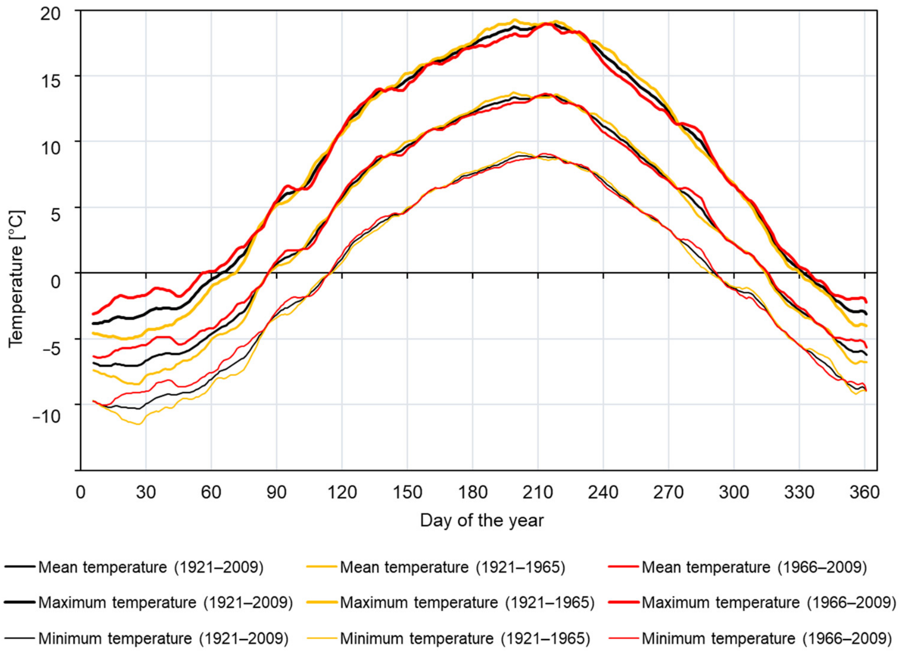
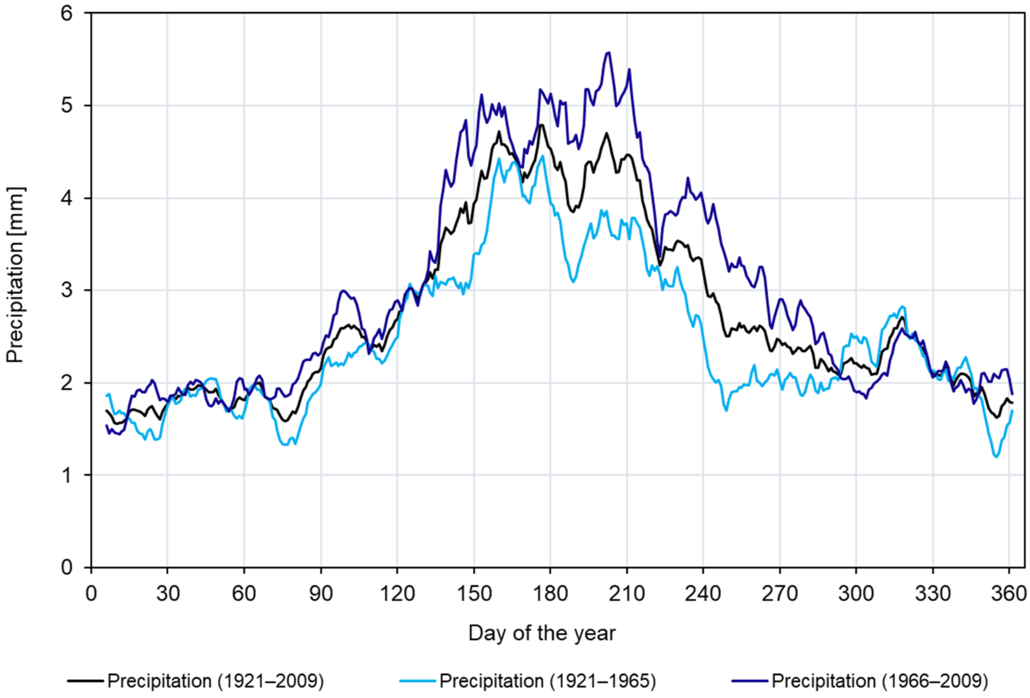


Figure 1. Map showing study site location (yellow dot) and the distribution of *Pinus cembra* in the Carpathian Mountains (blue areas) [35].



(**a**)

Figure 2. *Cont.*



(**b**)

Figure 2. Climatic diagrams for the analysed period (1921–2009) and two subperiods (1921–1965 and 1966–2009) based on daily data for the study area: (**a**) Eleven-day running means of the daily mean, maximum, and minimum temperature; and (**b**) eleven-day running means of the daily sums of precipitation.

2.2. Tree-Ring and Climatic Data

The increment cores were extracted at breast height (ca. 1.3 m) from stone pine trees growing in the study area with a Pressler borer. The cores were labelled, sanded, and then scanned at a 2400 DPI resolution. The ring widths were measured using the WinDendro software (https://www.regentinstruments.com/assets/windendro_about.html (accessed on 21 April 2023)). The accuracy of cross-dating was checked with COFECHA [36,37]. Time series that did not correlate with others were excluded to avoid potential errors in cross-dating. The diameter at breast height (DBH), height, and age of the studied trees as well as the tree-ring width (TRW) chronology characteristics were comprehensively described by Izworska et al. [20].

Daily climatic data: Temperature (mean, maximum, and minimum) and a sum of precipitation were obtained from the closest grid point for the study site (49°12′54.48″ N; 20°4′34.68″ E) from the E-OBS gridded climate dataset [38]. E-OBS version 25.0e (0.1-degree regular grid) covers the time from 1 January 1920 to now.

2.3. Analysis of Daily Climate–Growth Relationships

Climate–growth relationships were calculated using residual chronology (TRWI—tree-ring-width index) for the 1921–2009 period. To remove the age-related growth trends and competition effect, detrending was performed using the spline function (frequency response of 0.50 and cut off at 0.67 series length) in the ‘dplR’ (in R version 4.0.0) [39,40]. Statistics of the detrended chronology for the climate analysis (1921–2009), including interseries correlation (Rbar), expressed population signal (EPS), subsample signal strength (SSS) [41], and mean sensitivity (MS) [42], were calculated using the ‘dplR’ with the ‘rwi.stats’ functions [43].

Climate–growth relationships for the TRWI chronology and day-wise data for temperature (mean, maximum, and minimum) and the sum of precipitation during the 1921–2009 period, and the two subperiods of 1921–1965 and 1966–2009, were analysed. These subperiods were chosen as a comparable length (45 years and 44 years, respectively) series out of the 89-year climatic data to indicate possible changes in the growth reaction due to climate change over the last decades. We used the 'daily_response()' function from the 'dendroTools' [31,40]. The primary objective of the 'daily_response()' function was to examine changes over time in the relationships between tree rings and daily climatic data. The function used a moving window through daily data and aggregated data within each window by calculating its averages and then calculating statistical metrics (i.e., correlation coefficient). The moving window was based on the window width (number of days) and daily data within the position of the matrix [31]. The daily correlations were computed by taking into account all window widths ranging from 7 to 210 consecutive days from July of the previous year to September of the year of growth. To calculate partial correlations, a bootstrap procedure was applied within 1000 replicates.

3. Results

3.1. Site-Specific Chronology

The TRWI chronology for the 1921–2009 period covered the available daily climatic data (Figure 3); the statistical parameters are provided in Table 1. The chronology shows the EPS value, as well as SSS exceeding the threshold of 0.85, indicating the strong climate signal in the site chronology and allowing us to conduct further climatic analyses [44,45]. The relatively low value of Rbar might be because our sampled trees were not a homogenous group with a large number of samples (104 trees). Alongside that, the trees were of different ages and growing in various microhabitats, reflecting individual growth conditions in the cliffs. Rbar values are usually higher in more homogenous groups/areas.

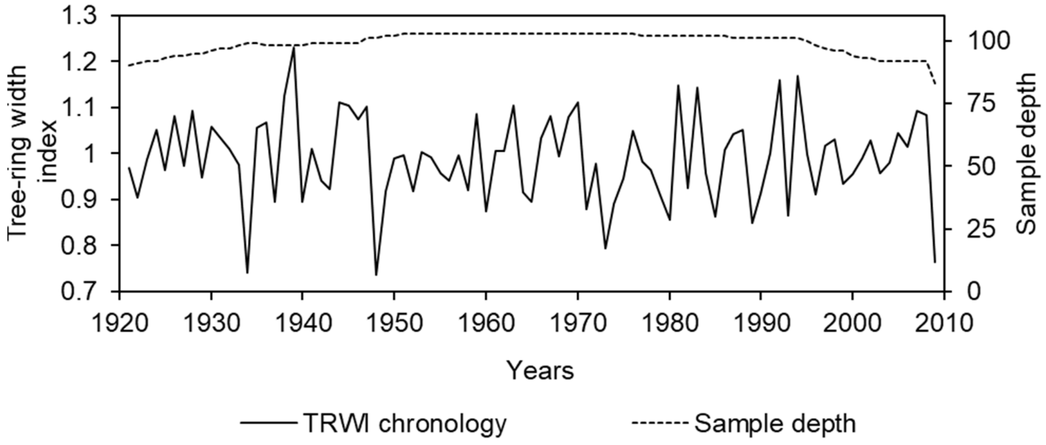


Figure 3. The TRWI chronology (solid line) and sample depth (dotted line) for 1921–2009 period.

Table 1. Statistics of the detrended chronology for the analysed period (1921–2009) and two subperiods (1921–1965 and 1966–2009).

Parameter	Number of Years	Number of Trees	Interseries Correlation (Rbar)	Expressed Population Signal (EPS)	Subsample Signal Strength (SSS)	Mean Sensitivity (MS)
1921–2009	89	104	0.16	0.951	0.998	0.196
1921–1965	45	104	0.17	0.953	0.997	0.187
1966–2009	44	104	0.14	0.942	0.998	0.188

3.2. Climate–Growth Relationships

3.2.1. Mean Temperature

The highest positive significant correlation coefficient (r = 0.44) between the TRWI chronology and the mean temperature was found for the 14-day window width between 21 June and 4 July (DOY 172–185) during the year of growth (Figure 4). However, an important period with a high correlation (r > 0.40) was found for the window width range between 14 and 50 days, spanning mid-June to the beginning of August (DOY 168–222). Additionally, tree growth was positively influenced by the mean temperature of autumn the previous year (0.20 < r < 0.30), and an important period with relatively high correlation coefficients for this period spanned mid-September to the end of October (DOY 257–306; 39–46-day window width) (Figure 4).

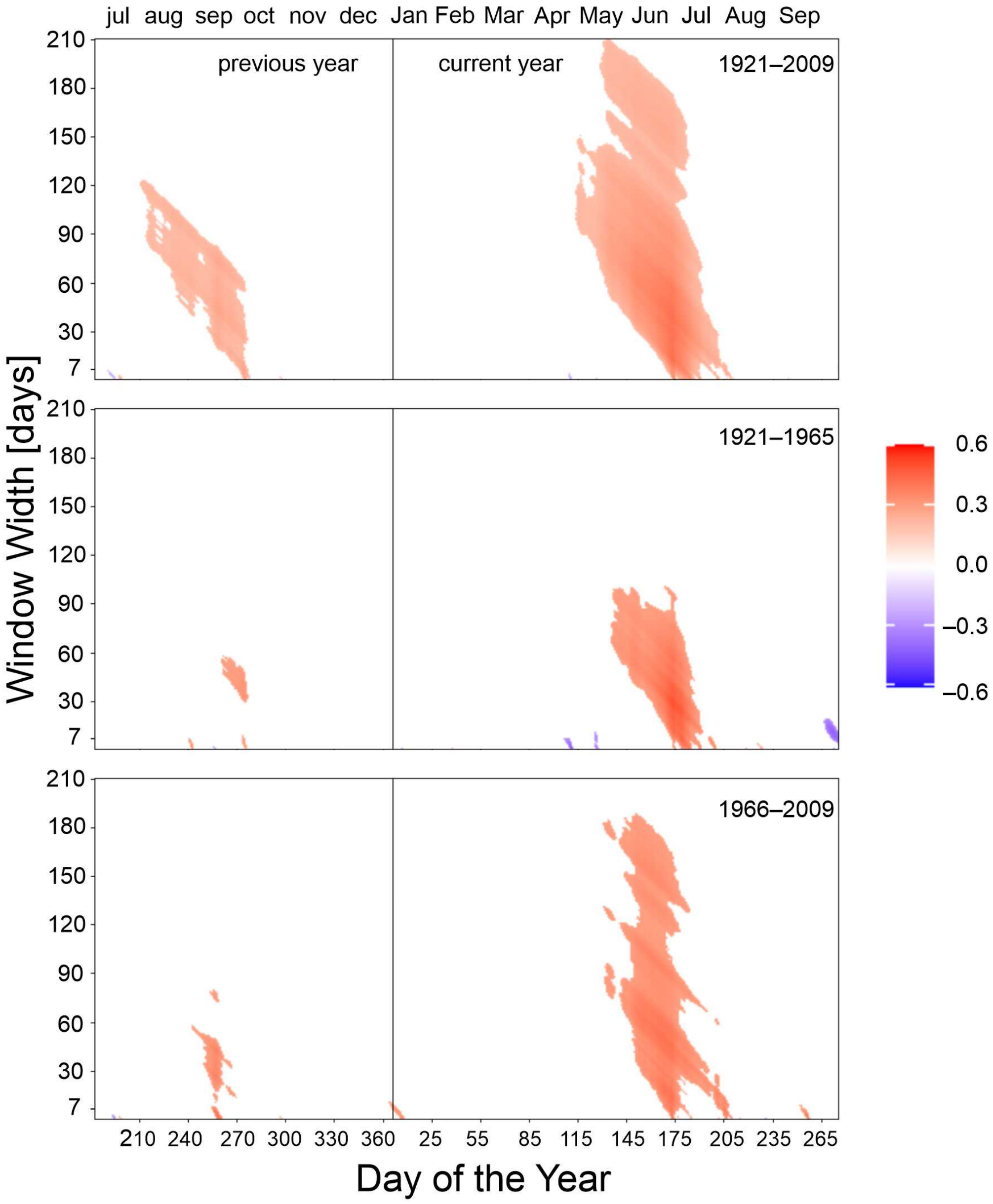


Figure 4. Correlations between the mean daily temperature and the TRWI chronology for the analysed periods. The colours show a significant ($p < 0.05$) correlation coefficient for consecutive window widths. The given values show the beginning of the specific time window.

In the first subperiod (1921–1965), the highest positive significant correlation coefficient (r = 0.51) between the TRWI chronology and the mean temperature was found for the 29-day window width between 21 June and 19 July (DOY 172–200) during the year of growth (Figure 4). The period with a high correlation (r > 0.40) was found for the window width range between 10 and 33 days and spanned the end of June to the end of July (DOY 172–211). Tree growth was positively influenced by the mean temperature of autumn the previous year (0.30 < r < 0.40), and an important period with relatively high correlation coefficients was found for the period spanning the end of September to mid-November (DOY 272–316; 35–43-day window width) (Figure 4).

In the second subperiod (1966–2009), the highest positive significant correlation coefficient (r = 0.44) between the TRWI chronology and the mean temperature was found for the 14-day window width between 20 June and 3 July (DOY 171–184) during the year of growth (Figure 4). The period with a high correlation (r > 0.40) was found for the window width range between 14 and 47 days and spanned mid-June to the beginning of August (DOY 168–218). Tree growth was positively influenced by the mean temperature of autumn the previous year (0.30 < r < 0.40), and an important period with relatively high correlation coefficients was found for the period spanning mid-September to the end of October (DOY 256–300; 23–43-day window width) (Figure 4).

3.2.2. Minimum Temperature

The highest positive significant correlation coefficient (r = 0.37) between the TRWI chronology and the minimum temperature was found for the 14-day window width between 21 June and 4 July (DOY 172–185) during the year of growth (Figure 5). However, an important period with a high correlation (r > 0.35) was found for the window width range between 14 and 38 days, spanning mid-June to the end of July (173–192). Additionally, tree growth was positively influenced by the minimum temperature at the end of summer and autumn the previous year (0.25 < r < 0.30). There were two important periods with relatively high correlation coefficients (r > 0.25), spanning the end of September to the end of October (DOY 267–302, 30–35-day window width) and mid-August to the first days of November (DOY 232–307; 64–70-day window width) (Figure 5).

In the first subperiod (1921–1965), the highest positive significant correlation coefficient (r = 0.49) between the TRWI chronology and the minimum temperature was found for the 13-day window width between 22 June and 4 July (DOY 173–185) during the year of growth (Figure 5). However, an important period with a high correlation (r > 0.45) was found for the window width range between 11 and 23 days, spanning the end of June to the end of July (DOY 171–202). There were two important periods with relatively high correlation coefficients (r > 0.33), spanning the end of September to mid-November (DOY 272–324, 7–50-day window width) and mid-August to mid-November (DOY 231–316; 73–83-day window width) (Figure 5).

No distinct impact of minimum temperature was observed in the second subperiod (1966–2009) during the year of growth and the previous year (Figure 5).

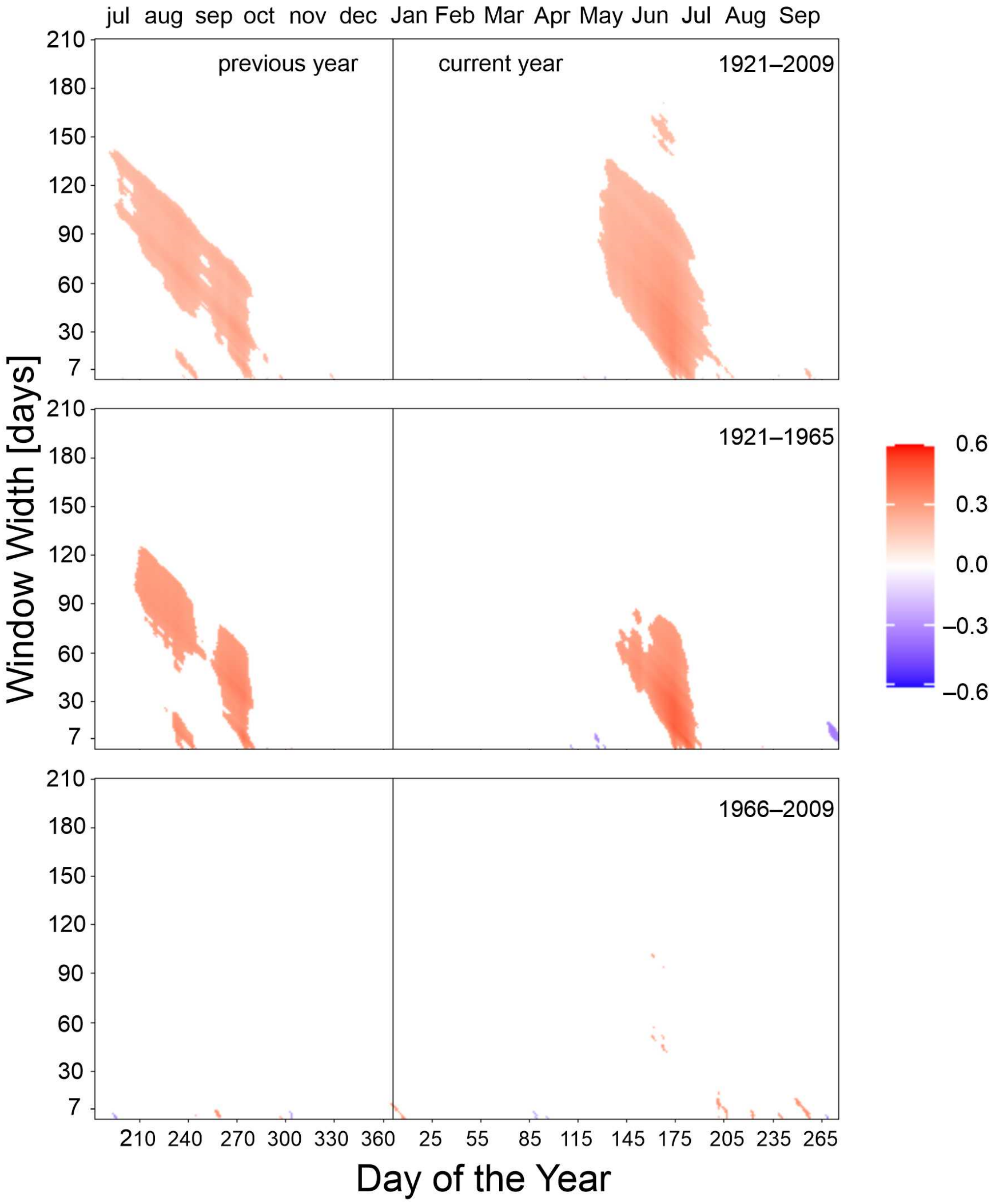


Figure 5. Correlations between the minimum daily temperature and the TRWI chronology for the analysed periods. The colours show a significant ($p < 0.05$) correlation coefficient for consecutive window widths. The given values show the beginning of the specific time window.

3.2.3. Maximum Temperature

The highest positive significant correlation coefficient (r = 0.48) between the TRWI chronology and the maximum temperature was found for the 38-day window width between 21 June and 28 July (DOY 172–209) during the year of growth (Figure 6). However, an important period with a high correlation (r > 0.44) was found for the window width range between 14 and 55 days, spanning mid-June to the beginning of September (DOY 160–250). Additionally, tree growth was positively influenced by the maximum temperature of autumn the previous year (0.20 < r < 0.26), and an important period with relatively high correlation coefficients was found for the period spanning mid-September and mid-November (DOY 256–315; 23–58-day window width) (Figure 6).

In the first subperiod (1921–1965), the highest positive significant correlation coefficient (r = 0.56) between the TRWI chronology and the maximum temperature was found for the 39-day window width between 21 June and 29 July (DOY 172–210) during the year of growth (Figure 6). However, an important period with a high correlation (r > 0.45) was found for the window width range between 15 and 45 days, spanning mid-June to the beginning of August (DOY 169–222). No significant impact of maximum temperature was observed in the first period of the previous year (Figure 6).

In the second subperiod (1966–2009), the highest positive significant correlation coefficient (r = 0.45) between the TRWI chronology and the maximum temperature was found for the 14-day window width between 20 June and 3 July (DOY 171–184) during the year of growth (Figure 6). However, an important period with a high correlation (r > 0.33) was found for the window width range between 11 and 55 days, spanning the end of June to mid-August (DOY 171–225). Additionally, tree growth was positively influenced by the maximum temperature of autumn the previous year (0.37 < r < 0.46), and an important period with relatively high correlation coefficients was found for the period spanning between mid-September and mid-October (DOY 255–292; 12–36-day window width) (Figure 6).

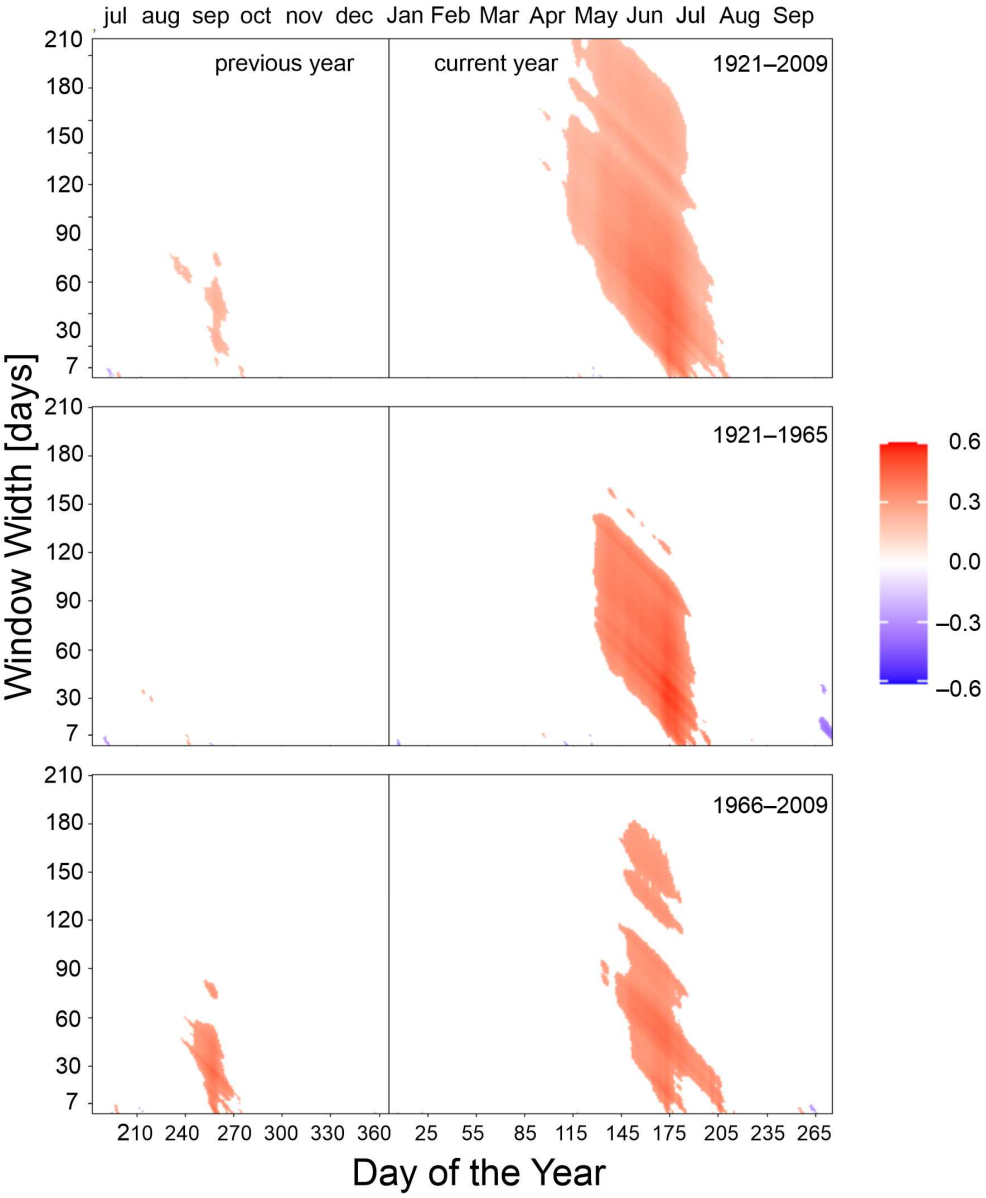


Figure 6. Correlations between the maximum daily temperature and the TRWI chronology for the analysed periods. The colours show a significant ($p < 0.05$) correlation coefficient for consecutive window widths. The given values show the beginning of the specific time window.

3.2.4. Precipitation

The strongest negative significant correlation coefficient (r = −0.35) between the TRWI chronology and the sum of precipitation was found for the 15-day window width between 19 June and 3 July (DOY 170–184) during the year of growth (Figure 7). An important period with a strong correlation coefficient (r < −0.33) was found for the window width range between 13 and 21 days, spanning mid-June to mid-July (DOY 169–192). No distinct impact of precipitation was observed in the previous year (Figure 7).

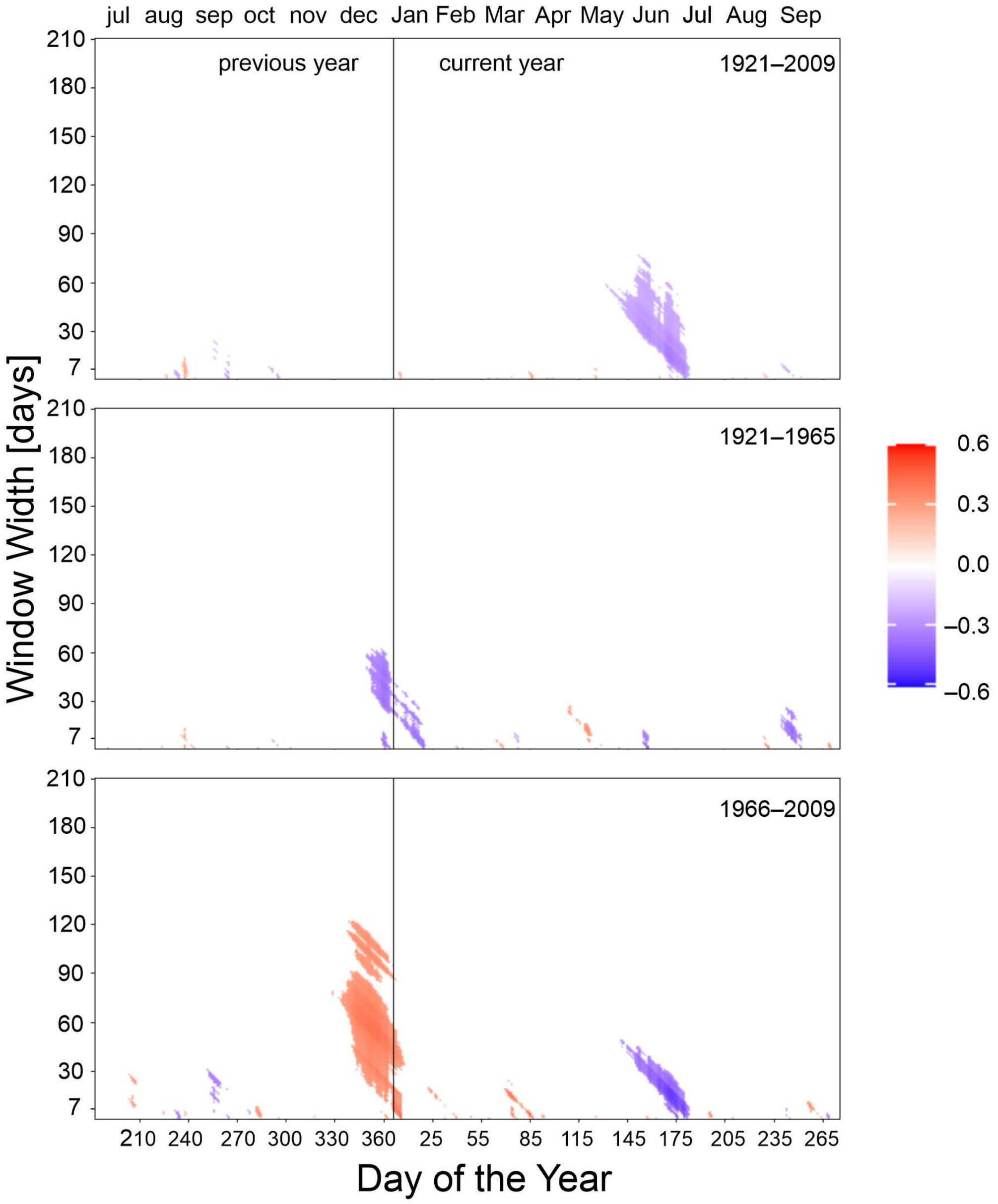


Figure 7. Correlations between daily precipitation and the TRWI chronology for the analysed periods. The colours show a significant ($p < 0.05$) correlation coefficient for consecutive window widths. The given values show the beginning of the specific time window.

In the first subperiod (1921–1965), the strongest negative significant correlation coefficient (r = −0.38) between the TRWI chronology and the sum of precipitation was found for the 39-day window width at the turn of the year from 25 December to 2 February (DOY 360–33) (Figure 7). An important period with a strong correlation coefficient (r < −0.30) was found for the window width range between 27 and 54 days, spanning the end of December to mid-February (DOY 358–49) (Figure 7).

In the second subperiod (1966–2009), the strongest negative significant correlation coefficient ($r = -0.53$) between the TRWI chronology and the sum of precipitation was found for the 15-day window width in the period between 19 June and 3 July (DOY 170–184) during the year of growth (Figure 7). An important period with strong correlation coefficients ($r < -0.40$) was found for the window width range between 11 and 20 days, spanning mid-June to mid-July (DOY 168–194). Additionally, the period with significant correlation coefficients ($r > 0.40$) was found for the window width range between 52 and 63 days, spanning mid-December to the end of February (DOY 348–54) (Figure 7).

4. Discussion

This is the first study that analyses the potential of applying daily climatic variables to enhance the precision and temporal resolution of the climate–growth correlation for stone pine in the Western Carpathians. Most previous dendroclimatic studies about the growth of *Pinus cembra* were based on monthly climatic data. Papers about the radial growth of stone pine discuss higher altitudes of the Alps and Carpathians [20,24–28,46,47]. Only a few authors used daily data for the dendroclimatic study and mostly with reference to wood anatomy. Day-wise aggregated climatic data were used by Ştirbu et al. [48] for the South-Western Carpathians and Carrer et al. [23] for the Eastern Alps to analyse xylem anatomical traits, maximum density (MXD), and the ring widths of stone pine.

From another perespective, summer temperature remains a key limiting factor of stone pine growth at higher elevations. Our analyses clearly show that the most important period for radial growth of stone pine is limited to two–three weeks in the second half of June and the first half of July, when the correlations between the ring widths and temperature are the strongest. By expanding the number of analysed days (the window width), significant reactions were found for the period between mid-June and the beginning of August (with a lower correlation coefficient). A similar pattern was found in the Alps and Carpathians, where the temperature from mid-June to the beginning of July was the most important factor for radial growth and explained by favourable conditions for the cell number and tangential cell-wall thickness. The radial cell-wall thickness was positively correlated with the temperature of a later period (from mid-July to the beginning of September) [23,48]. The lumen area was negatively correlated with the temperature from the end of June to the end of August [48]. The TRW analysed in this study was a parameter, which comprised all anatomical features; thus, the relationship between TRW and daily temperature data is not so strong. The changes in the growth–temperature relationship over time were more obvious when analysing the maximum and minimum daily temperatures. The minimum daily temperature, known as the night-time low, is probably the closest indicator limiting tree growth at high elevations [42]. The warmer day-time temperature cannot compensate for the cold nights, and what is more, the low minimum temperature in spring can delay the growing season [49]. The biggest difference between the subperiods of 1921–1965 and 1966–2009 was obvious for minimum temperatures. In the first period the minimum temperature of summer positively and significantly influenced the growth; while in the second subperiod, the minimum temperature lost its relevance. It is possible that the minimum temperature was greater than the threshold for affecting tree growth in the second subperiod.

The association between growth and the temperature of autumn the previous year is also well documented in the literature [25,46,50–52]. Our study allowed us to determine the period of importance more precisely. The most positive temperature occurred during the time between mid-September and mid-October of the previous year, but this interval expanded from the beginning of August to the beginning of November once the minimum temperature is taken into consideration. The crucial role of the autumn temperature results from the timing period was the bud set and the accumulation of reserves for building effective protection against winter frost, drought, or wind [18,53–55]. However, this pattern changed over time when considering shorter subperiods and the minimum and maximum temperatures. For example, this relationship disappeared for maximum temperatures in the years 1921–1965, which can be related to the cooler autumn during this period; however, it becomes clear in the second half of the 20th century when the maximum temperatures of autumn were higher. Our analysis did not reflect the temperature of the soil, which is crucial for the physiological activity of trees within their distribution limits (upper timberline), as soil retains heat for several days during unfavourable weather conditions, especially in autumn when trees enter dormancy [49,56].

Our research confirmed that summer precipitation had a negative influence on tree growth at high elevations [20,24,26]. In our study, this period of negative correlations almost completely overlaps with the days with the highest positive influence of the temperature and lasts between mid-June and the beginning of July. This relationship was not clear in the first half of the 20th century (1921–1965), which can be attributed to the lower precipitation during this time (Figure 2b). It is noteworthy that the radial growth of stone pine was influenced by winter precipitation from the preceding vegetation season during the shorter analysed periods. Additionally, the negative impact of winter precipitation on radial growth observed in the first subperiod (1921–1965) became positive in the second subperiod (1966–2009). The same trend was observed in the Alps [26,50]. This shift may be due to changes in precipitation patterns, possibly because of the amount and timing of precipitation having shifted. It is possible that warmer temperature during the dormant season with higher precipitation results in substantial snow depth, which can help prevent deep soil frost and mitigate the risk of damage caused by frost drought [17].

The general outcome of our study was that temperature became less important as a growth factor at high elevations in the Carpathians, which confirmed our hypothesis. The change in the temperature may potentially promote an upward shift of this species in the Tatra Mountains. Our study essentially validated the conclusions of Briffa et al. [57], Paulsen et al. [58], and Körner and Hoch [49]: The climate pattern fluctuates and reflects a threshold response. As the climate continues to warm, the treeline is also shifting upslope. One of the biggest challenges is to determine the rate and range at which local tree limits align with the warming climate [49]. As a result, trees that once grew within the treeline are now exposed to conditions that no longer resemble their boundary from the past. It means that stone pine in the Tatras has been growing in better climatic conditions over the last decades due to the shifting climatic treeline [59]. The warming climate opens space for the colonisation of higher elevations, and stone pine may benefit from these changes. As a zoochoric species dispersed by nutcracker (*Nucifraga caryocatactes*), stone pine can migrate upslope. This is especially important for the species due to their relatively small and fragmented, but stable, population with a significant degree of genetic variability in the Western Carpathians [22,60–62].

5. Conclusions

Our study showed that the temperature between mid-June and the beginning of July was a key factor for the growth Swiss stone pine in cliffs. The reaction of trees to climate was not stable over time. The changes in the growth–temperature relationship are the clearest with the minimum daily temperature. The negative influence of precipitation on growth almost completely overlaps in time with the highest positive influence of temperature (mid-June to beginning of July). Therefore, the potential migration of *Pinus cembra* to higher elevations is promoted by climate warming.

Dendroclimatic studies based on daily data define the periods (exact calendar days) that influence the radial growth of trees more precisely than monthly data. This is especially important in analysing the growth of trees at high elevations, where the vegetation season is short, and the climate factor strongly limits radial growth. Finally, the forest stands near the treeline are prone to climate change, and daily climatic data allow us to track these changes with a higher resolution.

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