



Chronic warming and dry soils limit carbon uptake and growth despite a longer growing season in beech and oak

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Abstract

Progressively warmer and drier climatic conditions impact tree phenology and carbon cycling with large consequences for forest carbon balance. However, it remains unclear how individual impacts of warming and drier soils differ from their combined effects and how species interactions modulate tree responses. Using mesocosms, we assessed the multiyear impact of continuous air warming and lower soil moisture alone or in combination on phenology, leaf-level photosynthesis, nonstructural carbohydrate concentrations, and aboveground growth of young European beech (*Fagus sylvatica* L.) and Downy oak (*Quercus pubescens* Willd.) trees. We further tested how species interactions (in monocultures and in mixtures) modulated these effects. Warming prolonged the growing season of both species but reduced growth in oak. In contrast, lower moisture did not impact phenology but reduced carbon assimilation and growth in both species. Combined impacts of warming and drier soils did not differ from their single effects. Under warmer and drier conditions, performances of both species were enhanced in mixtures compared to monocultures. Our work revealed that higher temperature and lower soil moisture have contrasting impacts on phenology vs. leaf-level assimilation and growth, with the former being driven by temperature and the latter by moisture. Furthermore, we showed a compensation in the negative impacts of chronic heat and drought by tree species interactions.

Introduction

With air temperature rising chronically, forests will be more frequently exposed to a combination of hotter and drier conditions in the future (Breshears et al. 2005), inducing the climatic range shifting closer to the current distribution limit of species (i.e. rear edge). The co-occurrence of chronic warming and lower soil moisture could have contrasting impacts on climate-vegetation predictions because temperature and soil

moisture can have different effects on forest carbon cycling in terms of phenology, photosynthesis, and growth (Fu et al. 2020; Didion-Gency et al. 2022; Petrik et al. 2022; Vitasse et al. 2022). Hence, there is an urgent need to disentangle single effects from combined impacts of chronically elevated temperatures and lower soil moisture on tree carbon relations.

Most studies demonstrate that higher spring temperatures induce earlier leaf-out of trees, potentially leading to a longer

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growing season (Polgar and Primack 2011). However, the underlying leaf-level cues driving these effects and interspecific differences are not fully understood (Schaber and Badeck 2003). For example, the winter bud dormancy of European beech (*Fagus sylvatica* L.) is photoperiod sensitive and requires a high amount of winter chilling to be released (Way and Montgomery 2015). Contrastingly, some species, like sessile oak (*Quercus petraea* (Matt.) Liebl) and oriental oak (*Quercus variabilis* Blume), are mainly sensitive to variations in spring temperature, showing large advancement of leaf emergence with increasing temperature (Dantec et al. 2014; Han et al. 2014). One of the simplest models to predict budburst timing is to compute the amount of heat necessary to trigger this phenological stage, classically expressed as growing degree day (GDD) above a certain temperature threshold (generally set at 5 °C). However, previous work suggests that the amount of GDD reached at budburst varies depending on previous exposure to chilling temperatures responsible for dormancy release in winter, i.e. exposure to temperatures ranging between ca. –2 and 10 °C (Baumgarten et al. 2021). Thus, the GDD requirement gradually decreases with longer exposition to chilling conditions, reaching a minimum when chilling has been sufficient to fully release dormancy (Murray et al. 1989; Baumgarten et al. 2021). The interaction between chilling and heat requirement could explain the decline in phenological sensitivity to temperature increase recently found in European trees (Zhang et al. 2021), although this effect varies among species and may also be related to the nonlinear effect of temperature (Wolkovich et al. 2021). In contrast to spring phenology, the drivers of senescence timing are less understood. Contrasting patterns have been observed, including a warming-induced delay, advancement, or no effect on the date but an overall slower senescence process (Polgar and Primack 2011). Additionally, temperature impacts on phenology are dependent on soil moisture. For example, low soil moisture can delay leaf emergence and cause premature senescence, thereby shortening the growing season (Bigler and Vitasse 2021; Dallstream and Piper 2021). A delay in leaf flushing has been observed for beech trees under limited soil moisture and can be associated with a reduction of late frost risk and higher drought resistance by postponing the onset of transpiration (Spieß et al. 2012). A recent study suggests that the initiation of leaf senescence could largely be regulated by growth and development during early summer whereas leaf coloration and senescence progress is mediated by late summer/early autumn temperature (Zohner et al. 2023). Thus, the role of spring, autumn, and winter temperatures and their interactive effects with soil water availability remains unclear and need to be explored further to better predict phenological trends.

Phenological shifts induced by warmer and drier soils affect the timing of leaf-level photosynthetic activity, tree growth, and carbon stocks in several ways (Polgar and Primack 2011; Klein et al. 2016). An earlier leaf-out and extended growing season do not always result in an increase in carbon

uptake and higher nonstructural carbohydrate (NSC) concentrations at the yearly scale because of an earlier start of assimilation (Etzold et al. 2022; Grossiord et al. 2022), and it does not necessarily result in higher growth rates (Dow et al. 2022). Higher temperatures can harm trees when the optimal temperature for photosynthetic activity (T_{opt}) is exceeded, resulting in reduced assimilation (Dai et al. 2021). Therefore, variations in these responses depend on species-specific sensitivity to temperature. Beech typically grows in a mild climate and has a T_{opt} around 24.5 °C (Holišová et al. 2013) whereas downy oak (*Quercus pubescens* Willd.) usually grows in Mediterranean areas with a T_{opt} of about 26 °C (Il'nitsky et al. 2021). Consequently, hotter and drier conditions can lead to severe changes in assimilation during the growing season (Etzold et al. 2022), which may be reflected in carbon stocks, including a reduction in NSC pools (Hartmann and Trumbore 2016) and growth (Morin et al. 2009). Moreover, warmer temperature co-occurs with a rise in vapor pressure deficit (VPD) and reduced soil water availability, which further restrict stomatal conductance (Zhou et al. 2014), resulting in lower growth, assimilation (Grossiord et al. 2020; Trotsiuk et al. 2021), and potential depletion of NSC pools (Klein 2015).

Yet, while the single impacts of lower soil moisture and warming have been studied in various ecosystems, the combined effects of chronically higher temperature and drier soils on tree phenology and carbon relations remain uncertain. Work conducted in drylands reported a delayed and prolonged bud development under combined hot and dry conditions associated with a more rapid depletion of NSC (Adams et al. 2015). However, others have suggested an earlier spring phenology during hot droughts because of a more decisive temperature impact on phenology than soil moisture (Arzac et al. 2021). Although it remains untested, the contrast between these studies could be associated with species-specific tolerance to low soil water availability, the intensity of warming and soil moisture reduction, and the duration of these extreme conditions. Similarly, distinct responses have been observed from the impact of hot and dry conditions on leaf-level carbon relations. While most studies tend to agree that drier conditions have a more adverse impact on assimilation, NSC, and growth (Lukasová et al. 2020), some studies have reported an exacerbation of responses under additive conditions (Arend et al. 2016). Thus, a better understanding of the combined impacts of chronic temperature rise and dry soils requires studies where single and additive warming and low moisture impacts on different species with contrasting strategies are compared over multiple years.

Although better predictions of the fine-scale mechanisms that drive tree responses to continuous warmer and drier conditions is fundamental, these responses cannot be fully understood without considering the dynamics of the forest as an entire system, particularly when considering species diversity (Forrester 2014). Numerous studies have shown that forests with more than one tree species (i.e. mixtures) are

more resistant to extreme conditions than single-species forests (i.e. monocultures) (Vacek et al. 2021). Although these observations are species- and context-specific, they suggest that adverse impacts from chronic heat and low moisture can be mitigated in diverse forests. Two underlying mechanisms explaining biodiversity effects are usually applied. The “complementarity effect” is associated with species’ niche differences and/or facilitation. Complementarity occurs when trees with distinct crown architectures and light requirements—like beech and downy oak—interact, leading to a more efficient aboveground space occupation and increased biomass (Jucker et al. 2015). The “selection effect” reflects the dominance of more competitive species in mixtures (Loreau and Hector 2001; Grossiord et al. 2013), resulting in a lower reduction of productivity in mixtures compared to monocultures during drought (Dziedek et al. 2016). An approach to estimate the relative contribution of these two processes is to separate the net biodiversity effects into complementarity and selection effects (Loreau and Hector 2001). However, no studies to date have investigated if and how tree species interactions affect phenological, leaf-level carbon cycle, and tree growth responses to warming and low soil moisture acting individually or in combination.

Here, we aim to understand how carbon relations, including phenology, leaf-level gas exchange, and growth traits, of two co-occurring widely distributed and contrasting tree species, European beech and downy oak are impacted by chronic air warming and a moderate but continuous reduction of soil moisture acting alone or in combination over multiple years and how tree species interactions can alter these responses. We exposed 3-yr-old beech and downy oak trees in monocultures and mixtures to a continuous +5 °C air warming and a reduction of soil moisture by 50% acting individually or in combination using open-top chambers for 3 yr. European beech and downy oak trees were selected because they can be found growing together in natural ecosystems and they have different phenological cycles (Baumgarten et al. 2021) and different strategies to deal with low soil moisture and high temperature, with downy oak being more tolerant to moisture limitation and heat (Barigah et al. 2013).

Our objectives were to: (1) evaluate how beech and downy oak phenology (including bud swelling, duration of bud development, onset and duration of senescence, and growing season length) responds to chronic warming and moderate reduction of soil moisture acting individually or in combination, (2) assess how these climatic conditions influence leaf-level carbon relations (i.e. starch and sugar concentrations, light-saturated assimilation, A_{sat}) and growth (height, diameter, and aboveground woody biomass (AGWB) increment), and (3) determine if and through which mechanisms species interactions (i.e. monocultures vs. mixtures) influence chronic warming and reduction of soil moisture impacts on phenology, leaf-level carbon relations, and growth. Because of the strong photoperiodic control of spring phenology in beech compared to downy oak (Basler and Körner 2012), we hypothesize: (1) beech trees to show a weaker

phenological shift in response to warming compared to downy oak trees, manifested through earlier leaf-out and slower senescence process inducing a longer growing season. We expect reduction of soil moisture to delay leaf development and advance leaf senescence, especially for the more moisture-sensitive beech trees. Combined climatic treatments should differ between these two species as temperature changes more strongly drive downy oak phenology. Hence, weaker advances in leaf-out and senescence are expected for beech whereas a faster leaf emergence and slower senescence process may be observed in oak. Moreover, because of beech’s sensitivity to high temperature and low soil moisture, we hypothesize: (2) beech to have impaired assimilation and lower starch and sugar concentrations and aboveground growth under chronic warming and reduced soil moisture. On the other hand, while drier soils should reduce these traits in downy oak, chronic warming may enhance them because of its higher tolerance to temperature reflected in its distribution range. Combined treatments should exacerbate tree responses observed under drier soils because of enhanced water stress. Finally, we hypothesize: (3) both species to benefit from being grown in mixtures compared to monocultures under all climatic conditions because of complementarity in their crown architectures and light requirements.

Results

Phenology

We found substantial impacts of chronic warming but not soil moisture on the phenology of both species (Fig. 1, Supplemental Fig. S1). Higher daily air temperatures in spring were linked to an earlier bud swelling in both species, where beech was advanced by $-1.1 \text{ d } ^\circ\text{C}^{-1}$ and oak by $-2.3 \text{ d } ^\circ\text{C}^{-1}$ across the 2 yr and treatments. A shorter leaf development duration was also found, with a reduction of $-0.7 \text{ d } ^\circ\text{C}^{-1}$ in both species. Similarly, senescence duration was extended by $+3.4 \text{ d } ^\circ\text{C}^{-1}$ in beech and $+3.1 \text{ d } ^\circ\text{C}^{-1}$ in oak. The growing seasons were extended by $+4.5 \text{ d } ^\circ\text{C}^{-1}$ and $+5.7 \text{ d } ^\circ\text{C}^{-1}$ for beech and oak, respectively, with an increase in daily mean annual air temperature (Fig. 1). However chronic warming was more advantageous to oak than to beech as the advancement of bud swelling extension was higher in oak ($P = 0.004$ using Least-squares analysis). No relationship between the onset of senescence and fall daily air temperatures was found, suggesting that the onset of senescence is not driven by temperature changes in the fall for both species. We observed no significant relationship between phenology and soil moisture for both species (Supplemental Fig. S1), indicating that temperature has a more direct impact on tree phenology than soil moisture.

With an increase in the number of chilling days, both species had lower GDD requirements to budburst (Fig. 2), suggesting that trees exposed to chronic warmer winters in the warm and low soil moisture conditions were likely limited in chilling to fully break dormancy (i.e. to have the minimum of forcing requirement to budburst).

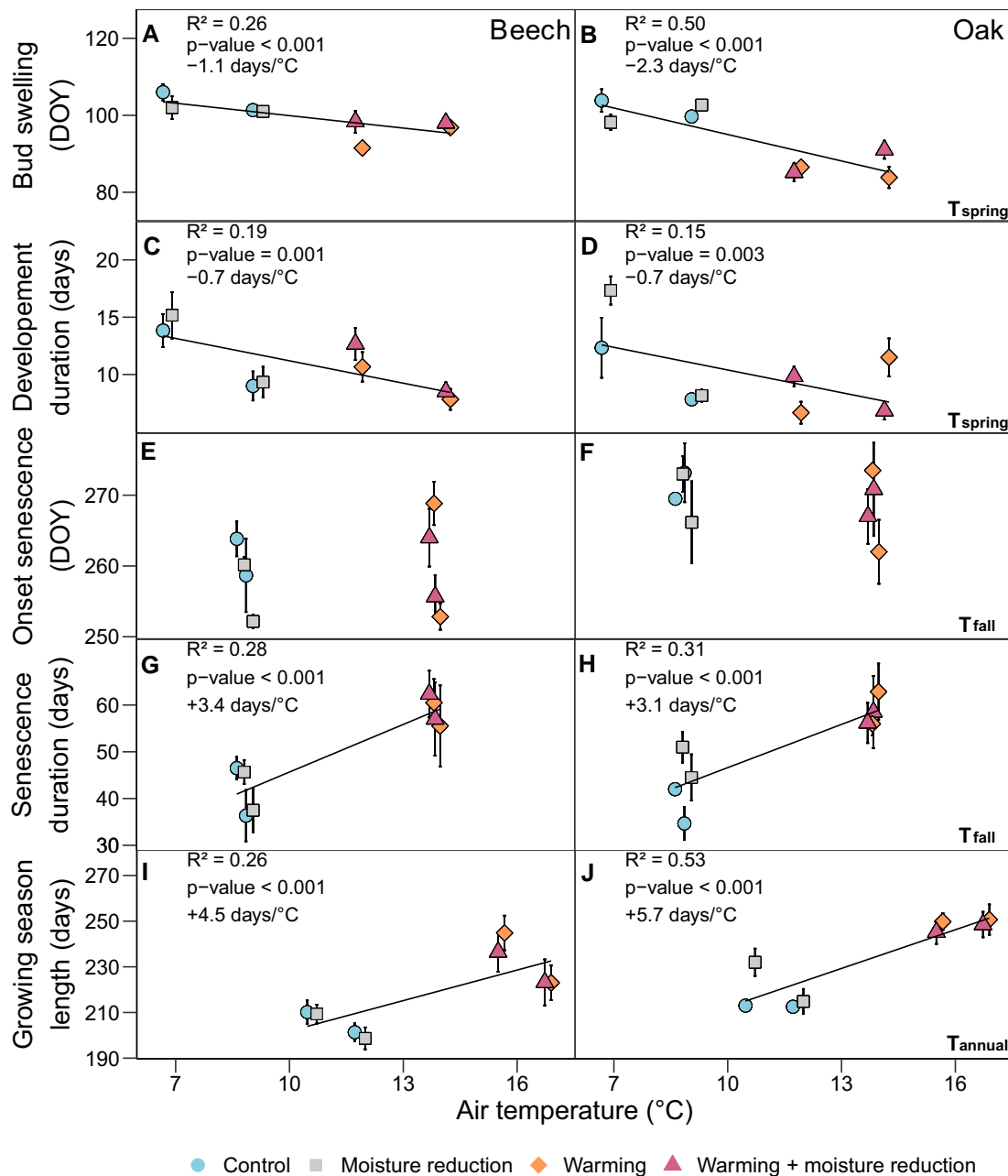


Figure 1. Bud swelling (A, B), leaf development duration (C, D), onset of senescence (E, F), leaf senescence duration (G, H), and growing season length (I, J) as a function of air temperature for beech and oak trees growing under control (blue), moisture reduction (grey), warming (orange), and warming + moisture reduction (purple) in monocultures in 2020 and 2021 (mean \pm SE per treatment, species and years, $n = 6$ trees). The bud swelling and leaf development duration are shown as a function of the daily mean air temperature in spring (from February to April, T_{spring}). Onset of senescence and leaf senescence duration are shown as a function of the daily mean air temperature in fall (from September to December, T_{fall}). Growing season length is shown as a function of the daily mean annual air temperature (T_{annual}). Linear regression lines across all treatments per species are shown when significant. R^2 , P -values and the change of day number for each degree are given in the top left corner when significant ($P \leq 0.05$). Additionally, DOY corresponds to the day of the year.

Leaf water potential

We found little effect of warming and soil moisture acting alone on predawn and midday leaf water potentials (Ψ_{PD} and Ψ_{MD} , respectively, Fig. 3). Warming resulted in more negative Ψ_{PD} in 2020 in both species and more negative Ψ_{MD} in

2020 but only in beech (Fig. 3). Moreover, lower soil moisture reduced Ψ_{PD} in 2020 but only in oak (Fig. 3), suggesting that the reduction in soil moisture was moderate. However, combined warming and drier soils resulted in more negative Ψ_{PD} in 2021 in both species (Fig. 3, Supplemental Table S1).

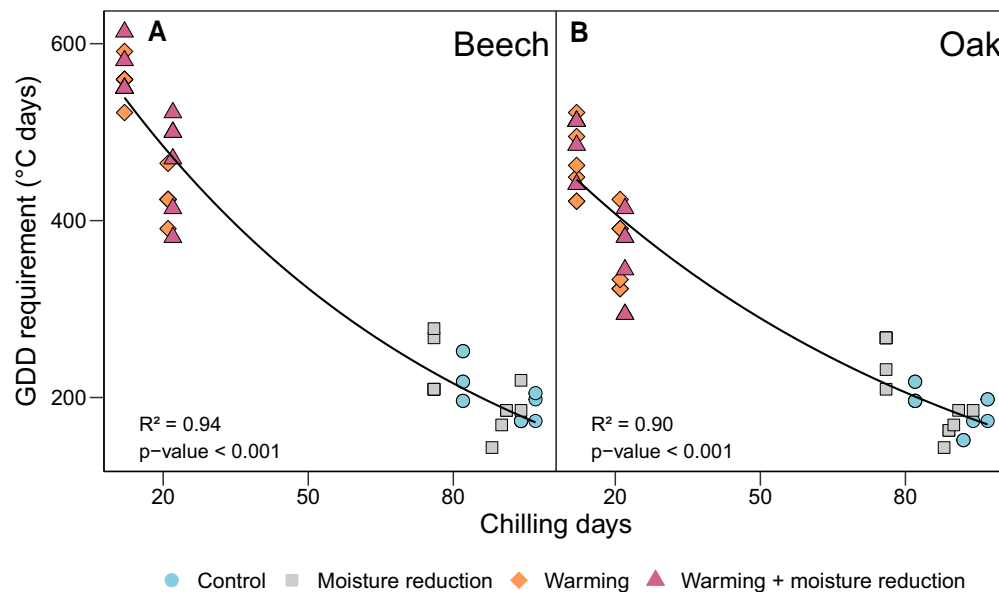


Figure 2. GDD requirement (i.e. accumulated the daily mean temperature above a threshold of 5 °C from January 1 to the date of bud swelling; **A, B**) as a function of the number of chilling days (i.e. days with average temperature below 5 °C from November 1 to the date of leaf flushing) for beech and oak trees growing under control (blue), moisture reduction (grey), warming (orange), and warming + moisture reduction (purple) in monocultures in 2020 and 2021 (each point represents one tree). Negative exponential regression lines across all treatments per species are shown when significant. R^2 and P -values are given in the bottom left corner when significant ($P \leq 0.05$).

Leaf-level carbon relations and tree growth

While lower soil moisture reduced leaf-level assimilation and growth, we found only a few impacts of chronic warming (Fig. 4). In beech, warming had no impact on leaf-level carbon relations and growth (Fig. 4, Supplemental Table S1). In oak, warming reduced height increment, diameter increment, and AGWB increment but only in 2021 (Fig. 4, Supplemental Table S1). In beech, lower soil moisture led to a significant reduction of A_{sat} in 2021, height increment in 2021, diameter increment in 2020 and 2021, and AGWB increment in 2021. Similarly, we observed a substantial reduction in A_{sat} , height increment, diameter increment, and AGWB increments in oak in 2020 and 2021 (Fig. 4, Supplemental Table S1). Under combined warming and low moisture, we observed a reduction of A_{sat} and diameter increment in 2020 and 2021 in beech. In oak, a reduction of A_{sat} , height increment, diameter increment, and AGWB increment in 2020 and 2021 was observed (Fig. 4, Supplemental Table S1). No significant differences were found between responses to lower moisture alone and combined warming and soil moisture reduction (Fig. 4, Supplemental Table S1).

Impact of species interactions

In both species, no impact of species interactions on phenology was found in any treatment, except in oak where we observed a slightly shorter development duration of 2 d in mixtures compared to the monocultures under lower moisture (Supplemental Table S2), but the net biodiversity effect was not significant. Similarly, we observed limited species

interaction effects in control or when warming and lower soil moisture acted alone in 2020 and 2021. However, a positive effect of species mixture under combined warming and drier soils was found (Fig. 5).

In beech, no impact of species interactions on leaf-level carbon relations or growth was found under the warming treatment in 2020 and 2021 (Supplemental Table S3). Consequently, beech did not show any impact of net biodiversity in response to warming in terms of leaf-level carbon relations or growth in 2021 (Fig. 5). However, we observed a positive selection effect on beech A_{sat} under warming (Supplemental Fig. S2), suggesting positive interactions in the mixtures; although, this effect was not strong enough to influence the overall net biodiversity effect. For oak, no differences between mixtures and monocultures were found under warming, except for lower diameter increment of approximately 0.3 cm per year in mixtures compared to monocultures (Supplemental Table S3). Moreover, oak trees showed a negative net biodiversity effect for the AGWB increment in response to warming in 2020 (Fig. 5), explained by a negative complementarity effect (Supplemental Fig. S3).

Under lower soil moisture, we found a reduced diameter increment in mixtures compared to the monocultures in beech (Supplemental Table S3). Similarly, a negative net biodiversity effect on sugar concentration in response to low soil moisture was found in beech (Fig. 5), driven by a negative complementarity effect (Supplemental Fig. S3). In contrast, we observed no impact of species interactions and net biodiversity effect in oak (Supplemental Table S3, Fig. 5).

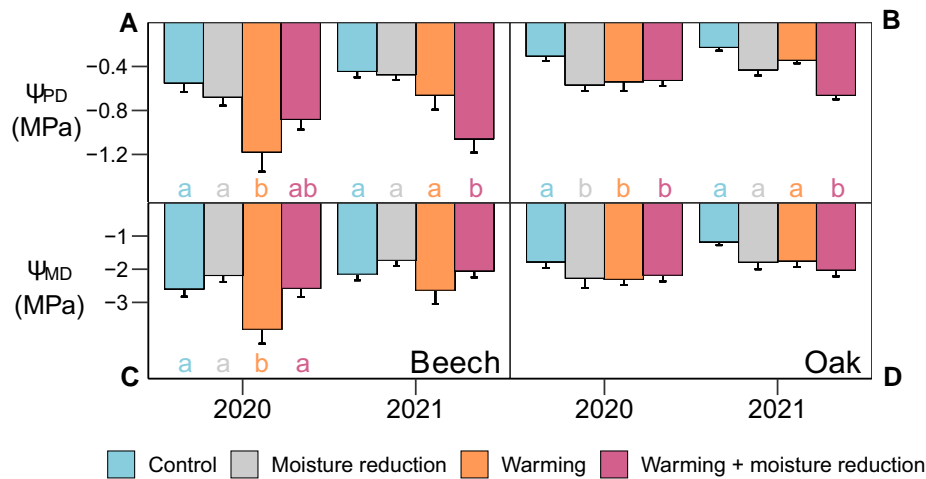


Figure 3. Predawn (Ψ_{PD} ; **A, B**) and midday leaf water potential (Ψ_{MD} ; **C, D**) for beech and oak trees growing under control (blue), moisture reduction (grey), warming (orange), and warming + moisture reduction (purple) in monocultures in 2020 and 2021 (yearly mean \pm SE per treatment and species, $n = 6$ trees per histogram). Significant differences between climatic treatments are highlighted for each year and species with letters (Tukey's HSD post-hoc test, $\alpha = 0.05$).

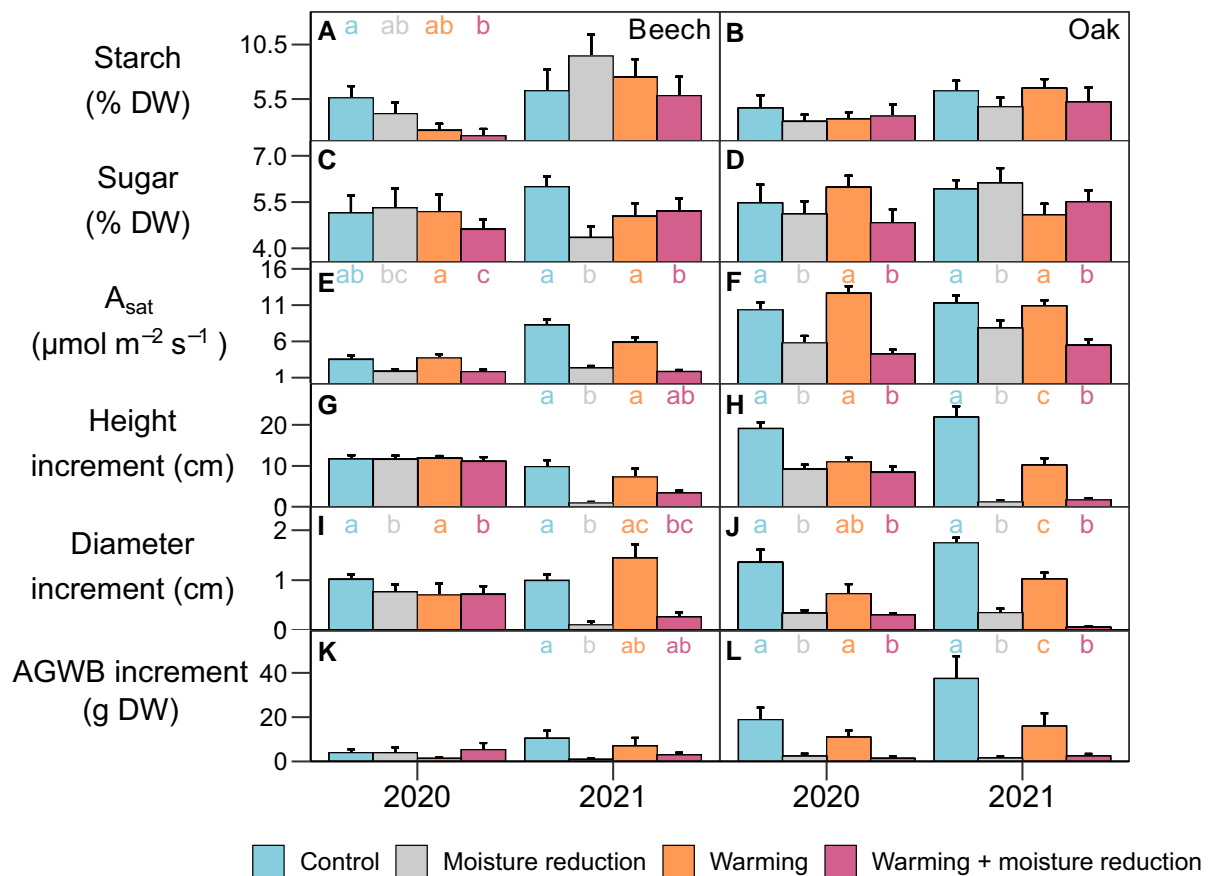


Figure 4. Starch (**A, B**), sugar (**C, D**), light-saturated assimilation (A_{sat} ; **E, F**), height increment (**G, H**), diameter increment (**I, J**), and estimated AGWB increment (**K, L**) for beech and oak trees growing under control (blue), moisture reduction (grey), warming (orange), and warming + moisture reduction (purple) in monocultures in 2020 and 2021 (yearly mean \pm SE per treatment and species, $n = 6$ trees \times 3 campaigns = 18 trees for the physiological traits, and $n = 6$ trees for the growth traits once a year). Significant differences between climatic treatments are highlighted for each species with letters (Tukey's HSD post-hoc test, $\alpha = 0.05$). Additionally, DW corresponds to the dry weight.

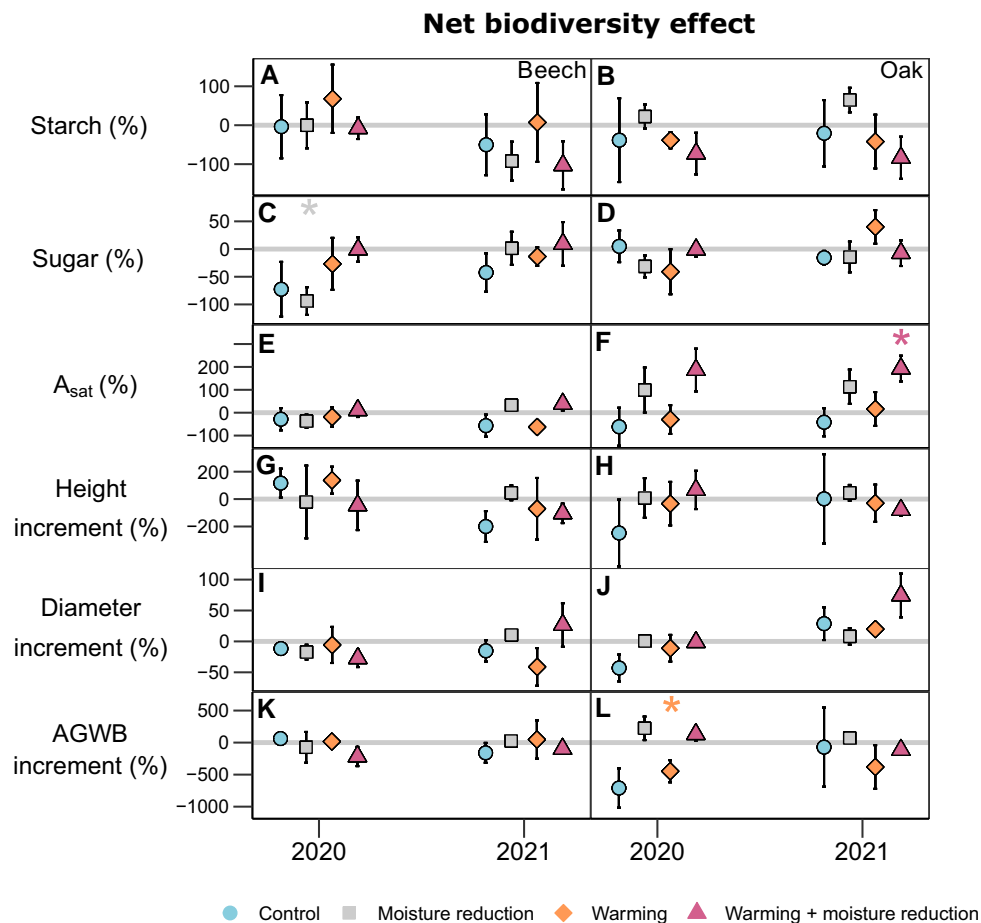


Figure 5. Starch (A, B), sugar (C, D), light-saturated assimilation (A_{sat} ; E, F), height increment (G, H), diameter increment (I, J), and estimated AGWB increment (K, L) net biodiversity effect for beech and oak trees growing under control (blue), moisture reduction (grey), warming (orange), and warming + moisture reduction (purple) in 2020 and 2021 (yearly mean \pm SE per treatment and species, $n = 6$ trees \times 3 campaigns = 18 trees for the physiological traits, and $n = 6$ trees for the growth traits once a year). Positive values indicate higher rates in mixtures compared to the monocultures. Significant differences from 0 are highlighted per treatment, year and species (Tukey's HSD post-hoc test, P -value: $0.05 \geq * > 0.01$, $0.01 \geq ** > 0.001$, $*** \geq 0.001$).

Under combined warming and lower moisture, a larger height increment by approximately 2 cm per year was found in monocultures compared to the mixtures in beech (Supplemental Table S3). In oak, diameter increment was larger by 1.4 cm in mixtures compared to the monocultures (Supplemental Table S3). We also observed a positive net biodiversity effect for A_{sat} in 2021 in oak (Fig. 5). This effect was explained by complementarity effects, indicating a resource complementarity under warmer air and drier soils (Supplemental Fig. S3).

Discussion

Contrary to our expectations, chronic warming had similar effects on spring phenology advancement in both species. Bud swelling was advanced by approximately -1.1 and -2.3 $\text{d } ^\circ\text{C}^{-1}$ in beech and downy oak, respectively (Fig. 1), confirming previous work in beech (Dantec et al. 2014). These findings in downy oak suggest a similar response to

continuous warming as other previously studied oak species (e.g. sessile oak—Charlet de Sauvage et al. 2022; and oriental oak—Han et al. 2014). Budburst onset in beech was less sensitive to temperature than in downy oak, which was likely due to the stronger photoperiod and chilling temperature dependency compared to oak species (e.g. common oak (*Quercus robur* L.) and sessile oak—Lebourgeois et al. 2010; Fu et al. 2013). Moreover, we found that a lower amount of winter chilling increases the demand for bud flushing for cumulative forcing temperatures in spring (Fig. 2) (Murray et al. 1989). However, while most studies showed an exponential relationship between GDD and chilling days, suggesting that trees exposed to a lower number of chilling days require higher temperatures in spring to flush, our results indicate that the climatic conditions of the open-top chambers might be in the more linear section of the negative exponential relationship between these two parameters. This suggests that the winter temperature did not fulfill the required chilling for both species. A study showed that beech and sessile

oak need more than 160 and 90 d (Vitasse and Basler 2013), respectively, with a temperature below 5 °C to reach the chilling requirement. In our experiment, trees were exposed to a maximum of 97 d even in the absence of warming (Fig. 2), which could partially explain the more extensive heat-induced budburst advancement in downy oak compared to beech, as another oak species, i.e. sessile oak, has already shown lower chilling requirements than beech. Nevertheless, while the trees may not have been ultimately released from winter dormancy, higher spring temperatures in the warmed treatments compensated for the warming-induced reduction in chilling and still induced an earlier bud break in both species, as found previously (Zhang et al. 2021). However, these findings should be interpreted with caution because photoperiod is another parameter that affects the relationship between chilling and GDD requirements (Fu et al. 2019). While further experiments with distinct gradual chilling and forcing temperatures are needed to better disentangle the environmental cues driving budburst, our results suggest that warmer springs alone significantly promote the start of the growing season in tree species with contrasting temperature and moisture tolerances. Hence, we expect the trend in spring advancement observed over past decades (Vitasse et al. 2018) to continue with the ongoing shift toward warmer conditions, irrespective of higher winter temperatures, but likely at a slower rate due to chilling and photoperiodic limitations (Fu et al. 2015) or due to nonlinear effects of temperature increase on development (Wolkovich et al. 2021).

Moreover, while our treatments did not change the onset of senescence, we found that the process of senescence and the growing season was extended for both species with warming (Fig. 1). Previous work has reported similar results (Jiang et al. 2022). Leaf senescence is driven by the interaction of multiple environmental factors, including light conditions (Vitasse et al. 2021), cold and warm temperatures (Schuster et al. 2014), and soil moisture (Holland et al. 2016), with some species being more sensitive to specific parameters than others. Our results indicate that senescence of beech and oak trees show minor sensitivity to chronic temperature changes and may, therefore, be more dependent on photoperiod. Nevertheless, according to a recent study by Zohner et al. (2023), presummer solstice warming accelerates senescence whereas post-solstice warming delays it. Thus, our year-long warming treatment could have compensated these opposing effects. Consequently, it is essential to note that our experiment did not allow us to distinguish the single effects of spring, fall, and winter temperatures because warming was applied throughout the experimental period to reflect changes in the climatic range toward warmer and drier conditions. Further studies applying warming only in spring, fall, and/or winter would allow us to better understand the exact cues driving senescence and/or the impact of single heat waves to incorporate phenological shifts in models that do not consider climate-induced phenological changes.

Contrary to temperature, we found no effect of lower soil moisture on the phenology of both species (Supplemental Fig. S1). We anticipated a shorter growing season under drier soils, as previously described in several studies (Adams et al. 2015), which also included oak species (Spiess et al. 2012; Dallstream and Piper 2021). This suggests that the effects of water availability on phenology vary depending on the moisture level. Using an experimental approach, one study showed that a 60% soil water reduction in acidic and calcareous soils induced leaf flushing 2 d earlier in different oak provenances (i.e. sessile, common, and downy oak; Kuster et al. 2014). Contrastingly, others found that 30% precipitation reduction delayed budburst in holm oak in a dry, Mediterranean forest (*Quercus ilex* L.; Limousin et al. 2012). As the predawn (Ψ_{PD}) and midday leaf water potential (Ψ_{MD}) of our trees were slightly affected by our low moisture treatment (Fig. 3), we considered the water availability level as moderate. Indeed, trees reached Ψ_{PD} of about -1.9 and -1.2 MPa in beech and downy oak, respectively. In comparison, in a temperate forest in Switzerland, researchers found Ψ_{PD} values between -2 and -3.3 MPa in adult beech trees during the drought in 2018, which led to premature leaf senescence in late July (Schuldt et al. 2020). Hence, our work suggests that exposure to moderate soil moisture conditions has limited impacts compared to extreme dryness and that moisture impacts on phenology do not follow any relationship. Moreover, similar responses were found under warmer and drier conditions (Fig. 1), supporting our finding that a chronic +5 °C warming has a more decisive impact on phenology than moderate reduction in soil moisture.

Warming under well-watered conditions had no effects on the leaf-level carbon relations and growth of beech (Fig. 4). This finding contradicts our expectations and previous studies suggesting high heat vulnerability in beech (Gessler et al. 2006). Trees experienced a mean annual temperature (MAT) of maximum of 17 °C (in 2020) in the warmed treatments, which is substantially above their optimum temperature range. However, beech can occur in environments where MAT reaches a maximum of 18 °C (Durrant et al. 2016). Hence, our constant treatments may not have been strong enough to induce substantially shift to this rear edge of this species. However, contrary to our expectations, downy oak, which occurs in environments of 19 °C MAT (Pasta et al. 2016), showed no effect of warming on A_{sat} and NSC but a substantial decrease in growth (Fig. 4). While this result contradicts previous studies where oak increased A_{sat} with a +0.8 °C and +1.5 °C warming (Arend et al. 2016), it supports recent studies finding reduced growth with higher temperature and VPD (Adams et al. 2015; Trotsiuk et al. 2021). However, growth reduction was not associated with lower carbon fluxes and storage (i.e. starch and sugar concentration and A_{sat}). While no respiration measurements were conducted in our study, we expect this trend to be partially driven by warming-enhanced leaf cellular respiration as observed in previous studies (Piao et al. 2008). Moreover, temperature could increase soil respiration and thereby

reduce the overall available carbon pools. Further research on whole-tree carbon losses through respiration, including the offsets in carbon gained during photosynthesis, would be necessary to assess chronic warming impacts on the carbon balance in this experiment.

Chronically drier soils strongly reduced the leaf-level carbon relations and growth of both species, except for NSC where we found no changes (Fig. 4). However, while both species were negatively impacted by low soil moisture, beech A_{sat} was more strongly impaired (Fig. 4), which corresponds with its rather isohydric stomatal behavior relative to others oak species (i.e. sessile oak, white oak (*Quercus alba* L.) and red oak (*Q. rubra* L.); Pretzsch et al. 2013). These findings support many studies showing that reduced soil moisture negatively affects A_{sat} and growth (Scharnweber et al. 2011) and indicate that although the reduction in soil moisture was moderate, it was sufficient to affect leaf carbon relations and growth of both species negatively. Homeostatic NSC concentrations under drier soils have also frequently been observed (Schönbeck et al. 2018) and may suggest that newly assimilated carbon was preferentially invested in storage and maintenance instead of growth. However, further measurements using carbon isotopes are required to validate this assumption.

As observed in phenological responses, no differences were observed for all physiological and growth traits under combined treatments and single stressors (Fig. 4). However, contrary to phenology which was driven mainly by temperature, leaf-level carbon relations and growth responded similarly under drier soils only. Thus, our results indicate that water resources strongly determine these responses than continuous +5 °C warming. These findings support the previous work (Didion-Gency et al. 2021) where warming does not necessarily worsen soil moisture levels (Grossiord et al. 2017). Exacerbated impacts of warming imposed on dry soils have been associated with faster exhaustion of soil moisture through VPD-enhanced transpiration and higher residual water loss, accelerating dehydration after stomatal closure. We found no differences in soil moisture conditions at 25 cm depth between single and combined treatments (Fig. 6), suggesting that neither processes occurred in our study. While this result could be explained by the high relative humidity inside the chambers, the extreme dryness of the soil in the superficial soil layers probably prevented any further evaporative water loss. Moreover, residual water loss sensitivity to soil moisture has often been observed under drier conditions after a few years (Grossiord et al. 2018, 2020) and could occur at our site in the future. Plastic trait responses are often involved in climate change studies but are rarely utilized to understand the responses to climatic range shifts toward the rear edge of a species. Our results further suggest that responses to chronic warming and low moisture in trees depend on the stress duration because most effects were found after 3 yr of treatment exposure (Fig. 4). We show that physiological traits have a relatively slower adjustment compared to the more rapid phenological

response. A shift in spring and autumn phenology was observed in the subsequent year following the initiation of the treatments (in 2020) whereas leaf-level gas exchange and growth mainly deviated from the control after 2 yr (in 2021). These findings support the previous work showing shifts in phenology only 1 yr after exposure to a new temperature regime (e.g. Morin et al. 2010). Similarly, studies that have exposed trees artificially to chronic mild drought over several years also found leaf-level gas exchange and growth rates to mainly respond after 2 yr (e.g. Schönbeck et al. 2020). Furthermore, our work was conducted with trees at the seedling life stage, and adult trees may respond differently to warmer and drier conditions. For example, young beech and oak trees have marcescent leaves, which provide protection from freezing temperatures, but they also reduce the exposure to heat through a reduction of the temperature exchange between the stem and the surrounding environment and potentially delay budburst timing independently of the climatic conditions (Heberling and Muzika 2023). Previous work found that young trees tend to have an earlier budburst as a compensatory mechanism for the overshadowing by taller trees in mature forests (Augsburger and Bartlett 2003; Vitasse 2013). However, studying juvenile phenology is still crucial for understanding establishment of trees and predicting carbon sequestration in forests because young trees are in the key stage where rapid evolutionary responses occur. Nevertheless, a lack in leaf area information could induce different responses between leaf-level measurement and the whole tree level.

We expected positive interactions between species because beech and downy oak trees exhibit contrasting functional strategies for uptake of resources (e.g. water) and light use, leading to a possible reduction of competition for resources (Fabiani et al. 2022). Yet, species interactions did not impact phenology, suggesting that microclimatic changes induced by biotic interactions were insufficient to impact the timing of flushing, senescence, and the growing season length (Supplemental Table S2). However, tree species interactions affected leaf-level carbon relations positively depending on the climatic treatments and species, (Supplemental Table S3).

When exposed to warming, beech showed no differences between mixtures and monocultures, and net biodiversity was close to zero for leaf-level carbon relations and growth traits (Supplemental Table S3, Fig. 5). Oak was negatively affected in mixtures compared to monocultures in 2020 (Fig. 5), which was driven by a positive complementarity effect (Fig. 5, Supplemental Fig. S3). This suggests a higher competitive ability of beech at an early life stage. However, trees may still have been impacted by their transplantation in the chambers during the first year. Some oak species, like northern red oak, are known to be highly sensitive to transplant shock because of their taproot systems (Harris et al. 2002). Moreover, no impact was observed during subsequent years under warming. A slightly shorter development duration in mixtures compared to the monocultures in oak trees and a

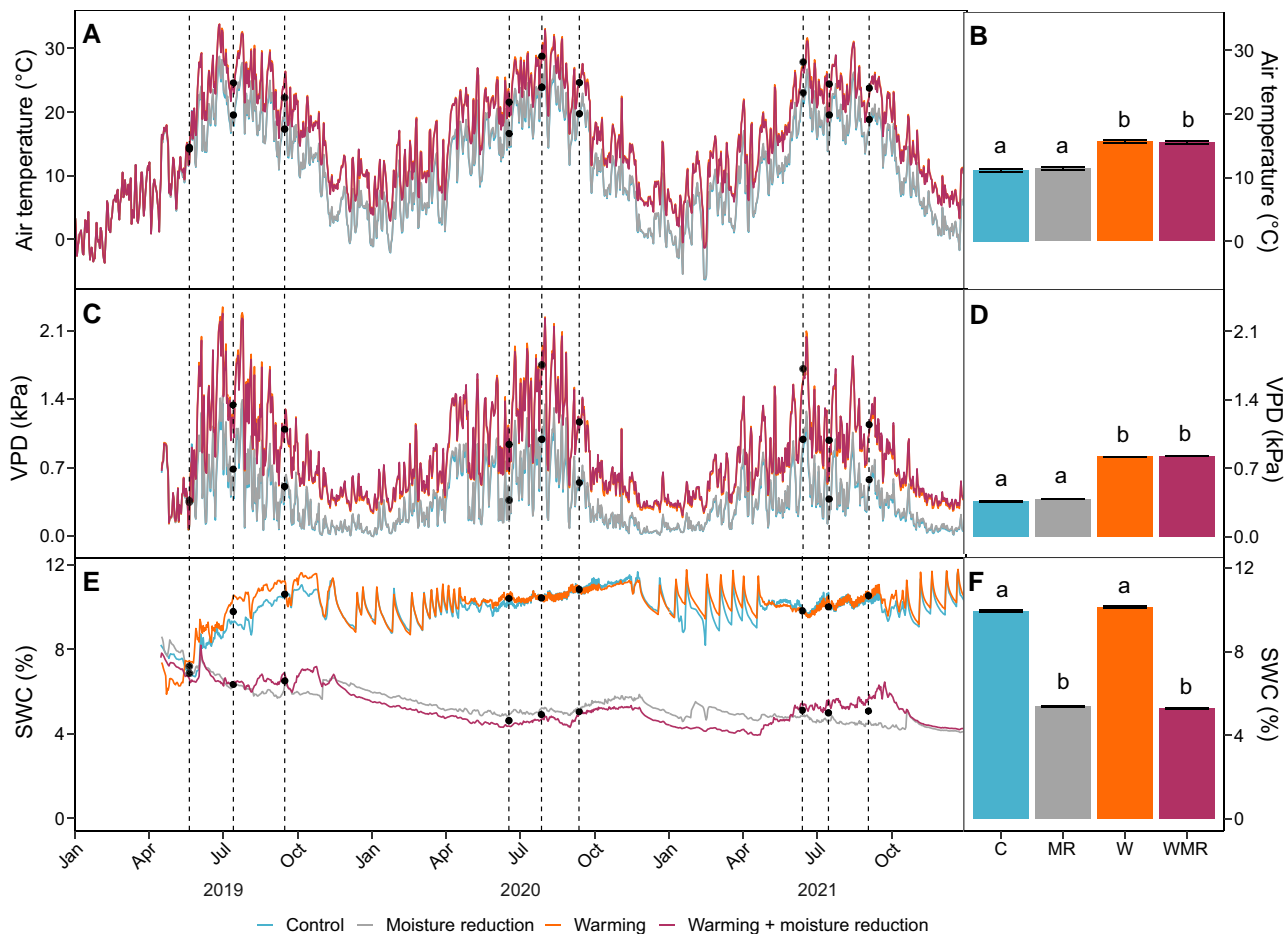


Figure 6. Air temperature (A, B), VPD (C, D), and soil water content (SWC; E and F) under control (C, blue), moisture reduction (MR, grey), warming (W, orange), and warming + moisture reduction (WMR, purple) treatments measured in the open-top chambers. Full lines show the daily averages ($n = 4$ chambers per treatment). Dashed vertical lines indicate the middle of the measurement campaigns (lasting approx. 6 d). Black filled dots stand for the nonheated and heated chambers for the air temperature and VPD, and high soil moisture and low soil moisture chambers for the SWC during the campaigns ($n = 8$ each). Color-filled bars show the averages (mean \pm SE) over the entire time in each climatic treatment, and the significant differences are highlighted with letters (Tukey's HSD post-hoc test, $\alpha = 0.05$).

lower diameter increment in mixtures compared to the monocultures in beech were found on in drier soils (Supplemental Tables S2 and S3). A negative net biodiversity effect on sugar concentration in response to low water availability, driven by a positive complementarity effect, was observed in 2020 (Fig. 5, Supplemental Fig. S3). Overall, these results suggest little impact of tree neighbors on leaf-level carbon relations and growth when drier soils act alone.

However, when warming and lower moisture co-occurred, oak trees had higher A_{sat} in mixtures compared to the monocultures after 3 yr, leading to a positive net biodiversity effect (Fig. 5), driven by complementarity between species (Supplemental Fig. S3). These findings support previous work showing strong resource partitioning between beech and downy oak and beneficial interaction effects under warmer and drier climate (Grossiord et al. 2015). Nevertheless, the effect of species interactions was not constant throughout the experiment and treatment, indicating a

shift in the type of interactions over time. Potentially, beech trees had faster root development after planting, allowing better access to soil nutrients and water resources in the first 2 yr (2019 and 2020). One study observed similar results where more rapid root development was found in beech compared to oak when grown together at a young life stage (Leuschner et al. 2001). However, further work on root growth is required to validate this hypothesis. The positive complementarity effect found in oak after 3 yr supports many studies suggesting the interactions between trees are change over time and often get stronger (Domisch et al. 2015; Haase et al. 2015). Our experiment was still at an early stage of tree development (6-yr-old trees), and tree interactions can take multiple years to establish (Domisch et al. 2015). Thus, further measurements are needed to determine how the interactions will change with tree age and to confirm the apparent advantage of oak in older mixtures with beech during hotter and drier conditions.

Overall, our study highlights that European beech and downy oak will extend their growing season with chronically rising temperatures, even under lower soil moisture, with a longer extension in oak. Therefore, oak may become more competitive, especially in spring, as earlier bud break and photosynthetic activity would provide access to resources before other species start their growing season. While we found that a chronic +5 °C warming will reduce the chilling conditions in winter required for the release of winter bud dormancy, a stronger force due to warmer springs will compensate for cold requirements in both species, and spring phenology will contribute to advance bud break but at a slower rate than before. Contrary to phenology, prolonged water shortage will severely reduce tree gas exchange and growth, with stronger impacts on beech. However, although temperature and low soil moisture impacted the phenology and leaf-level carbon relations differently, their additive effects did not differ from their single effects in our experiment. Therefore, our work suggests that trees may have lower carbon uptake during hotter and drier conditions and that an extension of their active period through chronic temperature rise may not compensate for this reduction because lower growth was still observed overall. Large uncertainties remain regarding the concurrent CO₂ fertilizing impact on all these processes in the long term, and future work should focus further on additive climatic drivers (see Zani et al. 2020). Furthermore, we showed that species interactions could actively shape tree responses after a few years, with a positive effect of mixtures compared to monocultures but only under warmer and drier conditions.

Materials and methods

Experimental set-up

The study was conducted in open-top chambers (OTCs) designed to investigate the impact of tree species interactions under chronic warming and low soil moisture (Didion-Gency et al. 2022). The site is located at the Swiss Federal Research Institute for Forest Snow and Landscape Research (WSL) in Birmensdorf, Switzerland (47°21'48"N, 8°27'23"E, 545 m a.s.l.), and contains 16 hexagonal glass-walled OTCs (3 m height, 6 m² area each, Fig. 7), where mobile roofs are kept above the chambers during the entire experiment to exclude natural precipitation and control the soil water status. The glass walls, roofs, and shadows between chambers reduce the photosynthetic photon flux density (PPFD) inside the OTCs by about 50% compared to the outside conditions (but still reach up to 1,700 µmol m⁻² s⁻¹ PPFD during sunny days, Supplemental Fig. S4). The belowground part of each OTC is divided into two semicircular lysimeters (1.5 m deep, 2.5 m²) with concrete walls, which are divided into four compartments using plexiglass walls, leading to a total of eight soil compartments per OTC (each with an area of 0.625 m²). The soil compartments were filled with a 1 m deep layer of gravel for fast water drainage, covered with fleece to prevent root growth into the gravel below the soil layers but allow the water to pass through, and topped with 50 cm of an artificial

forest soil provided by Ökohum (Herbertingen, Germany; pH 6.3, 40% quartz sand, 20% white peat, 20% expanded shale, 16% pumice stone, and 4% clay). In all compartments, annual soil fertilization was conducted in spring using granules (Unikorn I, Hauert, Grossaffoltern, Switzerland) with 30 g per compartment (20% potash, 14% nitrogen, 12% sulfur, 4% phosphate, and 3% magnesium). During the entire experiment, the leaf litter was left in each compartment.

In October 2018, a total of 336 3-yr-old seedlings of European beech (*F. sylvatica* L.) and downy oak (*Q. pubescens* Willd.) were planted into three species interaction treatments: single-trees to avoid any effects of species or individual interactions ($n = 1$ tree); monocultures to evaluate the effect of intraspecific interactions (i.e. four trees from the same species, $n = 4$ trees); and mixtures to assess the impact of interspecific interactions (i.e. diagonally two trees from each species, $n = 4$ trees). In this study, we only considered monocultures and mixtures because we aimed to compare interaction effects. One tree per species was randomly selected for measurement out of the two or four trees from the same species in each compartment. Tree seed originated from local nurseries from the canton of Solothurn (Biberist, Switzerland) and Valais (Leuk, Switzerland) for beech and oak trees, respectively, and were both grown by Schweizerpflanzen in the canton of Bern (Wiler bei Utzenstorf, Switzerland). Tree sizes were statistically similar when delivered and planted (Supplemental Table S4). In June 2019, after the first leaf flushing and measurement campaign, trees were subjected to a combined manipulation of an air temperature and soil moisture regime. This resulted in four climatic treatments, including a control treatment with ambient air temperature and soil moisture maintained at field capacity (C), an air warming treatment with an increase of around 5 °C (i.e. $+5.19 \pm 0.2$ °C) relative to the (ambient) air temperature in the control (W) (leading also to an increase in VPD), a soil moisture reduction treatment with a reduction of soil moisture of around 50% (i.e. $-52.77 \pm 9.7\%$) relative to the control (moisture reduction, MR), and a combined air warming + soil moisture reduction treatment where both air warming and reduction of soil moisture were applied simultaneously (WMR, i.e. $+5.02 \pm 0.2$ °C and $-51.96 \pm 10.3\%$, Fig. 6, Supplemental Table S5). The soil field capacity was determined using pF-curves (corresponding to approximately 12% relative water content in the sandy soil). Our study aimed to understand the physiological mechanisms under chronic warming of +5 °C and reduction of soil moisture conditions by 50% rather than predict the response of trees to periodic extreme events. The selected conditions have been chosen at our facility to match a possible future shift in mean air temperature leading also to constantly drier soils (Lyon et al. 2022). From March to November, trees were irrigated every second day using an automated irrigation system. Irrigation levels were adjusted throughout the year to maintain soil moisture reduction in the low soil moisture and warming + soil moisture reduction treatments. To prevent frost damage to the pipes, the irrigation system was not used from December to March, and irrigation was applied manually twice a month to maintain treatment

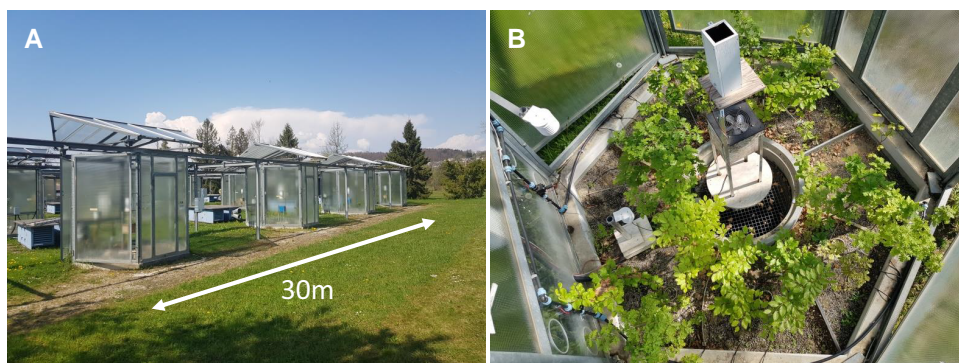


Figure 7. A) Side picture of the 16 open-top chambers. B) Aerial picture from a control chamber including a central fan and eight compartments with different species interaction treatments, taken in August 2021.

differences. Air temperature and relative humidity were monitored inside each OTC at 50 cm and 2 m above the ground every 10 s, and averaged every 10 min (ATMOS 14, METER Group Inc., Pullman, WA, USA). Soil conditions, including soil temperature and moisture, were monitored at 25 cm depth every minute and averaged every 10 min (STM, Decagon Devices, Pullman, WA, USA). Each of the four climatic treatments was repeated in four OTCs ($n = 4$). In each climatic treatment, beech and downy oak trees ($n = 2$ species) and species interaction treatments (monocultures and mixtures, $n = 2$) were replicated six times ($n = 6$ trees per climatic treatment, species and species interaction treatment = 96 trees in total). Phenology, leaf-level assimilation, starch and sugar concentrations, and growth were measured in the selected trees for 3 yr (2019 to 2021). Phenology and growth were measured annually, and leaf-level parameters were measured three times a year during the growing season (early, middle, and late growing season). The first year of measurements (2019) was not included in this study because trees may still have been recovering from their transplant in the chambers (but see Supplemental Figs. S5 and S6). Moreover, phenological shifts were likely impacted by the climatic conditions of the previous years (e.g. Marchand et al. 2020), when the plants were still growing in the nursery.

Phenology

From February to April, the timing of leaf flushing was monitored three times a week by the same observer. The bud development stages, from no bud activity to full leaf unfolding, were determined using a scale with five intermediate stages according to the species (Vitasse et al. 2009; Supplemental Fig. S7, Supplemental Method S1). The bud swelling stage was reached in each tree when at least one bud reached stage 1. The development duration of leaf flushing represents the number of days needed to pass from stages 1 to 4. From September to December, the timing of leaf senescence was assessed once a week by the same observer using leaf coloration and leaf fall. We considered that the onset of senescence was reached when trees had 10% of their leaves had either colored or fallen, using a linear interpolation between two measuring

dates if necessary. The senescence duration was estimated as the number of days between the stage of 10% and 90% of either colored or fallen leaves. For each tree, the growing season length was calculated as the number of days between the bud swelling stage and the onset of senescence.

GDD were calculated for each tree and year by accumulating the daily mean temperature above a threshold of 5 °C from January 1 to the date of bud swelling as determined in previous work on our focal tree species (Vitasse and Basler 2013; Vitasse et al. 2019). The GDD requirement to budburst is an index used to determine the winter and spring temperatures that trigger budburst. GDD requirement to budburst is known to be influenced by the previous exposition of the plant to cooler temperatures, called chilling temperatures, that exponentially reduce the amount of GDD required to budburst (Murray et al. 1989). We also estimated the duration of chilling conditions for each tree during each winter by counting the number of days below a threshold of 5 °C from November 1 to the date of bud swelling.

Foliar gas exchange

Measurements of light-saturated assimilation (A_{sat}) were conducted by means of CO_2 response curves (A/C_i curves) during the most active time of the day (between 9 AM and 5 PM) using LI-COR 6800 infrared gas analyzers (LI-COR, Lincoln, USA), except in the late growing season of 2020 when LI-COR 6400 infrared gas analyzers were used. For the measurements, one fully mature and sun-exposed leaf per tree was selected from the top one-third of the crown. A_{sat} was extracted from the first point of the A/C_i curves at 400 ppm CO_2 concentration, 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, block temperature matching mean daytime air temperature in the different treatments, and relative humidity at 50% (for the reference cell). The measurements are fully described in a previous study (Didion-Gency et al. 2022).

Leaf water potential

Predawn and midday leaf water potential (Ψ_{PD} and Ψ_{MD} , respectively) were measured on one fully mature and sun-exposed leaf per tree from the top one-third of the

crown that was stored in a plastic bag previously inhaled in. Predawn samples were collected before sunrise, and midday leaf water potential samples were collected in the middle of the day (solar time). Measurements were conducted on-site within 1.5 h after sample collection using a Scholander-type pressure chamber (PMS Instruments, USA).

Nonstructural carbohydrates

Leaves used for the midday leaf water potential measurements were heated in the microwave at 600 W for 90 s and dried in the oven for at least 48 h at 65 °C until a stable weight was achieved. Leaves were then ground into a fine powder and used for NSC concentration measurements according to the previously described protocols (Schönbeck et al. 2018; Supplemental Method S2).

Growth traits

Tree height and diameter were annually determined in September. Height was measured on the whole tree, and diameter was evaluated at the trunk base (15 cm above ground) using an electronic digital caliper. As no destructive measurements could be carried out in this ongoing experiment, we estimated the AGWB, excluding leaves, following the allometric equation from Annighöfer et al. (2016) (Supplemental Method S3). The growth rate per year of each parameter was calculated by subtracting the current values from the value of the previous year. These parameters were then called height increment, diameter increment, and AGWB increment.

Biodiversity, complementarity, and selection effects

Net biodiversity, complementarity, and selection effects were determined for each measured trait and species following the equations of Loreau and Hector (2001) and Grossiord et al. (2013) (Supplemental Method S4).

Statistical analysis

Relationships between bud swelling, development duration, onset of senescence, senescence duration, and growing season length, and daily air temperature and soil moisture content were determined through linear regression (*lm* function) for both species in monocultures. Different air temperatures and soil moisture contents were tested to explain phenological variations: the daily mean air temperature and soil moisture content in spring (from February to April, T_{spring} and M_{spring} , respectively), in fall (from September to December, T_{fall} and M_{fall} , respectively), and annually (T_{annual} and M_{annual}). Similarly, the relationship between the number of chilling days and GDD requirement was determined through negative exponential regression (*nls* function) for both species in monocultures because this relationship is best represented by a negative exponential regression (Vitasse and Basler 2013).

The response of all measured traits (i.e. starch concentration, sugar concentration, NSC concentration, A_{sat} , height, diameter, and AGWB increments) to the climatic treatments was determined through linear mixed-effects models for both species in

monocultures. The interactive effects of warming (yes/no), soil moisture reduction (yes/no), and year (2019, 2020, and 2021) were used as fixed effects. As leaf-level responses (assimilation and starch and sugar concentrations) did not vary during the growing season, we averaged them per year before the analyses (Supplemental Table S6). The individual chambers were treated as a random effect. Tukey-type post-hoc tests were used to reveal significant differences between treatments for each year (*multcomp* function).

To determine the impact of species interactions on all our traits, a second linear mixed-effects model was conducted for both species using an additional species interaction effect (monocultures vs. mixtures) as a fixed effect. Tukey-type post-hoc tests were used to reveal significant differences between mixtures (*multcomp* function). When a significant species interaction effect was found, we used *t*-tests to determine if the net biodiversity, complementarity, and selection effects were significantly different from zero for each climatic treatment, year, and species (*t*-test function; Grossiord et al. 2013).

All analyses were performed using the R v.4.2.0 statistical platform (2022).

Author contributions

M.D.-G. and C.G. conceived and designed the study; M.S. and J.G. provided and managed the OTC facility and implemented measurement and control systems; M.D.-G. and C.G. collected the data; M.D.-G. analyzed the data and led the writing of the manuscript. All authors critically contributed to the manuscript and gave final approval for publication.

Supplemental data

The following materials are available in the online version of this article.

Supplemental Figure S1. Phenological traits as a function of soil moisture for beech and oak trees growing under control, moisture reduction, warming, and warming + moisture reduction in the monocultures in 2020 and 2021.

Supplemental Figure S2. Selection effect on leaf-level carbon relations and growth traits for beech and oak trees growing under control, moisture reduction, warming, and warming + moisture reduction in 2020 and 2021.

Supplemental Figure S3. Complementarity effect on leaf-level carbon relations and growth traits for beech and oak trees growing under control, moisture reduction, warming, and warming + moisture reduction in 2020 and 2021.

Supplemental Figure S4. Photosynthetic photon flux density measured by the closest weather station from the open-top chambers.

Supplemental Figure S5. Leaf water potential for beech and oak trees growing under control, moisture reduction, warming, and warming + moisture reduction in monocultures in 2019.

Supplemental Figure S6. Physiological and growth traits for beech and oak trees growing under control, moisture

reduction, warming, and warming + moisture reduction in monocultures in 2019.

Supplemental Figure S7. Description of the bud development for beech and oak trees.

Supplemental Table S1. Summary of the ANOVA tests of the linear mixed-effects models where the interactive effects of warming, moisture reduction, and year were evaluated on leaf-level carbon relations, and growth traits for beech and oak trees in monocultures.

Supplemental Table S2. Summary of the ANOVA tests of the linear mixed-effects models where the interactive effects of warming, moisture reduction, year, and interaction were evaluated on phenological traits for beech and oak trees.

Supplemental Table S3. Summary of the ANOVA tests of the linear mixed-effects models where the interactive effects of warming, moisture reduction, year, and interaction were evaluated on leaf-level carbon relations, and growth traits for beech and oak trees.

Supplemental Table S4. Height and diameter for each species before trees grew in the different climatic.

Supplemental Table S5. Summary of the climate for the different years, treatments, and times.

Supplemental Table S6. Summary of the ANOVA tests of the linear mixed-effects models where the interactive effects of warming, moisture reduction, and season were evaluated on leaf-level carbon relations.

Supplemental Methods S1. Description of bud development stages.

Supplemental Methods S2. NSC concentration determination.

Supplemental Methods S3. Equation for the estimation of AGWB.

Supplemental Methods S4. Calculation of the net biodiversity, complementarity, and selection effect.

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Conflict of interest statement. None declared.

Data availability

Data used in this manuscript are available from the Dryad Digital Repository (doi:10.5061/dryad.4j0zpc8hz). Data supporting the findings of this study are also available from the corresponding author, M.D.-G.

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