RESEARCH ARTICLE

Warming may extend tree growing seasons and compensate for reduced carbon uptake during dry periods

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Abstract

1. Warming and drought alter plant phenology, photosynthesis and growth with important consequences for the global carbon cycle and the earth's climate. Yet, few studies have attempted to tease apart their effects on tree phenology, particularly leaf senescence, and on source and sink activity.

2. We experimentally assessed the single and combined effects of warming and reduced soil moisture on the phenology (leaf-out and senescence date, growing season length) and above-ground sink (height and diameter growth, leaf area and Huber values) and source activity (net photosynthesis, photosynthetic efficiency, chlorophyll concentration and total carbon [C] uptake) of two tree species with distinct strategies to deal with drought: European beech and pubescent oak.

3. Warming advanced leaf-out, irrespective of soil moisture levels, particularly in oak and to a lower extent in beech, leading to a prolonged growing season in oak but not beech. No impacts of warming on senescence timing were found for both species. Reduced moisture had little impact on the phenology of both species. Warming-induced advances in phenology and higher photosynthetic efficiency increased the annual C uptake for oak and compensated for the reduced photosynthetic activity in the presence of reduced moisture. Conversely, for beech, source activity, including yearly C uptake, was lower in all treatments than the control, indicating no compensation of the C budget by phenological shifts.

4. *Synthesis.* Our results demonstrate that a warming-driven earlier activity and higher photosynthetic efficiency compensates for reduced photosynthesis during hot and dry periods, but only for pubescent oak, which is a rather drought-tolerant species. Current predictions of warming-induced mitigation effects through extended C uptake seem incorrect for beech.

KEYWORDS
Fagus sylvatica L., growth, J_{max}, photosynthesis, *Quercus pubescens* Willd., senescence, SPAC model, V_{cmax}, warming

1 | INTRODUCTION

Reduced precipitation and rising temperature are among the most critical environmental stresses for vegetation because of their impacts on plant sink and source activity (i.e. growth and photosynthesis, respectively) and phenology. For instance, warmer climate and hotter droughts have led to important phenological shifts (e.g. Geng et al., 2020; Piao et al., 2019), a widespread reduction in plant carbon assimilation (e.g. Rödenbeck et al., 2020; Santos et al., 2018) and forest productivity (e.g. Ciais et al., 2005; Fu et al., 2020). Yet, although high temperature and reduced precipitation tend to co-occur in nature and few studies have attempted to tease apart their effects, they are thought to have very different impacts on tree' phenology (Fatichi et al., 2014).

In broadleaved trees, the timing of leaf-out and senescence are important phenological events that arbitrate the length of the growing season, the duration of sink/source activity and consequently affect the global carbon (C) cycle (Keenan et al., 2014; Richardson et al., 2013). It is widely recognized that global warming has generally advanced the leaf-out of temperate trees (Piao et al., 2019). However, temperature impacts on leaf senescence timing, and thus on the growing season length, are less consistent (e.g. Chen et al., 2020; Estiarte & Peñuelas, 2015; Xie et al., 2018) and may depend on moisture availability (Xie et al., 2015). For instance, while drought can lead to premature leaf fall (Bigler & Vitasse, 2021; Dallstream & Piper, 2021), for some species such as *F. sylvatica*, reduced C uptake because of soil moisture stress can be compensated by delayed senescence and higher photosynthesis later in the season (Leuschner, 2020). High temperature and drought may also cause embolism in the vascular system, leading to the desiccation of branches and earlier leaf fall (e.g. Cochard et al., 2021; Schuldt et al., 2020). Contrary to leaf-out timing, the exact underlying processes driving senescence remain unclear, but temperature and drought impacts on autumn phenology have been linked to sink/source activity. For instance, a recent study showed that increasing photosynthetic productivity in spring and early summer due to warming drives earlier autumn leaf senescence (Zani et al., 2020, but see Norby, 2021). Indeed, during periods of limited growth demand, photosynthesis can be downregulated by an excess of accumulated carbohydrates (Paul & Foyer, 2001), which can induce degradation of chlorophyll and photosystems and lead to the acceleration of leaf senescence (e.g. Juvany et al., 2013). However, it is unclear whether high carbon supply during periods of low growth demand accelerates the initiation of senescence, the velocity of the senescence process or both. Hence, the link between warming- and drought-induced changes in C assimilation, growth and phenological events remains to be tested experimentally to understand better how global warming will alter carbon sequestration.

Source activity is known to reach a maximum efficiency within a given temperature range and declines after that. For instance, photosynthetic electron transport of *F. sylvatica* peaks at around 34°C (Dreyer et al., 2001; Leuschner, 2020), and net C uptake reaches a temperature optimum at 15–28°C (Schulze et al., 1973). However,

above a given threshold (>40°C), hot spells may impact the integrity of the photosynthetic apparatus (Qu et al., 2013). Contrary to temperature, soil moisture stress is commonly thought to impair source activity because of CO_2 diffusion limitation through the stomata (Chaves et al., 2009). Water stress results in decreasing leaf water content and leaf water potential, leading to stomatal closure and a reduction of intercellular CO_2 concentrations (Flexas et al., 2004). Furthermore, temperature and soil moisture impacts are not entirely independent: reduced stomatal conductance during drought leads to lower leaf evaporative cooling (e.g. Muller et al., 2021), thereby enhancing thermal stress and restricting C uptake. Contrary to photosynthetic properties, far less is known on temperature impacts on sink activity. We can expect cell expansion and tissue growth to cease before C uptake decreases when temperatures rise, resulting in an increase in non-structural carbohydrates (NSC) concentration with higher temperatures. However, higher maintenance respiration under warming (Teskey et al., 2015) might reduce NSC reserves under these conditions. Similarly, drought inhibits sink activity at less negative water potentials than photosynthesis (Tardieu et al., 2011). Plants would thus first stop growth before photosynthesis and accumulate NSC (Körner, 2003; Weber et al., 2019; Woodruff & Meinzer, 2011). The differential sensibility of the sink and source activity to warming and moisture stress could lead to an imbalance between C supply and C demand, which should influence NSC dynamics and could feedback to plant phenology (Estiarte & Peñuelas, 2015).

Moreover, temperature and drought impacts on phenology, and sink/source responses will likely differ between coexisting species. Some species tend to close their stomata at more positive water potentials than others (Tardieu & Simonneau, 1998), leading to lower photosynthesis, reduced growth and NSC storage during drought and/or heat stress (Dickman et al., 2015; Manrique-Alba et al., 2018). Furthermore, the temperature optimum for photosynthesis is highly variable between species because of adaptation to their climate of origin (Berry & Bjorkman, 1980; Fryer & Ledig, 1972) and rapid acclimation to changes in temperature (Gunderson et al., 2010; Kumarathunge et al., 2019). For instance, many studies have shown that the photosynthetic thermal optima can shift by 0.3–0.5°C per degree change in daytime temperature (e.g. Gunderson et al., 2010; Yamori et al., 2014). Plants can also acclimate to soil moisture to optimize their C uptake efficiency under more restrictive moisture conditions. These processes involve cellular adjustments to maintain leaf turgor to whole-plant allometry adjustments to reduce water loss (reviewed in Bréda et al., 2006; Niinemets, 2010). In addition to addressing species differences, we further need to explore heat and drought impacts independently and combined under controlled conditions (e.g. Grossiord et al., 2016, 2017). Such experiments have shown that high temperature and soil moisture limitation reduce photosynthesis and growth in semi-arid systems, thereby reducing foliar NSC concentrations and delaying leaf-out timing in the following spring (Adams et al., 2015). Whether a similar response can be expected in temperate systems is unclear as no study has experimentally

investigated the relative and combined impacts of warming and drought on the phenology of temperate trees, including their link to sink/source activities.

We used an open-top chamber facility where European beech (*Fagus sylvatica* L.) and pubescent oak (*Quercus pubescens* Willd.) seedlings were exposed for multiple years to warming and soil moisture reduction acting alone or together. Beech and oak present essential differences in their strategy to deal with drought, with oak being more tolerant to low moisture and heat (e.g. Barigah et al., 2013; Nardini et al., 2012; Robson et al., 2009; Urli et al., 2013). Our objectives are to (1) determine how individual and combined effects of warming and soil moisture reduction influence phenology and above-ground sink in two temperate trees with contrasting strategies to deal with drought and (2) assess the relationship between source activity, sink activity, and autumn phenology under warming and soil moisture reduction. We expect warming to advance leaf-out timing, accelerate leaf development time, and delay and/or slow down leaf senescence, resulting in longer growing seasons. On the contrary, we expect soil moisture reduction to slow down leaf development in spring and advance and accelerate senescence, resulting in a shorter growing season than in ambient conditions. These responses should be stronger in oak, which is under lower photoperiodic control than beech and has lower chilling requirement to break winter dormancy (Baumgarten et al., 2021). Warming may increase the photosynthetic capacity (i.e. net photosynthesis, rubisco carboxylation, electron transport rate, chlorophyll concentration) in these temperate trees, which could lead to higher C uptake and growth, particularly for the Mediterranean pubescent oak, while soil moisture reduction should decrease these same functions but more severely in European beech (González de Andrés et al., 2021). We further expect changes in autumn phenology, and thus growing season length, to be linked to shifts in the sink/source activity with earlier and accelerated senescence under high carbon assimilation but low growth demand, independently of the species. Finally, we expect the combination of warming and soil moisture reduction to exacerbate the responses observed under moisture reduction-only conditions because of enhanced moisture stress (Adams et al., 2015), particularly for the more vulnerable beech trees (González de Andrés et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Site description

The study was conducted at the model ecosystem facility of the Swiss Federal Research Institute WSL (47°21′48″N, 8°27′23″E, 545 m a.s.l.). The facility comprises 16 hexagonal glass-walled open-top chambers (3 m height, 6 m² each, Figure S1). The roofs were kept closed during the entire experiment to exclude natural precipitation. The lower parts of each chamber are divided into two lysimeters (1.5 m deep, 2.5 m² each) that are each divided into four compartments using PVC shields leading to eight compartments per chamber. The compartments are filled with a 1 m-deep layer of gravel for fast drainage, covered with a fleece layer that is impermeable for roots (to restrict root growth below the soil layers) but permeable for water, and topped by a 50 cm layer of sandy soil (pH = 6.3). This artificial soil with high sand content was selected to ensure good drainage (Ökohum Gmbh). Long-term mean annual and mean summer (June, July and August) air temperature are 9.5 and 17.7°C, respectively, and the average yearly and summer precipitation are 1124 and 377 mm (MeteoSwiss, Station Zurich-Fluntern).

In winter 2018, compartments within each chamber were planted with one 2-year-old individual of common beech and pubescent oak to avoid effects related to competition. In addition, some compartments were planted with monocultures (four trees from the same species) and mixtures (two trees from each species) of the two species but they were not considered in this study. Tree saplings (70.8 cm height ± 12.0 cm and 71.8 cm ± 15.0 cm for beech and oak, respectively) were purchased from a local nursery and originate from canton Aargau, northern Switzerland (for beech) and canton Valais, southern Switzerland (for oak). Fertilizations were conducted yearly in spring using granules (Unikorn I, Hauert, Switzerland). In the open-top chambers, the trees were subjected to a fully crossed combination of soil moisture and an air temperature treatment since April 2019 (i.e. after leaf emergence). This resulted in four treatment combinations: (1) control, where trees were exposed to ambient air temperature, and soil moisture was maintained at field capacity (corresponding to approximately 10% relative volumetric water content in these sandy soils); (2) warming, where the air temperature inside the chambers was maintained at 5.0°C (±0.4°C) above the temperature of the control using heating units; (3) moisture reduction, where irrigation was reduced by 70% leading to a reduction in soil moisture of 51.5.0% ± 11.8% relative to the control; and (4) warming + moisture reduction, where both treatments were applied simultaneously (i.e. +4.8°C ± 0.4°C and irrigation reduction of 70% leading to a soil moisture of −47.8% ± 12.4%, Figure S2). The trees were irrigated every second day using an automatic irrigation system between April and November 2019. The amount of water added to each treatment was adapted throughout the year to maintain field capacity in the control and the treatment differences (Figure S2). The irrigation system was removed from December 2019 to March 2020 to prevent frost damage to the pipes, and watering was done manually bi-monthly to maintain differences between treatments during the winter. An increase in air temperature of 5°C and a decrease of approximately 70% in irrigation was selected at our facility to match values observed during extreme hot droughts in this region, such as the one that occurred during summer 2018 (Peters et al., 2020; Schuldt et al., 2020). In 2020, the treatments resulted in a mean annual temperature of 11.6, 11.8, 16.5 and 16.3°C in the control, moisture reduction, warming and warming + moisture reduction treatments, respectively. During the summer 2020, the maximum daytime temperature in

the chambers reached 37.0, 37.6, 43.8 and 44.4°C in the control, moisture reduction, warming and warming + moisture reduction treatments, respectively. Each climatic treatment was replicated four times ($n = 4$ chambers per climatic treatment) with six replications per species and climatic treatment ($n = 48$ trees in total, i.e. 24 trees per species). Air temperature and relative humidity (ATMOS 14; Meter Group Inc, USA) were measured under a white radiation shield inside all chambers at two heights (0.5 and 2 m above ground) and used to control the heating units. Soil water content and temperature were measured automatically (5TM; Decagon Devices, USA) every minute at 25 cm depth in all chambers (one probe per compartment).

2.2 | Phenology and growth

In March 2020 (during the second growing season, i.e. approximately 11 months after the beginning of the treatments), one observer monitored bud development three times per week until early June using a categorical scale from '0' (no bud activity) to '4' (leaves out and flat) (Vitasse et al., 2013). At stage 1, buds were swollen, elongating and became green; at stage 2, buds were open, and leaves were partially visible; at stage 3, leaves had fully emerged from the buds but were still folded, crinkled or pendant, depending on the species; at stage 4, at least one leaf was fully unfolded. We considered the bulk of the foliage for each tree and assessed the proportion of the buds having reached the most advanced phenological stage, allowing for a tree-level estimate of leaf unfolding. In addition, each phenological score from '1' to '4' was reached by a given tree when at least one bud was at the corresponding stage. We present here only the results of stage 4 (i.e. leaf-out date) and the development time (i.e. the number of days needed to pass from stage 1 to 4) for the analyses. Starting in September, we monitored leaf senescence by estimating the percentage of coloured and dropped leaves of each tree. We then calculated the date when 50% of the leaves were either coloured or had fallen using linear interpolations between two monitoring dates when necessary. The velocity of the senescence process was estimated as the number of days between the stage of 10% and 80% of either coloured and dropped leaves. Every individual tree's growing season length was calculated as the number of days between leaf-out (i.e. stage 4) and leaf senescence date.

At 10 cm above the ground (i.e. below the first branches), tree diameter was measured twice in 2020 using an electronic digital calliper: in spring before leaf-out and autumn after leaf fall. At the same time, tree height was measured on all trees. The difference between the spring and autumn growth measurements was used to calculate yearly height and diameter increment per tree. As no destructive measurements could be carried out in this ongoing experiment to estimate whole-tree biomass, we cut a 15-cm long branch in September 2020 to estimate the mean branch leaf area (cm^2) and Huber value (i.e. ratio of sapwood area over leaf area, cm^2 m^{-2}) from each tree.

2.3 | Leaf-level photosynthetic capacity, non-structural carbohydrates, leaf water potential and percentage loss of conductivity

We measured leaf-level light-saturated photosynthesis (A_{sat}, µmol m^{-2} s^{-1}), stomatal conductance (g_s, mmol m^{-2} s^{-1}), maximum rate of rubisco carboxylation (V_{cmax}, µmol m^{-2} s^{-1}) and electron transport rate (J_{max}, µmol m^{-2} s^{-1}) on one leaf from the highest part of the crown of all 48 trees three times per year in 2020 (i.e. after the trees had been exposed to a full year of treatment manipulation). Chlorophyll concentration (µmol m^{-2}) was measured on the same leaves with a chlorophyll content meter (MC-100; Apogee Instruments, Inc., USA). Measurements took place during three campaigns: once the leaves were fully mature (June), in the middle of the growing season (July/August), and before the first sign of leaf senescence (early September). Gas exchange measurements were conducted using A/C_i (i.e. intercellular CO_2 concentration) curves between 9 AM and 5 PM (local time) using two LI-6800 infrared gas exchange analyser systems (LICOR Biosciences). We used the Auto program 'CO2_response' with relative humidity set to 50% to match average daily environmental conditions inside the chambers. Based on light response curves conducted on our trees (Figure S3), we used a photosynthetic photon flux density (PPFD) of 1500 µmol m^{-2} s^{-1} to ensure saturating light conditions. The air temperature inside the cuvette was fixed to 20, 25 or 30°C to fit the mean midday air temperature during the measurements (i.e. 20°C in June and September and 25°C in July) with +5°C for the warming and hot drought treatments. The A/C_i response curves were measured by stepping down CO_2 inside the cuvette from 400 ppm to 300, 200, 100, 50, 0 ppm and then returned to 400 ppm. The CO_2 concentration was then stepped up to saturation from 400 ppm to 600, 800, 1000, 1200, 1500 and 2000 ppm. When the leaves did not fully cover the LI-6800 cuvette, the projected leaf area of the measured foliage was determined to correct A_{sat} using a flatbed scanner (EPSON Perfection V800 Photo; EPSON) and the Silver Fast 8 software (Laser soft imagine AG, Germany).

A_{sat} (A at 400 ppm), g_s, V_{cmax} and J_{max} were extracted from the A/C_i curves using the Farquhar, von Caemmerer & Berry model computed in the 'PLANTECOPHYS' R-package (Duursma, 2015). Several criteria were used to manually clean the A/C_i curves before fitting, following the recommendations by Gu et al. (2010). To ensure a saturating plateau, all curves that did not reach a C_i of 600 ppm and did not have a minimum of 7 measurement points (because of outlier exclusion) were excluded. Using the default method in the 'PLANTECOPHYS' R-package, the model used a temperature correction to fit all curves to 25°C (see Duursma, 2015 for more details on the modelling procedure). After cleaning the data, 133 out of 144 A/C_i curves were further considered in the analyses. On the same day as gas exchange measurements, one leaf per tree was collected at midday (between 11:30 AM and 1:30 PM). The leaf was microwaved at 600 W for 90s and oven-dried for at least 48 h at 65°C. The leaves were ground to a fine powder and analysed for non-structural carbohydrates (NSC) content following the protocol by Hoch et al. (2002). See Hoch et al. (2002) and Schönbeck

et al. (2020) for more details on the NSC extraction steps. NSC concentrations are expressed on a percent dry matter basis. During each campaign, we sampled one leaf per tree before sunrise and measured leaf water potential (MPa) with a Scholander-type pressure chamber (PMS Instruments).

One 10- to 15-cm-long stem per tree was cut underwater in the field between 07:00 and 10:00 AM during the last campaign. Branches were transported to the laboratory and kept with their cut ends immersed in water and with foliage enclosed in a plastic bag. After at least 30 min of immersion, the stem was cut again in its current-year part and connected to a hydraulic apparatus (Xyl'Em *Plus*—Xylem Embolism Meter; Bronkhorst) and perfused with deionized filtered water with 10 mM KCl and 1 mM $CaCl_2$ that had been previously degassed. After measuring the initial hydraulic conductivity at low pressure, the segment was flushed at 1.5 bar for 1 min to measure its maximal conductivity. A second flush at 1.5 bar for 30 s was conducted to confirm the maximal conductivity value. The initial hydraulic conductivity and the value measured after embolism removal were used to estimate the percentage loss of conductivity (PLC).

2.4 | SPAC modelling of leaf-level photosynthesis

We simulated leaf-level net photosynthesis with a mechanistic soil–plant atmosphere continuum (SPAC) model proposed by García-Tejera et al. (2017), which allows calculating photosynthetic CO_2 uptake based on plant physiological parameters and environmental drivers. The model uses an iterative optimization process to determine the equilibrium between the photosynthetic demand (A) for C_i and the supply of extracellular CO_2 (C_a) through stomatal conductance (g_S). First, the potential A under a given photosynthetic photon flux density (PPFD), V_{cmax} and J_{max} determine the required g_S for sufficient CO_2 supply (i.e. CO_2 supply that is not limiting A by keeping C_i at the concentration of C_a). Second, g_s determines the transpirational water loss (E), which is used to calculate the leaf water potential (Ψ_{leaf}) as a function of T, soil water potential (Ψ_{soil}), and the soil, root and xylem hydraulic resistances. Finally, Ψ_{leaf} is used to calculate the hydraulic restriction on g_s, limiting A due to a restricted supply of intercellular CO_2. The iteration procedure starts again until the demand and supply for CO_2 converge (difference of less than 0.1%). The initial g_s is based on Farquhar's equation for biochemical photosynthesis (Farquhar et al., 1980) and reformulated according to García-Tejera et al. (2017) as:

$$g_{S_{max}} = \frac{B(C_i - \Gamma) - R_d(V C_i + D)}{(E C_i + D)(C_i - C_a)} \qquad (1)$$

with B representing the V_{cmax} or J_{max} limited rates of CO_2 uptake, Γ the CO_2 compensation point of photosynthesis and D is a combination of Michaelis–Menten coefficients for carboxylation and oxygenation rates (K_C, K_O), or the light compensation point of photosynthesis. V is a constant parameter. D is derived from K_C, K_O and the O_2 partial pressure (O_i) as:

$$D = K_C \left(1 + \frac{O_i}{K_O}\right). \qquad (2)$$

The actual g_s is then calculated with Ψ_{leaf} using the equations of Tuzet et al. (2003):

$$g_s = g_0 + \frac{m A}{C_i - \Gamma} f_{\psi leaf} \qquad (3)$$

and

$$f_{\psi leaf} = \frac{1 + e^{[S_f \Psi_f]}}{1 + e^{[S_f (\Psi_f - \Psi_{leaf})]}} \qquad (4)$$

with g_0 as g_S when A_{net} equals 0, m an empirical proportionality factor between A and g_s, and $f_{\psi leaf}$ a factor for reducing g_s as a function of Ψ_{leaf}. S_f is the stomatal sensitivity to Ψ_{leaf} and Ψ_f the leaf turgor loss point (measured using pressure–volume curves). C_i and g_s are then used to obtain A with:

$$A = g_s(C_a - C_i). \qquad (5)$$

We used the SPAC model to simulate A based on soil water content, air temperature and humidity measured at 10-min intervals in the chambers, and PPFD recorded at a nearby long-term forest monitoring site. As the chamber structures intercept part of the incoming radiation, we additionally recorded PPFD with quantum sensors (Apogee Instruments Inc., USA) in 8 of the 16 chambers during 1 week in June 2021. We calculated the fraction of transmitted light (43%) from these measurements, which we used to correct the radiation measured at the nearby forest monitoring site. Model parameters were measured if possible at the study site (tree hydraulic traits), taken from literature, or calibrated (Table S1). We calibrated the model parameters using a Bayesian approach, which allows the inference of parameters from observations via the likelihood (Hartig et al., 2012). We used instantaneous and hourly A and g_s measurements of beech and oak saplings taken during three campaigns in June, July and September 2020 from sunrise to sunset. As prior knowledge for each parameter, we used values inferred from literature (García-Tejera et al., 2017) and calculated a truncated normal distribution. For the calibration, we used a joint Gaussian likelihood based on A and g_s measurements. As A and g_s are expected to be autocorrelated during the diurnal measurements, we used an autoregressive (AR1) likelihood using the function likelihoodAR1 from the R package BAYESIANTOOLS (Hartig et al., 2018). The parameters of the two likelihood components (σ^2 and the AR1 term) were included in the calibration. We obtained the posterior distributions of the parameters used by the SPAC model with a differential evolution (DEzs) Markov chain Monte Carlo (MCMC) sampler (Ter Braak & Vrugt, 2008) using the R package BAYESIANTOOLS (Hartig et al., 2018). In all, 10,000 iterations of three independent chains were run, and convergence after burn-in (50% of the chain) was confirmed with the Gelman–Rubin diagnostic (Gelman & Rubin, 1992). The chain was considered to have converged if the potential scale reduction factor (psrf) was below 1.1. We then used the maximum a-posteriori values as parameters for the SPAC model. The model calibration was evaluated by

simulating A for the conditions during three diurnal campaigns in June, July and September 2020, and calculating the root mean squared error (RMSE) and percentage of bias for the simulated compared to measured value A (Figures S4 and S5). We calculated the yearly assimilated leaf-level carbon A_{tot} (gC) of beech and oak trees in all chambers as the cumulative A multiplied with the molar weight of CO_2 from leaf flushing date to leaf senescence date.

2.5 | Data analysis

The response of the measured variables (leaf-out date, leaf development time, senescence date, senescence development time, growing season length, height increment, diameter increment, leaf area, Huber value, A_{sat}, g_s, V_{cmax}, J_{max}, chlorophyll content, A_{tot}) to the treatment combinations was determined for each species through linear mixed-effects models. The temperature (control temperature/warming) and soil moisture treatment (control irrigation/moisture reduction) and their interactions were fixed effects, and the individual chamber was considered a random effect. The measurement campaign was included as a fixed effect for measurements repeated during multiple campaigns (i.e. A_{sat}, g_s, V_{cmax}, J_{max}, chlorophyll content). Post-hoc analysis was performed with Tukey's HSD test, with FDR correction for multiple testing. Linear regressions were used to test the relationship between senescence date, growing season length, source (A_{tot}) and sink activity (height and diameter growth increment). All analyses were performed using the software R Studio (3.5.1, R Core Team, 2018).

3 | RESULTS

3.1 | Phenology and growth

In both species, warming advanced leaf-out (Table 1), which occurred on average 4.5 or 15 days earlier than ambient conditions, for beech and oak, respectively (Figure 1). Moisture reduction did not affect leaf-out timing in beech but advanced leaf-out in oak by 4.9 days. Warming combined with moisture reduction advanced leaf-out by more than 5 days for beech and 12 days for oak (Table 1 & Figure 1, significant warming×moisture reduction interaction). In spring, oak leaf development time (i.e. number of days between stages 1 and 4) was significantly prolonged by 3.5 days in response to warming (Table 1). No significant impact of the other treatments was found for beech and oak leaf development time (Table 1). No significant effect of the treatments on the senescence date was found for either species (Figure 1, Table 1). However, leaf senescence occurred over a more extended period under warmed conditions for oak (20 days longer), while no other effects of the treatments were found for both species (Figure 1, Table 1). For oak, the growing season length was significantly prolonged by warming (by 27.3 days), while no changes were observed for beech in response to the treatments (Figure 1, Table 1). No impact of the treatments or their interaction was found

on diameter and height increment, leaf area and Huber values for either species (Figure S6, Table 1).

3.2 | Leaf-level photosynthetic capacity, NSC, leaf water potential and PLC

While moisture reduction significantly reduced A_{sat} and g_s compared to ambient conditions, warming had no impact on A_{sat} and g_s in either species (Figure 2, Table S2). Treatment impacts on A_{sat} and g_s did not vary seasonally (i.e. no interaction between treatments and campaigns). A_{sat} and g_s did not differ between campaigns for oak but were significantly reduced during the last campaign compared to previous ones for beech (Figure 2). V_{cmax} was significantly reduced by moisture reduction for oak, whereas warming increased V_{cmax} in both species. Similarly, J_{max} was significantly reduced by moisture reduction for oak, but neither warming nor moisture reduction affected J_{max} for beech (Figure 2, Table S2). Warming had no impact on oak J_{max}. V_{cmax} and J_{max} varied during the season for both species, but the treatment effects were not affected by seasonality (Table S2). Chlorophyll content varied between campaigns for beech but was not impacted by moisture reduction and warming for both species (Figure 2, Table S2). For oak, we observed higher total NSC and starch concentration in September 2020 in the warming treatment compared to the control, while for beech no effect was found (Figure S7). No effect of the treatments was found for PLC for both species (Figures S7 and S8). Predawn leaf water potential was reduced by warming for both species (only in the single warming treatment for beech), and by drought for oak with lower values in the warming and moisture reduction treatments acting alone and together compared to ambient conditions (Figure S9).

3.3 | Modelled leaf-level carbon uptake during the growing season

The SPAC model captured diurnal and seasonal changes, as well as treatment effects and species differences of A (Figures S4 and S5). Total root-mean square deviation of the simulated A was 2.35 and the bias was −13%, indicating that the model generally underestimated photosynthesis. This was mostly due to an underestimation of assimilation peaks of oak trees in the ambient and warmed treatment (Figure S4).

In oak, while warming led on average to a 14.5% increase in A_{tot}, soil moisture reduction reduced total leaf-level C uptake by 12.4% (Table 1). The negative moisture reduction effect was to a certain degree mitigated by warming (significant warming×moisture reduction interaction, Figure 3). Consequently, the warmed oak trees had the highest C uptake (1760 gC m^{-2} year^{-1}), whereas the ones exposed to moisture reduction had the lowest A_{tot} (1359 gC m^{-2} year^{-1}). In beech, A_{tot} was on average 12.5% and 16.4% lower in response to warming and soil moisture reduction, respectively (Figure 3, Table 1).

TABLE 1 Linear mixed model results (*F*- and *p*-value) of the effect of warming (W) and moisture reduction (MR) and their interactive effect (W×MR) on the leaf-out date, leaf development time, senescence date, senescence development time, growing season length, diameter and height increment, leaf area, Huber value and the yearly assimilated carbon in beech and oak. Significant effects are highlighted in bold

Explained variables	Species	Treatment W	MR	W × MR
Leaf-out	Beech	**27.02 (<0.001)**	0.34 (0.572)	2.78 (0.129)
	Oak	**54.55 (<0.001)**	0.85 (0.519)	**5.78 (0.033)**
Leaf development	Beech	0.41 (0.528)	0.07 (0.789)	3.61 (0.073)
	Oak	**5.48 (0.041)**	1.92 (0.194)	0.01 (0.990)
Senescence	Beech	0.31 (0.579)	0.82 (0.375)	2.51 (0.131)
	Oak	2.67 (0.118)	0.34 (0.561)	0.04 (0.827)
Senescence development	Beech	2.07 (0.166)	0.49 (0.488)	2.56 (0.126)
	Oak	**10.19 (0.005)**	0.53 (0.472)	0.57 (0.459)
Growing season length	Beech	2.03 (0.171)	1.23 (0.281)	3.69 (0.070)
	Oak	**12.11 (0.003)**	0.13 (0.713)	0.14 (0.706)
DBH increment	Beech	0.17 (0.686)	2.43 (0.145)	3.39 (0.090)
	Oak	0.39 (0.541)	0.01 (0.917)	1.64 (0.225)
Height increment	Beech	0.30 (0.589)	0.33 (0.571)	0.01 (0.897)
	Oak	1.08 (0.319)	0.55 (0.472)	0.10 (0.753)
Leaf area	Beech	0.19 (0.667)	0.685 (0.370)	0.76 (0.696)
	Oak	0.24 (0.625)	0.23 (0.631)	0.24 (0.626)
Huber value	Beech	0.31 (0.587)	0.14 (0.710)	0.02 (0.870)
	Oak	1.49 (0.236)	0.20 (0.652)	1.09 (0.308)
Yearly assimilated carbon	Beech	**29.63 (<0.001)**	**63.04 (<0.001)**	0.01 (0.915)
	Oak	**70.40 (<0.001)**	**85.27 (<0.001)**	**16.41 (0.002)**

The warming and moisture reduction effects were additive so that the highest C uptake was found in beech seedlings from the ambient treatment (637 g C m^{-2} year^{-1}), whereas the lowest C uptake was in the warming + moisture reduction treatment (467 g C m^{-2} year^{-1}, i.e. 26.5% less).

In both species, warming (alone and in combination with moisture reduction) advanced leaf-out, which contributed considerably to their surplus of A_{tot} compared to trees in ambient condition: warmed beech and oak gained 3.8% and 8.4%, respectively, of their annual C during the period before ambient tree activity started. Similarly, beech and oak in the warming + moisture reduction treatment gained 4.4% and 7.9% of their yearly C before ambient trees flushed. Moisture reduction, in contrast, increased the annual C uptake by only 0.4% and 3.3% for beech and oak, respectively. In both species, warming and moisture reduction slightly delayed senescence compared to ambient trees (but not significantly), which contributed to 0.6% and 3.5% of their annual C uptake in warmed beech and oak, 0.8% and 1.4% in the moisture reduction treatment, and 1.7% and 4.1% in the warming + moisture reduction treatment. During the period where all trees were simultaneously active, beech assimilated 19.6%, 18.5% and 31.1% less carbon in the moisture reduction, warming and warming + moisture reduction treatment, respectively, compared to ambient conditions. In contrast, oak only reduced their assimilation by 9.8% and 11.8% in the moisture reduction and warming + moisture reduction treatment, respectively, and increased their C uptake by 7.9% in the warming treatment compared to ambient conditions.

3.4 | Relationship between autumn phenology and sink/source activity

In both species, delayed senescence and a longer growing season were related to a higher A_{tot} (Figure 4). However, none of the phenological measurements were correlated with sink activity (i.e. height and DBH increment).

4 | DISCUSSION

4.1 | Warming and moisture reduction effects on spring and autumn phenology

Our results support previous studies showing that global warming induces earlier tree activity (e.g. Beil et al., 2021; Piao et al., 2019; Vitasse et al., 2018). In addition, our results demonstrate that temperature impacts on spring phenology are independent of soil moisture in temperate trees as an advanced leaf unfolding occurred even when warming was combined to a substantial irrigation reduction (i.e. warming + soil moisture reduction treatment; Figure 1). These impacts were observed only 1 year after the treatment started, demonstrating the importance of winter and spring temperature for spring phenology and explaining the high year-to-year variability of this phenological event (Meier et al., 2021). However, the magnitude of the phenological shift induced by warming differ widely between the two species with an advance of 15 days for oak and only 4.5 days
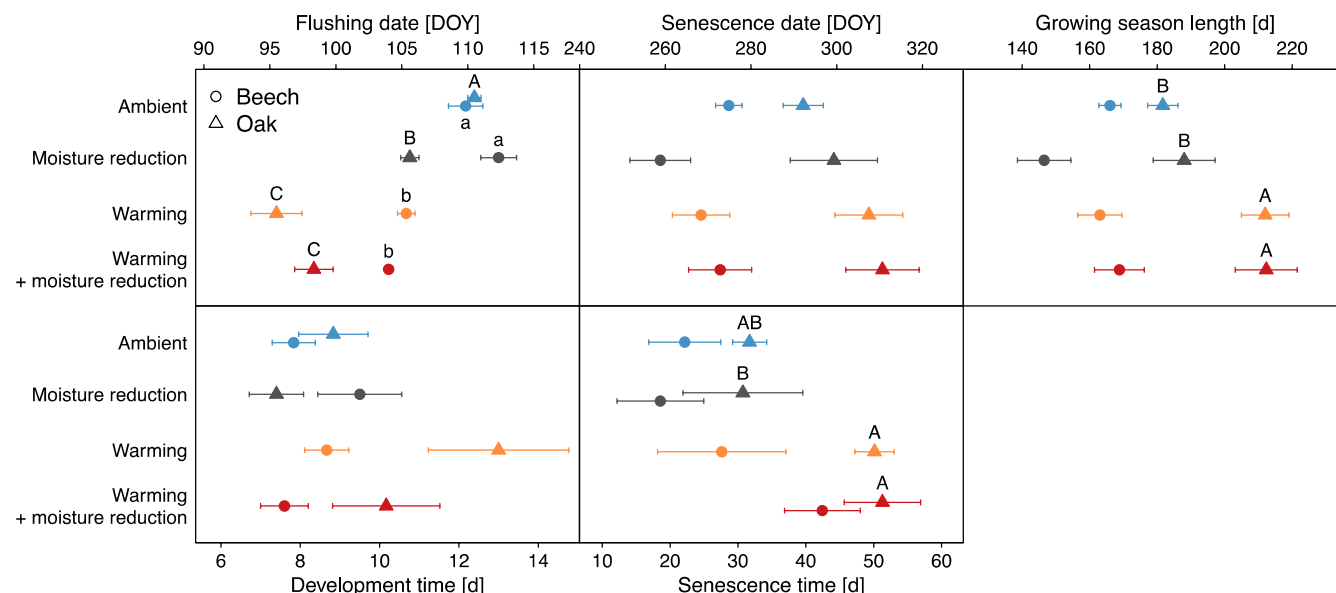
FIGURE 1 Mean leaf flushing date, senescence date, growing season length, leaf development time and senescence development time (mean ± SE; $n = 5$–6 trees per treatment and species) for European beech (circles) and pubescent oak (triangles) grown under control, warming, moisture reduction and warming + moisture reduction conditions. Significant differences between treatments for each species are indicated with capital (pubescent oak) and small (European beech) letters (Tukey's HSD post-hoc test, alpha = 0.05)

for beech, a difference that remains similar when soil moisture reduction co-occurs with warming (Figure 1). These differences, which are consistent with previous work (e.g. Vitasse et al., 2009), may be driven by a higher control of the photoperiod in beech trees compared to oak (Baumgarten et al., 2021). Our findings contradict, however, some work showing an earlier leaf-out in diffuse-porous species compared to ring-porous ones (e.g. Lechowicz, 1984), which has been attributed to greater embolism in trees with larger vessels by the end of winter, thereby impairing the supply of water to emerging leaves. As little loss of stem hydraulic conductivity was observed in our study (Figure S8) and leaf water potentials did not go beyond typical P_{50} (i.e. xylem pressure inducing a 50% loss of conductivity) values for those species (Figure S9), it is not surprising that treatment-induced phenological shifts were not associated with xylem vulnerabilities. Overall, our findings suggest that pubescent oak could benefit more than European beech from climate warming since it may become more competitive for resources such as water, nutrients and light earlier in the growing season, particularly in stands where the two species co-occur. However, this response could also expose trees to other climate-associated stressors such as frost and herbivory damages (Chamberlain & Wolkovich, 2021; Vitasse et al., 2014).

Our results differ strikingly from previous work in semi-arid systems where similar warming of 5°C delayed the start of the growing season (Adams et al., 2015). The contrast between the two studies highlights the context dependency of temperature impacts and suggests an essential role of the background climate. Indeed, as our results tend to show, temperate ecosystems, which are not yet limited by extreme drought and heat, are more likely to take advantage of warming-induced phenological shifts (Moritz &

Agudo, 2013). Adams et al. (2015) further showed that soil moisture reduction exacerbates high temperature impact in semi-arid conditions, which contradicts our observations. Contrary to the strong effects found on source activity (Figure 2), we observed no impact of soil moisture reduction on spring phenology for European beech, suggesting that temperature was solely responsible for shifts in leaf-out timing. Yet, opposite to our expectations, an earlier leaf-out occurred for pubescent oak in response to soil moisture reduction, even if only by 4.9 days. Few studies have investigated moisture impacts on spring phenology in temperate regions. Using a similar experimental design, Kuster et al. (2014) also observed an earlier moisture-induced leaf-out in three oak species, including pubescent oak. However, the underlying mechanisms driving this response remain unknown. In Mediterranean ecosystems, Peñuelas et al. (2004) showed that precipitation correlates well with the timing of leaf development. Nevertheless, even in this dry ecosystem, the effects of moisture on leaf-out date were still weaker than those associated with temperature (Peñuelas et al., 2002).

Despite our expectations and contrary to previous work (Arend et al., 2016), warming and soil moisture reduction had no impact on beech autumn phenology, but they prolonged the period of senescence in oak. Consequently, a longer growing season was observed for oak but not for beech, where temperature impacts on spring phenology were not as strong. This result suggests that different underlying processes are driving leaf-out and senescence timing. The initiation of senescence may be more controlled by the photoperiod (Keskitalo et al., 2005) even if, as shown in our study (Figure 1), the duration of the senescence process can be extended with warming in more plastic species such as pubescent oak.
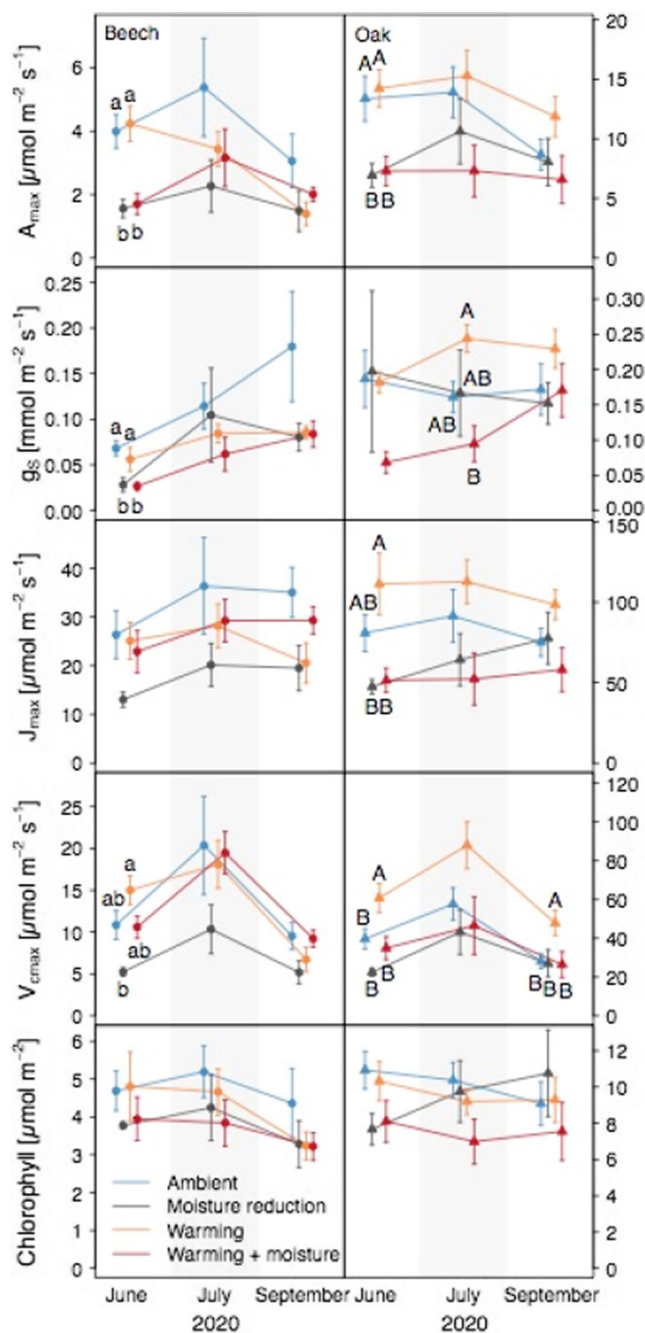
FIGURE 2 Light-saturated photosynthesis (A_{sat}), stomatal conductance (g_s), maximum electron transport rate (J_{max}), maximum rate of rubisco carboxylation (V_{cmax}) and leaf chlorophyll content (mean±SE; $n = 5–6$ trees per treatment, species and measurement campaign) for European beech (circles) and pubescent oak (triangles) growing under control, warming, moisture reduction and warming + moisture reduction conditions. Measurements took place in June, July and September 2020. Significant differences between treatments for a given campaign and species are indicated with capital (pubescent oak) and small (European beech) letters (Tukey's HSD post-hoc test, alpha = 0.05)

4.2 | Warming and soil moisture reduction effects on sink and source activity

Warming led to higher total modelled leaf-level C uptake in oak trees, mainly due to an extended growing season and earlier

source activity. Warming further enhanced oak V_{cmax} throughout the growing season, resulting in higher modelled C uptake when all trees were active. We found no changes in chlorophyll content, which indicates that warming-exposed trees increased the amount and activity of the Rubisco enzyme but not necessarily the harvesting of the light energy (i.e. leaf absorbance), which is largely determined by the chlorophyll pigment concentration (Collatz et al., 1991). Hence, both a warming-extended growing season and increased C assimilation through warming-enhanced photosynthetic efficiency (i.e. enhanced amount of CO_2 catalysed by Rubisco) led to a higher annual C uptake in warmed pubescent oaks. These findings are in agreement with previous work on pubescent oak from open-top chamber experiments where elevated temperature led to higher net photosynthesis (Arend et al., 2013). As we could not obtain whole-tree leaf area estimates, it is difficult to predict temperature impacts at the whole-tree scale. Moreover, care should be taken with modelled results as they are not as reliable as empirical data, particularly during periods of high photosynthesis (Figure S5). Yet, no changes in leaf size and Huber values were observed, suggesting that our leaf-level findings could be representative of whole-tree C uptake strategy. We also observed substantial reductions in CO_2 uptake, stomatal conductance, V_{cmax}, and J_{max} in response to reduced soil moisture, supporting many previous studies (e.g. Arend et al., 2013; Vaz et al., 2010; Xu & Baldocchi, 2003). Consequently, oaks exposed to irrigation reduction had 12% less C uptake during the period when ambient trees were also active. This reduction was entirely compensated in trees exposed to combined warming and irrigation reduction because of the extended growing season (Figure 3). These findings are crucial as they suggest that advanced spring phenology and a longer growing season driven by higher temperature compensate for a drought-induced reduction in C uptake in pubescent oak (Ciais et al., 2005). C compensation under warming increased the amount of stored NSC concentrations, especially starch levels (Figure S7), which could play a significant role in the long term for pubescent oak vulnerability to and recovery from climate extremes (Piper & Paula, 2020). Our study is the first to show this delicate balance existing between C-fixation limitations under limited soil moisture, increased photosynthetic efficiency and growing season length with warming, potentially allowing some species to persist under rising temperature by shifting their C uptake to the edge of the growing season. If these results can be validated for numerous species and if we could determine how it translates into annual carbon fixation, such compensation could substantially affect the strength of the carbon-climate feedback.

For European beech trees, an earlier photosynthetic activity was insufficient to compensate for the substantial reduction in modelled C uptake due to warming and limited soil moisture (Figure 3). As strong reduction in stomatal conductance together with no changes in J_{max}, V_{cmax} and chlorophyll content was observed, these results indicate that stomatal closure and thus reduced intercellular CO_2 concentrations must be driving climate impacts on beech C uptake (Flexas
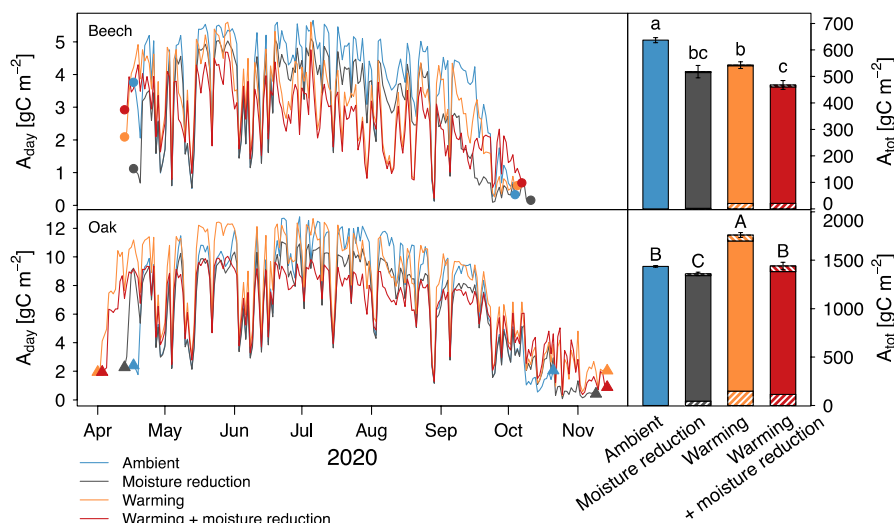
FIGURE 3 Mean simulated daily carbon uptake (A_{day}, $n = 4$ chambers per treatment and species) of European beech and pubescent oak growing under control, warming, moisture reduction and warming + moisture reduction conditions during the growing season of 2020 and their respective annual carbon uptake (A_{tot}). The surplus of carbon uptake in warming, moisture reduction and warming + moisture reduction treatments before the leaf-out and after senescence of ambient trees are shown with right and left dash, respectively. Significant differences between treatments are indicated with capital (pubescent oak) and small (European beech) letters (Tukey's HSD post-hoc test, alpha = 0.05)
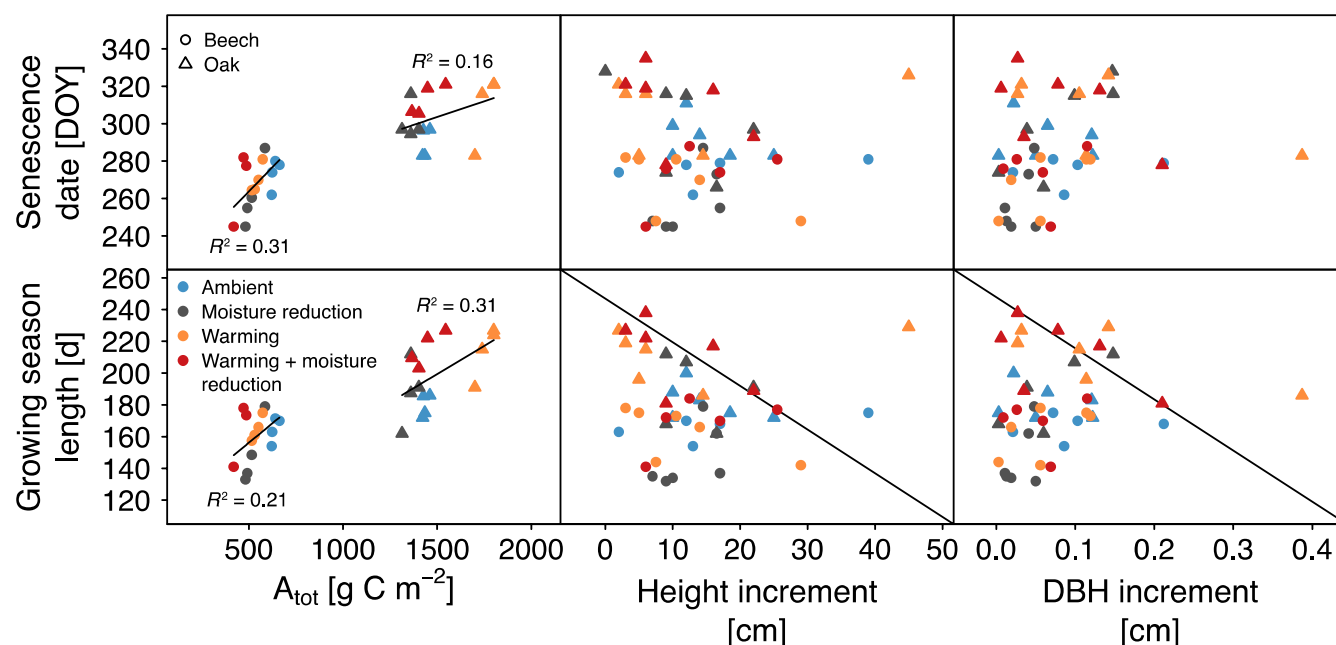

FIGURE 4 Phenology of European beech and pubescent oak growing under control, warming, moisture reduction and warming + moisture reduction conditions in relation to the source (modelled annual carbon uptake, A_{tot}) and the sink (increments of height and diameter at breast height, DHB). Significant linear relationships of each species (alpha = 0.05) are indicated with regression lines

et al., 2004). Large reductions of up to 44% in net photosynthesis and in the allocation of C resources below-ground were also previously found for beech in response to warming and soil drought in such manipulative experiments (Hagedorn et al., 2016). Taken together, these findings suggest that, in the coming years, European beech may have to rely more often on an early-season C uptake when the air temperature is still low. Our results thus also contradict predictions of a longer growing season with global warming and climate mitigation effects through extended C uptake for temperate species such as European

beech. Still, this finding corroborates many studies reporting that beech trees will likely experience population decline with future warming (Hanewinkel et al., 2013; Leuschner, 2020), likely because of the absence of warming-induced compensation through phenological adjustments. Moreover, as a species known for its low sensitivity to temperature compared to photoperiod limitation and chilling requirement (Vitasse & Basler, 2013), European beech may not have strong potential to adapt to global warming via phenological shifts. Nevertheless, care must be taken when interpreting these findings as

beech showed low assimilation rates (Figure 2) compared to previous work using the same experimental settings (Pflug et al., 2018). Low photosynthesis could be associated with high stress levels already under control conditions, which could explain the absence of C compensation found for this species (Figure 3).

The absence of warming and soil moisture reduction impacts on sink activity (i.e. growth increment in height and DBH) is surprising but coherent with the absence of changes in leaf area, Huber values and non-structural carbohydrates (Figure S7). Even if a large variability between trees restricts our interpretation and raises uncertainties about sink activity results (Figure S6), these findings could suggest no imbalance or strong compensation between the sink and source activity. Previous studies have found reductions, increases and no changes in productivity in response to warming and soil moisture limitation (e.g. Liu et al., 2017; Manrique-Alba et al., 2018; Taeger et al., 2015; Vanhellemont et al., 2019). For instance, using a similar experimental design, Arend et al. (2011) found that soil moisture stress decreased above-ground growth in pubescent oak by approximately 45% while warming enhanced it by 14%. Similarly, several studies reported that beech growth was severely reduced by higher vapour pressure deficit and soil moisture stress using open-top chamber experiments (e.g. Lendzion & Leuschner, 2008; Liu et al., 2017). The divergent findings could be attributed to local environmental factors, measuring approaches or contrasting drought and warming levels. For instance, Arend et al. (2011) used different provenances and increased daytime air temperatures by approximately 2°C while soil moisture was reduced by 50% in the warmed and moisture reduction treatments, respectively, compared to the control. Moreover, an essential part of the sink activity is taking place below-ground, particularly in the earlier life stages and under temperature and soil moisture stress (Hertel et al., 2013). A higher allocation of assimilates below-ground has been demonstrated in many species, including European beech (Hagedorn et al., 2016). However, as the actual contribution of the below-ground sink activity is poorly known, future work should include a whole-tree sink and source activity perspective, as well as temperature and soil moisture gradients, to shed more light on the mechanisms driving phenological shifts. Further assessments across years would also be needed to confirm our observations and provide additional insight into sink/source feedbacks, mainly as warming effects in manipulative experiments can sometimes dissipate with time (Wolkovich et al., 2012).

4.3 | Effect of sink and source activity on autumn phenology

We hypothesized that changes in the source (i.e. net photosynthesis and total C uptake) and sink activity (i.e. height and diameter increment) would be associated with shifts in leaf senescence and growing season length. Our findings show that higher C uptake was consistently related to delayed leaf senescence and longer growing seasons, independently of the treatment, as highlighted by the positive relationships observed between variables (Figure 4). Leaf senescence responses to warming and soil moisture changes are complex because they are determined by the interaction of many internal and external factors, among them hormones, sugar concentration, temperature, photoperiod and water availability. In this context, while the cross-correlation of all these factors limits interpretation from long-term observations, manipulative experiments allow us to decipher more precisely the underlying processes, and our study tends to show that leaf senescence occurs later in plants that have assimilated more C. Yet, we urge caution in interpreting the significant relationships between senescence, growing season length and A_{tot} observed here as the exact link between the two may be associated with other processes not accounted for. Recent work has associated senescence to source and sink activity whereby elevated CO_2 and temperature stimulated photosynthesis earlier in the growing season, creating a sink limitation that subsequently causes earlier senescence (Zani et al., 2020). These findings are contradicting evidence provided by free-air CO_2 enrichment (FACE) experiments where, similarly as in our work, a warmer (and/or a CO_2-richer) environment lead to advanced and enhanced sink/source activity in temperate trees but no change or even delayed senescence depending on the species and duration of the manipulation (Norby, 2021). These inconsistencies may be related to the timing of warming and soil moisture limitation. If warming occurs early in the growing season, it should stimulate photosynthesis when growth demand is high and prolong senescence. However, warming could accelerate autumn phenology if it occurs towards the end of the growing season when growth demand is low (Beil et al., 2021). As our treatments were applied all along the growing season, the two effects may have been triggered and compensated for each other. More work on the importance of the soil moisture and warming timing would be needed to understand better the drivers of leaf senescence and their interactive effects. Overall, senescence drivers have not been well studied, and our results highlight the need to further evaluate these drivers in numerous species and across broad gradients of temperature and soil moisture.

5 | CONCLUSIONS

Shifts in plant phenology due to global warming may mitigate negative drought impacts on plant C uptake. Yet, we have little evidence for validating this hypothesis because few studies have combined phenological assessments with leaf-level photosynthesis measurements, and even fewer studies have been able to separate the impact of temperature from other environmental factors. Our experimental study demonstrated that year-round air warming advances leaf flushing but has no impact on senescence, thereby leading to a longer growing season. On the contrary, reduced soil moisture acting alone had little impact on phenological events. Moreover, while warming and soil drought did not affect above-ground growth, leaf-level photosynthetic capacity was enhanced by air warming and reduced by low soil moisture. Consequently, an air warming-induced extension of the growing season buffered

the reduction in C uptake during dry periods for pubescent oak but not for European beech, a species whose phenology is under strong photoperiodic control. These results support previous predictions suggesting high vulnerability for European beech and high temperature-related mitigation potential for pubescent oak through shifts in the growing season. Future work should investigate broader temperature and soil moisture gradients to better understand the mechanisms driving phenological shifts, and their impact on sink and source activity.

AUTHORS' CONTRIBUTIONS

C.G. planned and designed the research; C.G., J.G., E.M. and M.D.-G. conducted fieldwork; C.G. and C.B. analysed the data; C.G., C.B., J.G., E.M., Y.V. and M.D.-G. wrote the manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings are openly available on Dryad Digital Repository https://doi.org/10.5061/dryad.3bk3j9kmx (Grossiord et al., 2022).

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