PERSPECTIVE

Four ways to define the growing season

Christian Körner [ID] | **Patrick Möhl** [ID] | **Erika Hiltbrunner** [ID]

Department of Environmental Sciences, Botany, University of Basel, Basel, Switzerland

Correspondence
Christian Körner, Department of Environmental Sciences, Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland.
Email: ch.koerner@unibas.ch

Editor: Johannes Knops

Abstract

What is addressed as *growing season* in terrestrial ecosystems is one of the main determinants of annual plant biomass production globally. However, there is no well-defined concept behind. Here, we show different facets of what might be termed growing season, each with a distinct meaning: (1) the time period during which a plant or a part of it actually grows and produces new tissue, irrespective of net carbon gain (growing season sensu stricto). (2) The period defined by developmental, that is, phenological markers (phenological season). (3) The period during which vegetation as a whole achieves its annual net primary production (NPP) or a net ecosystem production (NEP), expressed as net carbon gain (productive season) and (4) the period during which plants could potentially grow based on meteorological criteria (meteorological season). We hypothesize that the duration of such a 'window of opportunity' is a strong predictor for NPP at a global scale, especially for forests. These different definitions have implications for the understanding and modelling of plant growth and biomass production. The common view that variation in phenology is a proxy for variation in productivity is misleading, often resulting in unfounded statements on potential consequences of climatic warming such as carbon sequestration.

KEYWORDS
climate, development, dormancy, phenology, plant growth, primary production, roots, seasonality, window of opportunity

INTRODUCTION

Seasonality affects nearly all aspects of life on earth. Life conditions vary seasonally throughout the year. Even in the humid tropics, plant communities exhibit seasonality with regular periods that are less or more supportive for development and growth (e.g., Girardin et al., 2016; Ilondea et al., 2021; Würth et al., 2005). It was long recognized that the length of such favourable periods determines annual plant production and that plants not only track these conditions, but anticipate their arrival and end through evolutionary selection of signal perception and internal timing of development. The net outcome of both, internal control and external forcing is what is often termed the 'growing season'. As it is the case with many practical concepts, a closer look at their actual meaning opens space for interpretation. Here, we aim

for a novel conceptual framework that identifies various approaches and arrives at a reproducible terminology.

In ecology, clear-cut principles and terminology for effective communication and applications are often hard to frame. In part, this is due to the complexity of organisms and their interactions, but also owing to the probabilistic nature of life. Variation is the essence of life, the substrate as well as the outcome of evolution, often rendering sharp definitions impractical. Yet, vague terminology can be misleading and paves the way to scientific misunderstandings and conflicting interpretations. For example, the two most widely used terms in scientific ecology, stress and limitation, have rather different meaning in agronomy and ecology (Körner, 2003a, 2018). The very same 'stress' that reduces crop yield, determines the composition of a plant community, with the relief from such 'limitation' causing the community's extinction and

subsequent replacement by another type of community. The century-long debate about 'treeline' was fueled by ill-founded definitions of the life-form 'tree', the notion of a 'line', and the confusion of the realized versus fundamental niche concept (Körner, 1998, 2021b; Körner & Hoch, 2023). Similarly, the term growing season covers a suite of potential definitions with very different meanings and functional consequences.

Because many phenomena in ecology have a gradual nature, definitions of thresholds often cut through a continuum, causing shades of grey to become a step-change. It boils down to a convention where, along such gradients (e.g., advent of spring), one assumes a threshold has been surpassed. While such decisions call for pragmatism, they would best be placed within a well understood framework, rather than assuming everybody agrees on which shade belongs to which type of grey. In this perspective, we will develop different lines of reasoning that arrive at four broadly applicable definitions of the growing season. The definitions may either be centered around plant responses or environmental conditions. We urge researchers in related fields to become aware of the different definitions and their consequences (Figure 1), and to explicitly state which one they employ.

THE DORMANCY AND ITS END

Attempts at defining and understanding seasonality of plant life date back to the 19th century (De Candolle, 1855; Harrington, 1894), with most 20th century plant physiological approaches focusing on understanding the opposite of a plant's active growing season: the dormant season. Starting with Vegis (1964) and culminating in Lang et al. (1987), the debate centered around physiological causes of inactivity, termed *dormancy*. These studies revolved mainly around seeds and buds of herbaceous species, crops in particular, and focused on the role of hormones. A great deal of the dormancy debate in Lang et al. (1987) is related to what would better be addressed as differential morphogenesis (the controls of plant architecture), namely, the correlative silencing of certain buds through the suppressive action of dominant apical meristems (termed *paradormancy*). Most of this literature falls in the domain of chronobiology (see review by Forrest & Miller-Rushing, 2010), while the ecological research community is interested in the active period of entire plants and vegetation.

The seasonal activity of plant life has internal and external controls, and both are driven by environmental cues (Figure 2). The internal ones operate via autonomous clocks, activating genes, regulatory loops, and releasing hormones, often integrating chilling or photoperiod signals (Dunlap, 1999; Forrest & Miller-Rushing, 2010; Körner & Basler, 2010). The external controls (often addressed as 'forcing') act directly on the rate of development, meristem activity, tissue differentiation and metabolism. Internal settings are either facilitating or constraining external influences on plant activity. When internal controls impose dormancy irrespective of environmental conditions, the term *endodormancy* is used. On the other hand, the state when endodormancy is broken, but external conditions prevent developmental advances and growth (too cold or too dry conditions),

FIGURE 1 Examples for periods (in days, full scale 365 days) associated with the term 'growing season' (green) in a temperate deciduous forest and in an alpine grassland. Timelines for the forest are roughly based on Burke and Reynal (1994) in the case of leaf phenology and root growth, on Etzold et al. (2022) for stem radial growth and on Greco and Baldocchi (1996) for net CO_2 uptake, on Möhl et al. (2022) for leaf and root growth of alpine grassland, on Scholz et al., 2018 for net CO_2 uptake.
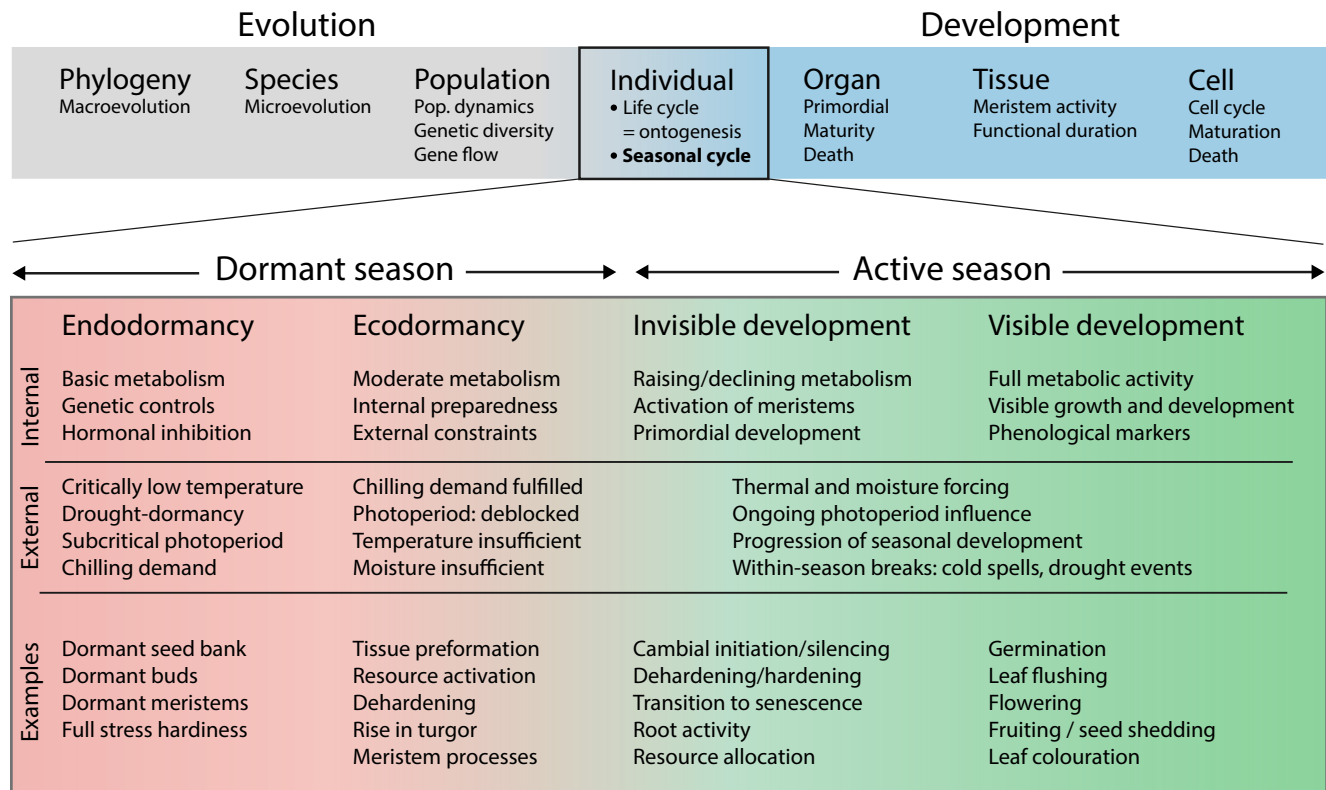
Evolution				Development		
Phylogeny Macroevolution	**Species** Microevolution	**Population** Pop. dynamics Genetic diversity Gene flow	**Individual** • Life cycle = ontogenesis • **Seasonal cycle**	**Organ** Primordial Maturity Death	**Tissue** Meristem activity Functional duration	**Cell** Cell cycle Maturation Death

← ——— Dormant season ——— → ← ——— Active season ——— →

	Endodormancy	Ecodormancy	Invisible development	Visible development
Internal	Basic metabolism Genetic controls Hormonal inhibition	Moderate metabolism Internal preparedness External constraints	Raising/declining metabolism Activation of meristems Primordial development	Full metabolic activity Visible growth and development Phenological markers
External	Critically low temperature Drought-dormancy Subcritical photoperiod Chilling demand	Chilling demand fulfilled Photoperiod: deblocked Temperature insufficient Moisture insufficient	Thermal and moisture forcing Ongoing photoperiod influence Progression of seasonal development Within-season breaks: cold spells, drought events	
Examples	Dormant seed bank Dormant buds Dormant meristems Full stress hardiness	Tissue preformation Resource activation Dehardening Rise in turgor Meristem processes	Cambial initiation/silencing Dehardening/hardening Transition to senescence Root activity Resource allocation	Germination Leaf flushing Flowering Fruiting / seed shedding Leaf colouration

FIGURE 2 A schematic representation of internal and environmental controls of seasonal activity in an individual plant. Note, invisible development refers to both, early spring and autumn.

is called *ecodormancy* (Lang et al., 1987). For an observer it remains hidden whether a plant is in endo- or ecodormancy. To predict phenological events, one needs to account for both, internal and external determinants of dormancy (e.g., Basler & Körner, 2012, 2014; Lundell et al., 2020). Because the drivers of endodormancy and ecodormancy, i.e., the chilling dose, photoperiod, and thermal forcing, interact non-linearly and species-specific, efforts for a general theory for modelling phenology failed so far (Basler, 2016). For instance, photoperiod restricts leaf flushing in response to exceptionally warm conditions too early in the season, while photoperiodic controls are weaker or absent later in spring. Past approaches to predict seasonal phenology of plants were mostly correlative, instead of aiming at truly mechanistic explanations. Recently, chilling-only effects on bud break had been quantified across six deciduous European tree species. Interestingly, chilling duration had a larger effect on dormancy release than absolute chilling temperature (Baumgarten et al., 2021).

THE ACTIVE SEASON BASED ON GROWTH OR DEVELOPMENT

In the literal sense, 'growing season' points to *plant growth*, referring to a period when plants exhibit an increase in volume or a net gain in biomass (dry matter), which introduces our first definition: *growing season sensu stricto*.

Development versus growth

It makes a fundamental difference whether growth is defined as a net gain in dry matter at the whole plant level (sensu productivity) or as any measurable volume or dry matter increment of certain plant organs by utilizing reserves, often addressed as stored growth. For instance, plants may produce flowers before leafing, or they may form new roots after above-ground senescence (Blume-Werry et al., 2016), involving metabolic activities of reserve mobilization and tissue formation without ongoing photo-assimilation. Hence, a dry matter allocation at a net loss of biomass should not be addressed as 'off-season' productivity.

Moreover, the dynamics of root and rhizome formation are rarely accounted for, but may represent a prominent part of a season defined by actual growth activity and of accumulated biomass (e.g., Warren et al., 2015; Figure 1). Due to high turnover and carbon (C) export, annual root production accounts for 33%–70% of terrestrial NPP (Jackson et al., 1996, 1997; Ma et al., 2021). Roots may grow and interact with soil microbes without concurrent visible shoot activity. Root growth is often termed 'root phenology', although it is a growth process

and may operate opportunistically depending on soil temperature. Root activity differs from shoot phenology, by commonly starting later but continuing longer in the season (Abramoff & Finzi, 2015; Liu et al., 2022; Steinaker et al., 2010). It is assumed that the asynchrony between above- and belowground growth activities is larger in forests than in grasslands (Sloan et al., 2016). Most studies are limited to fine root activity, and fine roots are more active than coarse roots (Körner, 1994). In forests, where fine root biomass constitutes a smaller fraction of total root biomass than in grasslands (McCormack et al., 2015), and where roots often extend below the sampling depth (Finér et al., 2011), the determination of the actual annual root production becomes challenging. While the study of belowground development and growth is highly laborious, a growing season definition based on above-ground parts only (as with remote-sensing) is likely to entail a serious bias, particularly when applied to C cycling and C budget calculations.

Although the term 'growing season' implies growth, much of the literature actually refers to the broader concept of plant development, the visible part of which is commonly addressed as *phenology*. Yet, growth and development are two different categories of plant responses that are often confused, and their hierarchic relationship is repeatedly ignored, namely that development controls growth.

In contrast to growth, *development* reflects the transitions across physiological states and has a life-long (ontogeny) and a seasonal (phenology) dimension (Figure 2). It includes the progression of the internal preparedness to grow and the advance of 'phenophases' of entire plants or organs, controlled by DNA and mediated by hormones, followed by activating and rebuilding specific meristematic tissues. For instance, a vegetative apical meristem that turns into a reproductive meristem in an otherwise 'quiet'-looking bud represents a key developmental transition (Guzicka et al., 2018). Accordingly, a large part of the seasonal development is invisible and remains unaccounted for by phenological observations. In general, we can observe such developmental shifts only to a very limited extent, and we simply assume that there must have been a state change (development) prior to observable activities (growth). For instance, plants may deharden from winter dormancy (an acclimative adjustment) or become photosynthetically active (in the case of evergreen plants) long before a visible developmental advance such as bud break (Fry & Phillips, 1977; Havranek & Tranquillini, 1995 for conifers; Lempereur et al., 2015 for evergreen oaks). Similarly, in autumn: plants complete tissue maturation, initiate leaf abscission layers and become freezing resistant without any change in leaf colour. The visible colour change often reflects the stochastic occurrence of a first frosty night and hence, leads to an overestimation of the significance attributed to colour change (Keskitalo et al., 2005; Körner & Basler, 2010; Tang et al., 2016), with key developmental

processes completed quite a while before. Delayed autumnal leaf colouration has often been assumed to add to seasonal productivity (e.g., Ma et al., 2022; Piao et al., 2008; Yang et al., 2017), while the signals obtained from either eddy-covariance flux towers or models using remote sensing data reflect ongoing CO_2 exchange by green foliage only (e.g., Keenan et al., 2014), such data cannot be used to infer annual (lasting) C sequestration, a rather popular inference.

Here, we propose to employ the term *phenological season* when referring to a timeframe based on phenological observations rather than growth. The contrast between invisible developmental states and processes (metabolism, hormones) on one side, and visible changes in appearance (phenology) on the other side, complicate definitions of the onset and end of a phenological season.

A growing season defined by phenological markers also depends on the type of indicator employed. For example, an NDVI-derived start and end of the season merely encompasses the number of 'green' days from leaf expansion to leaf browning, but that period is likely to be substantially different from the duration of cambial activity or root growth in the same ecosystem (Figure 1; examples for remote sensing of canopy or land surface greening, e.g., Choler, 2015; Chen et al., 2019; Tang et al., 2016). Such remotely sensed greening is matching with ground truth flushing in monospecific stands only. In mixed stands, the remote community-based signal reflects the abundance of species with different flushing patterns.

Potential versus realized plant development and growth

Plants devoted to growth by their internal developmental state will only grow and increase biomass when both cell turgor and tissue temperature jointly permit. This way, the number of days with a measurable size or volume increment may differ substantially from the number of days between the phenological onset of the season (bud break) and the end of the season (e.g., leaf shedding; Figure 1). Etzold et al. (2022) arrived at only 27–77 days of measurable radial increment of a total 89–117 days period between onset and end of radial increment of evergreen conifer and deciduous, broadleaved tree species (Table S1). Based on phenology only, the growing season lasted c. 250 days across the forest sites. For montane *Larix decidua*, Moser et al. (2010) arrived at 101–137 days of stem growth over a 150–180 days season by meteorological criteria. During days with no measurable radial growth, trees still assimilate CO_2, build reserves and mature tissues. It seems that the onset of xylogenesis is more strictly constrained, therefore better predictable, than the end of growth (Lupi et al., 2014). The cessation of xylogenesis often follows developmental controls to ensure timely maturation *before* it gets cold (Körner, 2012).

Thus, dendrometer and xylogenesis data underline the discrepancy between a growing season as defined by phenology or actual structural growth (Cuny et al., 2019). Furthermore, dendrometers revealed that tree growth was largely confined to night hours (when transpiration is at its minimum and turgor at its maximum; Zweifel et al., 2021), reducing the actual period of volume growth (expressed as net radial increment) to one quarter of the time measured in days. Similarly, dicot crops often stop growing when air humidity is low (potential transpiration high), and mainly grow at night or in early morning (Kronenberg et al., 2021; Nagelmüller et al., 2018), again related to cell turgor.

So, the actual hours or days with growth, measured at either the leaf or canopy level, differ substantially from a phenological season or period during which growth could (potentially) occur based on temperature and soil moisture only (e.g., Monson et al., 2002, Figure 1; Table S1). A pragmatic approach would best go by visible phenology markers that define the beginning and end of what is then believed to represent the 'growing' season, but such a season must not be confused with a period of continuous growth. In addition, even a favourable climate will not always induce the same responses in plants that either run their development-driven, autonomous program (internal clock; Möhl et al., 2022) or terminate vegetative growth activity during reproduction. In fact, most herbaceous plants stop growing when they switch to reproduction (Reekie, 1997) and trees show a trade-off between growth and reproduction (e.g., Hacket-Pain et al., 2018; Obeso, 2002).

THE PRODUCTIVE SEASON

Closely related to growth, productivity can be used as a surrogate for the 'active season' of entire ecosystems (forests, grass- and shrublands, arable crops). In this case, the *productive season* can be defined by the first and last passing across a minimum rate of biomass production or net carbon gain. Measures include repeated biomass harvests (ΔB), and net ecosystem exchange (NEE) or net ecosystem productivity (NEP) derived from eddy covariance (Box 1; for a recent example see Peichl et al. 2023).

BOX 1   The 'productive' season, an issue of definitions

The widely employed terms for plant biomass production or carbon gain are not synonymous, require a definition and imply different season lengths. In contrast to the term plant growth, the other four terms (ΔB, NEE, NEP and NPP) refer to processes per unit land area.

Net biomass increase (ΔB): The difference in dry matter of plant parts between two timepoints (both above- and belowground). For seasonal ΔB, the difference between the biomass at the onset of measurable (or visible) growth (in grassland frequently close to zero above ground) and the point when biomass stops increasing, often addressed as seasonal peak biomass. Thereafter, harvestable biomass either remains constant for a while or declines. Any biomass produced but lost between harvest dates is not included.

Net primary production (NPP): Historically, there have been divergent definitions for NPP. In the late 1970s, NPP was defined (based on earliest definitions by Boysen-Jensen, 1949) as the sum of all harvestable biomass produced between censuses *plus* all losses, that is, litter above and below ground, herbivory losses, exudation, investments to mycorrhizae, etc. (Fahey & Knapp, 2007; Sestak et al., 1971). More recently, NPP has been defined as the difference between gross primary production (GPP, representing canopy photosynthesis) and all autotrophic respiration (R_a). NPP is not really measurable and season boundaries are therefore hard to define by NPP.

Net ecosystem exchange (NEE): Is the net exchange of CO_2 of an ecosystem with the atmosphere, measured by the eddy covariance technique (Chapin et al., 2006; Schulze et al., 2019).

Net ecosystem production (NEP): The balance between an ecosystem's photosynthetic C-uptake and ecosystem respiration. NEP approximates NEE under most conditions, but the two measures differ, for instance, when dissolved, respiratory-derived inorganic carbon (part of NEP) is leached to groundwater. NEP and NEE have opposite signs (Chapin et al., 2006; Schulze et al., 2019).

The start and end of the 'productive season' can be defined as the period between the first and last passing of NEE or NEP through zero. This is the period with a net C gain at the ecosystem level. While NEE or NEP might still indicate a net C loss of the ecosystem early in the season, there may actually be a biomass or C gain by initial growth, not yet balancing heterotrophic respiration.

By these definitions, ΔB covers the shortest 'growing' season, followed by NEE/NEP, and the longest season by NPP, which comes closer to the 'green season' as defined by phenology markers (Figure 1).

NDVI-derived production indices have also become widespread and used as proxies for gross primary production (GPP), although NDVI is rather a surrogate for phenology (leaf greening) than productivity. Solar-induced fluorescence sensors (fluorescence of chlorophyll a) arrive at much better approximations of GPP (Shekar et al., 2022; Verma et al., 2014). NEP represents a conservative measure of the productive period, because biomass production (C fixation in plant structures) has to exceed the rate of auto- and heterotrophic respiration of the ecosystem before the net uptake becomes positive, cutting the length of the so-defined growing season substantially (by 21–26 days for spring-greening only; Balzarolo et al., 2016). Despite a vast literature in this field (e.g., references in Baldocchi, 2020), a NEP-based definition of season has not been deployed frequently. On the other hand, harvest-based definitions for productive seasons are error-prone due to imprecise estimates for the various losses (Box 1). Both, eddy covariance and harvest methods often select for ideal, homogenous vegetation stands and thus, yield maximum values rather than values representative for the heterogeneous vegetation across larger scales.

A METEOROLOGICAL DEFINITION OF SEASON

Because visible phenology markers and growth indices do not necessarily reflect actual shifts in developmental state and activity, meteorological thresholds are increasingly used for defining the growing season. Such a *meteorological season* rests on an assumed relatedness of plant activities to long-term climate and weather conditions across taxa and represents a practical convention rather than leaning on a plant-based mechanism.

There are two major environmental drivers that control the seasonal development and growth in plants globally: soil moisture availability and temperature.

The first affects larger fractions of land area than the latter and the two drivers obviously interact. However, unlike air temperature, water storage in soils is commonly not reported by weather services and is periodically decoupled from precipitation, depending on water storage capacity of the rooted soil profile. For plants to develop and grow, both drivers must pass critical thresholds (permanent wilting point, minimum temperature) that call for definitions. Thresholds may refer to gradual changes (e.g., spring warming) or to extreme events (e.g., frost risk). Favourable weather conditions at the 'wrong time', such as a warm spell in winter or a rain event during the dry season, must not cause plants to break dormancy. This exerts selective pressure for an evolutionary 'memory' of the *probability of returns* of fatal incidences. Becoming active too early bears a risk of failure, while a 'safe' late development may reduce competitiveness. Similarly, it would be disadvantageous

for plants if late season drought or freezing periods set in before reproduction and tissue hardening has been completed. So, there is a trade-off between risk mitigation and competitive success. For long-living plants, such as trees, it is a trade-off between vigour (and/or the advance of phenology) and stress tolerance (Körner et al., 2016; Loehle, 1998; Norby et al., 2003; Savage & Cavender-Bares, 2013). Additionally, there is a strong evolutionary selection for a common phenology among all individuals of a population in order to facilitate gene-flow by synchronized flowering.

Thus, *regular seasonality* promotes developmental adaptations that cause a periodic discrepancy between environmental conditions and plant activity, which may be precautionarily prevented because the time is not right. This leads to a disparity between (1) the potential climatic possibility to develop and grow and (2) the realized development and growth activity. In contrast, under *irregular seasonality*, the window of opportunity for plant life emerges randomly. Irregular seasonality induces full opportunism as employed by many terrestrial algae, mosses, lichens, ferns, resurrection plants, and by annual plant species, which compensate their risk of failure associated with tracking any short-term suitability of weather by either high stress tolerance (cryptogams) or high reproductive output and viable seedbanks (r-strategists; Figure 2).

Just as favourable periods at the wrong time escape any predictive tool for 'growing season', adverse conditions during the assumed favourable period, extreme events in particular, cannot be covered either. For instance, late freezing events and summer drought extremes introduce stochasticity that can stop or slow growth, phenology, and productivity, but a long-term probability of such events is hard to define and goes beyond of what a season concept can handle, particularly, one that rests on meteorological means. Inevitably, a meteorological season is a potential season.

A meteorological season needs a defined start and end, referring to an ecologically relevant threshold. Whether something is a threshold or not depends on both, temporal resolution and accuracy. All processes potentially relevant for development and growth of plants commence gradually as abiotic constraints are relieved. Thus, it matters whether critical abiotic conditions are defined per hour, per day or per week. The most popular thresholds are daily means. This may work with buffered soil moisture but not for the immediate action of air temperature. Means of temperature mask a wide range of temperatures that exceed or undercut a threshold and thus, bear little physiological meaning. This problem may be solved by using degree hours (°h) or degree days (°d), that is, the sum of hourly temperatures over a day or a defined longer period (Russelle et al., 1984) that requires the definition of a lower threshold (e.g., 0°C or 5°C). Whichever threshold-value is employed, the metric must account for an active plant's physiological

response time, which is commonly less than 1 h. It also matters when, in the course of a year, one starts to accumulate heat sums, an issue related to the transition between endo- and ecodormancy (see the dormancy section). Moreover, these thresholds may differ among species and plant ages (Wang, 1960). Including periods of endodormancy weakens the meaning of temperature sums. Of all possible metrics of environmental drivers, *mean annual temperature (MAT), although most popular, is the least suitable*. The longer the period of averaging, the more potentially relevant variation becomes buried (Körner & Hiltbrunner, 2018; Michaletz et al., 2017). To assess temperature effects on meristematic growth, temperature should be monitored as close as possible to the specific meristem (accuracy) and in the appropriate temporal resolution. Air temperatures taken or extrapolated from data archives often do not meet these criteria.

Low moisture thresholds of seasonal plant activity

In terms of soil moisture, a critical minimum of water is required along the rooted profile. Given that soils may store 200–400 mm of plant-available water in a rooted profile of one meter, depending on soil texture and stone content, wetting the top 5 cm by 10–20 mm of rainfall after several month of drought is insufficient to 'launch' a season (e.g., He et al., 2021). This amount of water will evaporate within 3–5 days in dry regions. Whenever the rooted soil space approaches the permanent wilting point, often around 10–15 vol-% soil water content, drastic turgor losses will restrict root and shoot growth. It is obvious that the timing (intervals) and amount per incident (Knapp et al., 2002, 2008) are important and complicate threshold definitions. The critical level of seasonal soil moisture either needs to be measured (soil matrix potential) or modelled. Models use daily precipitation and potential evapotranspiration in combination with plant available soil moisture storage capacity (e.g., Churkina et al., 1999), and by solving the water balance equation, a moisture driven season can be defined ('bucket model': Paulsen & Körner, 2014; SVAT model: Meusburger et al., 2022). A novel satellite-based approach is using estimates of actual evapotranspiration (ET) from a combination of surface temperature and net radiation (in essence by solving the Bowen-ratio equation for latent heat flux) and infer the size of the remaining water stores from time series of precipitation and ET (Stocker et al., 2023).

In recent years, it became obvious that cell turgor is a key driver of meristematic activity even under non-drought conditions (Körner, 2015; Muller et al., 2011; Peters et al., 2021; Tardieu, 2013). But its accurate assessment still represents a major challenge in non-woody plants. In trees, the turgor sensitivity of cell production is so high that radial increment halts during the day, even

in moist soil conditions, because 'normal' transpiration causes turgor to fall below the critical threshold (Zweifel et al., 2021). When soil moisture drops, meristematic activity is the first process to become inhibited, causing ongoing photosynthesis to produce carbohydrates in excess of demand (Körner, 2003b; Prescott et al., 2020; Würth et al., 2005). Dry phases will slow or interrupt growth (at least above-ground), whilst they do not fully stop gas exchange. Hence, the period of net CO_2 uptake is substantially longer than the period for structural growth in a moisture-driven season (Figure 1). A growing season defined by water availability may also become fragmented, or bimodal as is the case in a Mediterranean climate (e.g., Sarris et al., 2013; Valeriano et al., 2023), with the number of growing days (obtained by dendrometers) representing an adequate measure. For non-woody taxa, such continuous measurements with high temporal resolution are rare, especially under drought. Data obtained by automatic imaging tools in crops revealed diurnal patterns as well, with dynamics differing between monocot and dicot crops (Kronenberg et al., 2021; Nagelmüller et al., 2018; Yates et al., 2019). Under field conditions, it remains mostly unknown if and when plants have access to soil moisture deep in the rooted profile (e.g., Maysonnave et al., 2022). Therefore, it is difficult to delineate the local, moisture-driven seasonal plant activity by meteorological thresholds.

Low temperature thresholds of plant activity

Farmers and agronomists have already found in the 19th century that daily mean air temperatures around 6°C represent an adequate starting point for the growth of crops (Harrington, 1894; Rubinstein, 1924), while the end of the season remained undefined due to intentional harvests. Opportunistic plants such as winter crops can utilize each individual hour above a threshold at any time in winter, hence, there is no clearly defined start of season. Relative growth rates increased linearly with the daily number of hours above 0°C or 5°C in winter rape during winter (Körner, 2008; Nagelmüller et al., 2018).

For trees, the 'sustained' passing of a 5°C daily mean is often considered critical for the beginning of the season (in practice: 3–10 of such days in a row, mostly 5 days; Gao et al., 2022; Linderholm et al., 2008). Daily means >5°C are also considered effective for measurable tree growth within the season (Bootsma, 1994; Müller, 1981; Schiestl-Aalto et al., 2013; Sutinen et al., 2012). A range between 5.6 and 8.5°C was reported for minimum cambial activity (xylogenesis) by Rossi et al. (2007). Such temperature thresholds are an issue of resolution and cut-off conventions for growth data, given the asymptotic nature of the related cellular responses (Körner, 2003b, 2021a; Figure 3). For the end of the season in temperate and boreal forests, the first days with daily means <5°C, for instance
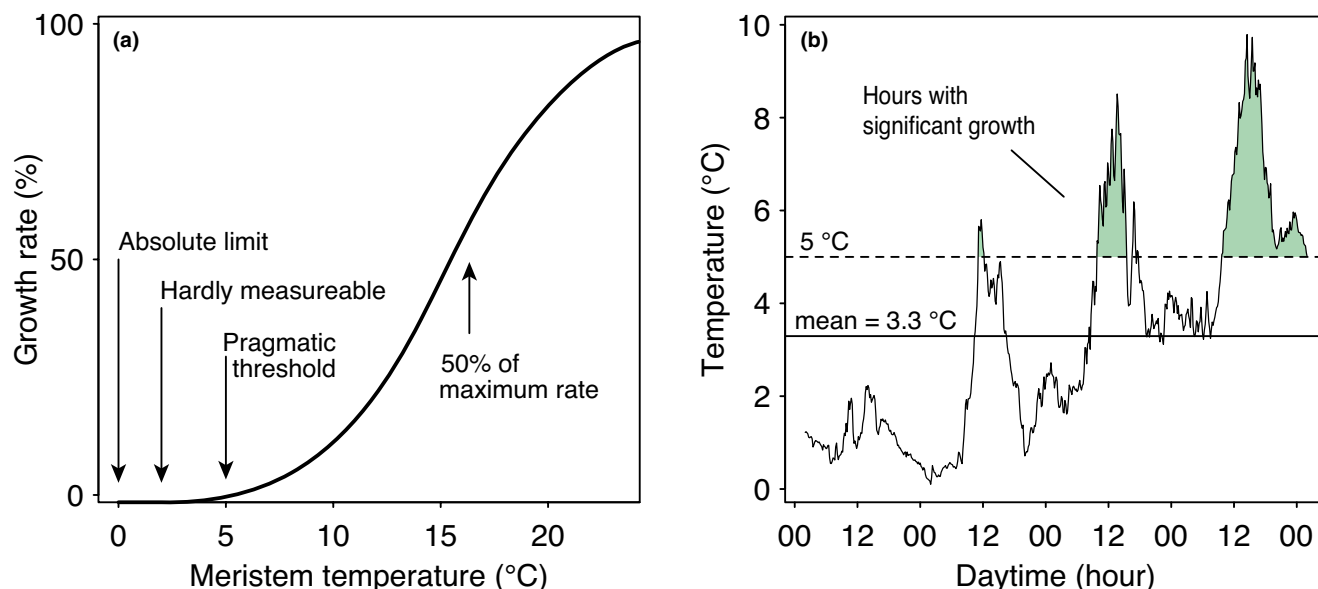
FIGURE 3 (a) Asymptotic responses challenge definitions of thresholds. Arrows illustrate different cut-off points (=thresholds), depending on the resolution and accuracy of growth and temperature measurements. (b) Means (in this case 3.3°C for the four dummy days shown) do not meet the nature of the biological temperature responses, given that temperatures below 5°C hardly contribute to growth and those above (green zone) do.

expressed as a 10-day running mean, had been regarded as a good proxy (Linderholm et al., 2008). As an example for rather cool adapted species, the position of the upper climatic treeline correlated best with on-site data when the growing season was defined by the first and last week with a weekly mean air temperature of 0°C; such a mean encompasses numerous warm hours that suffice to induce cambial activity (Körner & Paulsen, 2004; Paulsen & Körner, 2014). A correlation between air temperature and growth is meaningful in the case of trees, because trees are aerodynamically coupled to air circulation and hence, tree temperature corresponds to air temperature.

The definition of the meteorological growing season of small stature plants in alpine and arctic environments is much more demanding, because their body temperature does not reflect air temperature but is the net outcome of solar heat flux, the aerodynamic boundary layer resistance (canopy height and density), topography (exposure to the sun, wind shelter), and the presence or absence of snow at high latitude or high elevation (Körner & Hiltbrunner, 2018; Scherrer & Körner, 2009, 2011). Whenever seasonal snow cover comes into play, snowmelt is the decisive starting point (Vitasse et al., 2017; Vorkauf, Marty, et al., 2021), with buds and meristems of plants warming within hours after snowmelt to >10°C, and under bright sun to >20°C (Körner, 2021a) – temperatures not captured by weather stations. There is also no meteorological way to define the end of the season because the arrival of snow or frosty weather is unpredictable, with autonomous (in deciduous woody species, commonly photoperiod controlled) completion of above-ground plant senescence defining the end

(Möhl et al., 2022). In such cases, meteorology-based end-of-season definitions best use a fixed date for which it is known that above-ground seasonal activity largely ceased (for instance: 1st or 15th September in the alpine belt of the N-hemisphere temperate zone; Körner et al., 2022).

At the so far known coldest place on earth where a flowering plant has been found, the season is best described by the number of days during which plant temperature exceeds 0°C for at least 1 h, meaning there is no snow cover and plants are hit by direct solar radiation. From the available data it seems that at least 60 days with >1 hour above 0°C are required to make a living for extremely cold adapted flowering plants (at a mean of 2.6°C for such a season; Körner, 2011). Low growth-limiting temperatures do not substantially inhibit the rate of photosynthesis or mitochondrial respiration. In fact, photosynthesis may reach 30% of its full capacity at 0°C, and it is well known that evergreen conifer needles have a positive rate of CO_2 uptake for most of winter (Havranek & Tranquillini, 1995), unless the extracellular space is filled with ice and constrains gas diffusion (−5 to −6°C; Körner, 2003b, 2021a). This is one of the reasons why evergreen conifers are packed with photoassimilates (mainly starch and simple sugars) by the time of bud break, which is at the start of the phenological season (Hoch et al., 2002). Hence, temperatures that permit a positive rate of net photosynthesis are an unsuitable criterion for 'growing season' (Figure 1). Despite the limitations discussed above, a long-term meteorological season still has substantial potential to define windows of opportunity for growth and biomass production at a global scale.

THE WINDOW OF OPPORTUNITY: TIME MATTERS

'Window of opportunity' (WOP) is a phrase that became primarily known in economy. Here, it sets the environment-based timeframe for a 'potential growing season', similar to the meteorological season but based on long-term climate. For vegetation types in steady state conditions, it turned out that the WOP in terms of suitable months for biomass production explains almost exhaustively the global pattern of NPP across latitudes (Boxes 1 and 2), assessed by harvesting data (Saugier et al., 2001). For temperate deciduous forests within a 6-month meteorological growing season, annual NPP was estimated to be half that of humid tropical forests within a 12-month meteorological growing season. Hence, the two are equal per month of growing season and the same holds for boreal forests, once the shorter growing season is accounted for, and irrespective of the daylength differences (Körner, 2002, 2013; Huston & Wolverton, 2009; Table S1). These ground-truth data suggest that 'time for growth' (=WOP) is the overarching driver of NPP of major global biomes (Box 2).

In this context, the majority of gas exchange-driven models for global biomass production put 'the cart before the horse' (but see Fatichi et al., 2014), because gas exchange follows the demand of meristems set by moisture and thermal thresholds and by the local nutrient availability as a rate modulating factor (Körner, 2015,

2022). By applying simple WOP thresholds for forests (T_{min}, minimum season length, soil moisture), the global pattern of forest versus non-forest vegetation could be predicted surprisingly well (Paulsen & Körner, 2014), and yielded a potential global forest area of 88 Mio km^2, whereas additional 33 Mio km^2 were too dry for forest trees, although temperature alone did not preclude the presence of trees. In contrast to the application of such climatological WOP criteria to global patterns of NPP, models of climate change effects often use satellite based NDVI signals to define the 'productive season ', where a longer 'green' season with more CO_2 uptake is unwarrantedly assumed to represent a higher NPP (Kang et al., 2016; Liu et al., 2021; Park et al., 2016). The assumed gain in NPP is further confused with a gain in C stocking, in the sense of carbon sequestration, one of the most widespread misconceptions in the global change literature that also rests on the misperception of different season concepts. A phenology-delineated season length does not correspond to a season length defined by net ecosystem carbon uptake (Richardson et al., 2010).

A RECOMMENDED SET OF DEFINITIONS

Each of the various aspects of seasonality discussed here has its justification and accounts for different facets of plant activity. We recommend to explicitly specify which

---

BOX 2 The window of opportunity (WOP) hypothesis

We hypothesize that the length of the WOP (meteorological season, long-term climate) predicts the NPP of late-successional natural vegetation types globally, irrespective of the conditions during that period (Körner, 2002, 2013). This means that the within-season climatic differences from, for instance, boreal to tropical forests are compensated by physiological adjustments to the prevailing temperatures, except for marginal life conditions (e.g., the climatic treeline).

This WOP hypothesis needs to be tested in a global GIS-based approach, which requires accurate global data on the WOP and related ground-truth NPP. Several challenges are to be expected, owing to the following three reasons:

(1) Remote sensing data infer NPP for currently realized rather than potential land cover, i.e., regardless of land transformations by land uses, fire, etc. Gridded data for NDVI (e.g., by MODIS satellite) are including all land cover types. Filtering for undisturbed natural (= potential) vegetation will be required, because a WOP can obviously not predict land use effects.

(2) The translation of NDVI-type signals ('green periods') into modelled (potential) NPP rests on assumptions about effective season length that become circular when one aims at explaining NPP by a meteorological season length such as WOP.

(3) Definitions of the start and end of the WOP require suitable proxies, which may differ between ecosystems (air-temperature for trees; snow cover duration, meristem temperature for alpine plants). Predictions for trees appear most promising for their aerodynamic coupling to air temperature.

Global net ecosystem productivity (NEP) inferred from eddy covariance data does not disclose NPP (see Box 1), but allows a sharp delineation of a season, corresponding to the period of net carbon uptake. A NEE or NEP season will be much shorter than a WOP (Box 1).

FIGURE 4 A visualization of the four definitions of the 'growing season'. Note, the first two are individual plant based, the third is community or across species based, and the fourth refers to entire ecosystems. NPP for net primary production, based on repeated harvests, NEP net ecosystem productivity, expressed as net carbon gain. All images by C. Körner, except for the eddy tower (provided by UBC Micrometeorology Lab, Vancouver, CA).

of the four suggested categories of 'growing season' is being applied (Figure 4): (1) A season defined as the period during which any part of a plant grows, irrespective of whether this yields a net biomass increment at the whole plant level or whether growth occurs above- or belowground. One may address this as the true 'growing season' (*sensu stricto*) and it may cover almost a full year, even in a temperate climate. (2) A growing season associated with the period defined by the beginning and end taken from visible phenological events (e.g., bud break and autumnal leaf coloration). This type of 'phenological growing season' does not account for actual growth, biomass production and belowground processes and it suffers from the rather flawed meaning of autumnal phenology markers. Additionally, visible pheno-stages do not necessarily match the plant-internal progression in development. (3) A season defined as the period during which entire plants or plant communities exhibit a net biomass or net carbon gain, the 'productive season'. This type of season relies on direct measurements and cannot be deduced from the other definitions in Box 1. (4) A growing season defined as the period during which

environmental conditions could theoretically permit growth, thus representing a 'meteorological growing season' or 'window of opportunity'. This type of season rests on empirical data as well, and commonly refers to thresholds of measurable above-ground growth, but averaged across different taxa and vegetation types.

All four types of growing season do not incorporate metabolic activity during the non-growing season. For instance, significant photosynthetic assimilation in evergreen plants or respiratory activity and export of photo-assimilates to microbial symbionts (e.g., Druebert et al., 2009) are activities that also occur outside the growing season. Additionally, any physiological adjustments to drought or to freezing temperatures, and developmental advances within apical meristems are not considered to belong to the growing season in any of these four types. Type 1–3 seasons need a delineation by plant or vegetation data. The type 4 season, in part, requires environmental data that are not commonly available (Box 2). Modelling the C balance to determine the early and late crossing of zero (beginning and end of season) has been shown to be challenging (De Kauwe

et al., 2017), given our current understanding of the ecosystem C cycle.

THE GROWING SEASON IN A CLIMATE CHANGE CONTEXT

The previous sections made it obvious that there is not one overarching best definition of the 'growing season'. All four definitions of the growing season are valid, and the disparity among them holds valuable information, especially in the context of climate change: while spring and autumn warming leads to an extension of the meteorological season in temperature-driven, extratropical regions, its effects on plant growth and development are often ambiguous (Liu et al., 2018). Evolutionarily selected safety measures to prevent frost or drought damage through responses to short-term favourable conditions at the 'wrong time', cause late successional plant communities to lag behind the prolonging of the WOP (Box 2). The best example is the species-specific interference of photoperiod or chilling requirements with spring forcing by temperature, explaining the current slowing of phenological responses to ongoing climatic warming (for trees: Baumgarten et al., 2021; Wang et al., 2020; Zohner et al., 2020; flowering in alpine plants: Vorkauf et al., 2021). Photoperiod constraints are increasingly prohibitive for phenological advances, the earlier in the year warm temperatures occur (at the 'wrong time'). For forests, a change in local chilling conditions can lead to a similar departure from a temperature-only driven spring phenology. For that reason, Vitasse et al. (2017) found reduced elevation differences in tree flushing: from 34 to 22 days per 1000 m in elevation in the Swiss Alps between 1960 and 2016. Photoperiod commonly governs the initial steps (not the foliar colour change) towards late season senescence and hardening in trees, thus, preventing a simple tracking of climate warming effects (Jiang et al., 2022; Körner & Basler, 2010; Tang et al., 2016).

Several studies tested whether advanced phenology translates to growth responses, and they often do not, at least above the ground (e.g., tree ring width; Camarero et al., 2022; Dow et al., 2022; Rossi et al., 2013). Neither do responses of forest ecosystem productivity match stem growth of individual spruce trees (Krejza et al., 2022). For 108 forests across eastern North America, dendrometers indicated an earlier start of the season in warmer springs (beginning of tree ring formation), but no effect on annual increment (Dow et al., 2022). A study across 1773 sites in central Europe found that the 'green season' (a phenological season) lags significantly behind the prolonging of the thermal season (T-threshold of 5 °C; Fu et al., 2022). Yet, in the Harvard forest, a longer and warmer meteorological season (1992–2015) revealed a significant increase of NEP (based on eddy covariance data) in this relatively young forest, explained by enhanced growth above, but not below the ground (Finzi et al., 2020).

While the meteorology-based WOP is a reasonable proxy for the window of potential biomass production of upright (tall) life forms that are aerodynamically coupled to the surrounding air, it is less suitable for predicting the time for potential growth of small-stature plants such as alpine and arctic vegetation. Earlier snowmelt and sunny weather can cause within-canopy temperature far above the air-temperature-based season start, and some opportunistic species may track these warm early season conditions, whereas others are constrained by their 'evolutionary memory' and wait (Körner, 2021a). A high diversity of species and microhabitats within short distances can lead to large differences in season lengths related to growth and development at otherwise similar air temperatures (Körner & Hiltbrunner, 2021; Oldfather & Ackerly, 2019). Moreover, some plant species run a fixed internal program once growth was initiated in spring, as was observed in alpine sedge-dominated grassland (Möhl et al., 2022) and snowbeds (Baptist et al., 2010), while others are capable to extend growth (also in snowbeds: Carbognani et al., 2014). Thus, phenology indices and species-specific growth patterns must be related to relevant temperature measures (such as topsoil meristem temperature in the appropriate resolution) for predicting future vegetation responses to climate change.

Compared to aboveground phenology and growth, belowground processes are currently heavily understudied (e.g., Scartazza et al., 2023). From the little we know, asynchronies are likely. In a meta-analysis, Liu et al. (2022) observed for 43 herbaceous species across biomes an advanced start as well as an earlier end of the phenological aboveground growing season, but unchanged belowground phenophases. On the other hand, climate warming extended the belowground growing season for 38 woody species, but did not affect the aboveground phenology, according to these authors. Steinaker and Wilson (2008) showed that aspen forests significantly delayed root growth in relation to the onset of canopy greening, while adjacent grassland hardly did. Evidently, the seasonal responses of phenology and growth to climate change differ above and below the ground depending on plant functional type.

In summary, a warmer and longer meteorological growing season in the course of climate change does not necessarily translate into more growth or higher NPP in late successional vegetation, even when shifts in phenology do occur. This challenges the often-assumed proportionality between a lengthening of the meteorological season and plant growth or productivity (Hu et al., 2010; Rammig et al., 2010). The reasons for these discrepancies await testing and explanation, including the effect of altered seasonality on stress

mitigation and biotic interactions. The conservative responses to climatic warming of well adapted, late successional plant communities (forests, alpine grassland) are likely to cause a mismatch between the timing of nutrient demand (for growth), and the microbial provision of nutrients, a disparity that carries a risk of nutrient losses as well as further feedbacks on the soil microbiome.

CONCLUSIONS

Out of the many possibilities to describe what is commonly assumed to represent a 'growing season', we propose four major types that rest on either (1) actual growth, (2) phenological markers, (3) a period with a net ecosystem biomass production or net carbon gain, and (4) a meteorological season that delineates both, a short-term period of potential plant activity, and a longer-term climatological frame, defined as window of opportunity (WOP) for plant activity (potential for growth, development). We recall the importance of differentiating between development and growth, the former implying an advance in readiness for growth and senescence, and the latter addressing the formation of new plant tissue. The key message of this perspective is that the four definitions are not interchangeable, hence, assessing or modelling one, does not imply any of the three others. Most importantly, a season defined by phenomarkers must not be considered synonymous with a period of growth or NPP. Growth, although commonly implied by referring to 'growing season', does not always incur a net biomass gain, but can in fact cause a net biomass loss when non-photosynthetically active organs are growing (roots, flowers) while green leaves are absent. The length of the different types of growing season, measured in number of days, may differ considerably (Figure 1; Table S1). All four types of growing season can potentially respond to climate change, but they are not representing surrogates for each other.

Over the past decades, phenology turned out to be the dominant form of defining the 'growing season', and also became mainstream in the climate change research community, including meteorological services, remote sensing (continental 'greening') and citizen science programs (e.g., Cleland et al., 2007; Piao et al., 2019; Puchałka et al., 2022; Tang et al., 2016). In this perspective, we aimed at explaining that this phenology-based approach at defining the growing season covers one specific aspect only, namely the one related to visible markers of seasonal above-ground plant development. We find it inappropriate to assume that this type of growing season is a surrogate for the actual period during which plants grow or a net biomass accumulation does occur. While we hypothesize that in the longer-term and in a global comparison of biomes, the key driver of annual NPP is a meteorology and climate driven window of opportunity (Box 2), a suite of evolutionary constraints prevents

NPP from tracking rapid changes of actual climatic conditions.

ORCID
Christian Körner https://orcid.org/0000-0001-7768-7638
Patrick Möhl https://orcid.org/0000-0002-5058-8135
Erika Hiltbrunner https://orcid.org/0000-0002-0704-0780

REFERENCES
Abramoff, R.Z. & Finzi, A.C. (2015) Are above- and below-ground phenology in sync? *The New Phytologist*, 205, 1054–1061.

Baldocchi, D.D. (2020) How eddy covariance flux measurements have contributed to our understanding of global change biology. *Global Change Biology*, 26, 242–260.

Balzarolo, M., Vicca, S., Nguy-Robertson, A.L., Bonal, D., Elbers, J.A., Fu, Y.H. et al. (2016) Matching the phenology of net ecosystem exchange and vegetation indices estimated with MODIS and FLUXNET in-situ observations. *Remote Sensing of Environment*, 174, 290–300.

Baptist, F., Flahaut, C., Streb, P. & Choler, P. (2010) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biology*, 12, 755–764.

Basler, D. (2016) Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across Central Europe. *Agricultural and Forest Meteorology*, 217, 10–21.

Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, 165, 73–81.

Basler, D. & Körner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology*, 34, 377–388.

Baumgarten, F., Zohner, C.M., Gessler, A. & Vitasse, Y. (2021) Chilled to be forced: the best dose to wake up buds from winter dormancy. *The New Phytologist*, 230, 1366–1377.

Blume-Werry, G., Wilson, S.D., Kreyling, J. & Milbau, A. (2016) The hidden season: growing season is 50% longer below than above

ground along an arctic elevation gradient. *The New Phytologist*, 209, 978–986.

Bootsma, A. (1994) Long-term (100 yr) climate trends for agriculture at selected locations in Canada. *Climate Change*, 26, 65–88.

Boysen-Jensen, P. (1949) The production of matter in agricultural plants and its limitations. *Biol Meddeleser*, 21(2).

Burke, M.K. & Reynal, D.J. (1994) Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil*, 162, 135–146.

Camarero, J.J., Campelo, F., Colangelo, M., Valeriano, C., Knorred, A., Solef, G. et al. (2022) Decoupled leaf-wood phenology in two pine species from contrasting climates: longer growing seasons do not mean more radial growth. *Agricultural and Forest Meteorology*, 327, 109223.

Carbognani, M., Tomaselli, M. & Petraglia, A. (2014) Current vegetation changes in an alpine late snowbed community in the South-Eastern Alps (N-Italy). *Alpine Botany*, 124, 105–113.

Chapin, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M. et al. (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, 9, 1041–1050.

Chen, C., Park, T., Wang, X., Piao, S., Xu, B. & Chaturvedi, R.K. (2019) China and India lead in greening of the world through land-use management. *Nature Sustainability*, 2, 122–129.

Choler, P. (2015) Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. *Biogeoscience*, 12, 3885–3897.

Churkina, G., Running, S.W. & Schloss, A.L. (1999) Comparing global models of terrestrial net primary productivity (NPP): the importance of water availability. *Global Change Biology*, 5, 46–55.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, 22, 357–365.

Cuny, H.E., Fonti, P., Rathgeber, C.B.K., von Arx, G., Peters, R.L. & Frank, D.C. (2019) Couplings in cell differentiation kinetics mitigate air temperature influence on conifer wood anatomy. *Plant, Cell & Environment*, 42, 1222–1232.

De Candolle, A. (1855) *Géographie botanique raisonnée ou exposition des faits principaux et des lois concernant la distribution géographique des plantes de l'époque actuelle*. Paris: Imprimerie Martinet.

De Kauwe, M.G., Medlyn, B.E., Walker, A.P., Zaehle, S., Asao, S., Guenet, B. et al. (2017) Challenging terrestrial biosphere models with data from the long-term multifactor prairie heating and CO_2 enrichment experiment. *Global Change Biology*, 23, 3623–3645.

Dow, C., Kim, A.Y., D'Orangeville, L., Gonzalez-Akre, E.B., Helcoski, R., Herrmann, V. et al. (2022) Warm springs alter timing but not total growth of temperate deciduous trees. *Nature*, 608, 552–557.

Druebert, C., Lang, C., Valtanen, K. & Polle, A. (2009) Beech carbon productivity as driver of ectomycorrhizal abundance and diversity. *Plant, Cell & Environment*, 32, 992–1003.

Dunlap, J.C. (1999) Molecular bases for circadian clocks. *Cell*, 96, 271–290.

Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W. et al. (2022) Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439. Available from: https://doi.org/10.1111/ele.13933

Fahey, T.J. & Knapp, A.K. (2007) *Principles and standards for measuring primary production*. Oxford: Oxford University Press.

Fatichi, S., Leuzinger, S. & Körner, C. (2014) Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *The New Phytologist*, 201, 1086–1095.

Finér, L., Ohashi, M., Noguchi, K. & Hirano, Y. (2011) Factors causing variation in fine root biomass in forest ecosystems. *Forest Ecology and Management*, 261, 265–277.

Finzi, A.C., Giasson, M.-A., Barker-Plotkin, A.A., Aber, J.D., Boose, E.R., Davidson, E.A. et al. (2020) Carbon budget of the Harvard Forest long-term ecological research site: pattern, process, and response to global change. *Ecological Monographs*, 90, e01423.

Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3101–3112.

Fry, D.J. & Phillips, I.D.J. (1977) Photosynthesis of conifers in relation to annual growth cycles and dry matter production. II. Seasonal photosynthetic capacity and mesophyll ultrastructure in *Abies grandis, Picea sitchensis, Tsuga heterophylla* and *Larix leptolepis* growing in SW England. *Physiologia Plantarum*, 40, 300–306.

Fu, Y.H., Geng, X., Chen, S., Wu, H., Hao, F., Zhang, X. et al. (2022) Global warming is increasing the discrepancy between green (actual) and thermal (potential) seasons of temperate trees. *Global Change Biology*, 29, 1377–1389.

Gao, S., Liang, E., Liu, R., Babst, F., Camarero, J.J., Fu, Y.H. et al. (2022) An earlier start of the thermal growing season enhances tree growth in cold humid areas but not in dry areas. *Nat Ecol Evol*, 6, 397–404.

Girardin, C.A.J., Malhi, Y., Doughty, C.E., Metcalfe, D.B., Meir, P., del Aguila-Pasquel, J. et al. (2016) Seasonal trends of Amazonian rainforest phenology, net primary productivity, and carbon allocation. *Global Biogeochem Cycles*, 30, 700–715.

Greco, S. & Baldocchi, D.D. (1996) Seasonal variations of CO_2 and water vapour exchange rates over a temperate deciduous forest. *Global Change Biology*, 23, 183–197.

Guzicka, M., Pawłowski, T.A., Staszak, A., Rożkowski, R. & Chmura, D.J. (2018) Molecular and structural changes in vegetative buds of Norway spruce during dormancy in natural weather conditions. *Tree Physiology*, 38, 721–773.

Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M. et al. (2018) Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecology Letters*, 21, 1833–1844.

Harrington, M.W. (1894) The advent of spring. *Harper's New Monthly Magazine*, 523, 874–879.

Havranek, W.M. & Tranquillini, W. (1995) Physiological processes during winter dormancy and their ecological significance. In: Smith, W.K. & Hinckley, T.M. (Eds.) *Ecophysiology of coniferous forests*. San Diego p: Academic Press, pp. 95–124.

He, X.F., Wang, S.W., Sun, H., Körner, C. & Yang, Y. (2021) Water relations of "trailing-edge" evergreen oaks in the semi-arid upper Yangtze region, SE Himalaya. *Journal of Systematics and Evolution*, 59, 1256–1265.

Hoch, G., Popp, M. & Körner, C. (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggest sink limitation of growth at the swiss treeline. *Oikos*, 98, 361–374.

Hu, J., Moore, D.J.P., Burns, S.P. & Monson, R.K. (2010) Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biology*, 16, 771–783.

Huston, M.A. & Wolverton, S. (2009) The global distribution of net primary production: resolving the paradox. *Ecological Monographs*, 79, 343–377.

Ilondea, B.A., Beekman, H., Acker, J.V., Van der Bulke, J., Fayolle, A., Couralet, C. et al. (2021) Variation in onset of leaf unfolding and wood formation in a central African tropical tree species. *Front Forest Glob Change*, 4, 673575.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.-D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411.

Jackson, R.B., Mooney, H.A. & Schulze, E.-D. (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proc Nat Acad Sci*, 94, 7362–7366.

Jiang, N., Shen, M., Ciais, P., Campioli, M., Peñuelas, J., Körner, C. et al. (2022) Warming does not delay the start of autumnal leaf coloration but slows its progress rate. *Global Ecology and Biogeography*, 31, 2159–2380.

Kang, X., Hao, Y., Cui, X., Chen, H., Huang, S., Du, Y. et al. (2016) Variability and changes in climate, phenology, and gross primary production of an alpine wetland ecosystem. *Remote Sensing*, 8, 391.

Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y. et al. (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, 4, 598–604.

Keskitalo, J., Bergquist, G., Gardeström, P. & Jansson, S. (2005) A cellular timetable of autumn senescence. *Plant Physiology*, 139, 1635–1648.

Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M. et al. (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience*, 58, 811–821.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D. et al. (2002) Rainfall variability, carbon cycling, and plant species diversity in a Mesic grassland. *Science*, 298, 2202–2205.

Körner, C. (1994) Biomass fractionation in plants: a reconsideration of definitions based on plant functions. In: Roy, J. & Garnier, E. (Eds.) *A whole plant perspective on carbon-nutrient interactions*. The Hague: SPB Academic Publishing, pp. 173–185.

Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115, 445–459.

Körner, C. (2002) *German edition of Körner (2013) the English edition*.

Körner, C. (2003a) Limitation and stress - always or never? *Journal of Vegetation Science*, 14, 141–143.

Körner, C. (2003b) Carbon limitation in trees. *Journal of Ecology*, 91, 4–17.

Körner, C. (2008) Winter crop growth at low temperature may hold the answer for alpine treeline formation. *Plant Ecology and Diversity*, 1, 3–11.

Körner, C. (2011) Coldest places on earth with angiosperm plant life. *Alpine Botany*, 121, 11–22.

Körner, C. (2012) *Alpine treelines*. Basel: Springer.

Körner, C. (2013) Plant-environment interactions. In: Bresinsky, A., Körner, C., Kadereit, J.W., Neuhaus, G. & Sonnewald, U. (Eds.) *Strasburger's plant sciences, chap. 12*. Berlin: Springer. (translation of the 2002 German edition).

Körner, C. (2015) Paradigm shift in plant growth control. *Current Opinion in Plant Biology*, 25, 107–114.

Körner, C. (2018) Concepts in empirical plant ecology. *Plant Ecology and Diversity*, 11, 405–428.

Körner, C. (2021a) *Alpine plant life*, 3rd edition. Cham: Springer.

Körner, C. (2021b) The cold range limit of trees. *Trends in Ecology & Evolution*, 36, 979–989.

Körner, C. (2022) The forest's nutrient cycle drives its carbon cycle. *Tree Physiology*, 42, 425–427.

Körner, C. & Basler, D. (2010) Phenology under global warming. *Science*, 327, 1461–1462.

Körner, C., Basler, D., Hoch, G., Kollas, C., Lenz, A., Randin, C.F. et al. (2016) Where, why and how? Explaining the low-temperature range limits of temperate tree species. *Journal of Ecology*, 104, 1076–1088.

Körner, C., Berninger, U.G., Daim, A., Eberl, T., Fernandez-Mendoza, F., Füreder, L. et al. (2022) Long-term monitoring of high-elevation terrestrial and aquatic ecosystems in the Alps—a five-year synthesis. *EcoMont*, 14, 48–69.

Körner, C. & Hiltbrunner, E. (2018) The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 16–21.

Körner, C. & Hiltbrunner, E. (2021) Why is the alpine flora comparatively robust against climatic warming? *Diversity*, 13, 383.

Körner, C. & Hoch, G. (2023) Not every high-latitude or high-elevation forest edge is a treeline. *Journal of Biogeography*, 50, 838–845. Available from: https://doi.org/10.1111/jbi.14593

Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31, 713–732.

Krejza, J., Haeni, M., Darenova, E., Foltynova, L., Fajstavr, M., Svetlik, J. et al. (2022) Disentangling carbon uptake and allocation in the stems of a spruce forest. *Environmental and Experimental Botany*, 196, 104787.

Kronenberg, L., Yates, S., Ghiasi, S., Roth, L., Friedli, M., Ruckle, M.E. et al. (2021) Rethinking temperature effects on leaf growth, gene expression and metabolism: diel variation matters. *Plant, Cell & Environment*, 44, 2262–2276.

Lang, G.A., Early, J.D., Martin, G.C. & Darnell, R.L. (1987) Endo-, Para- and ecodormancy: physiological terminology and classification for dormancy research. *Horticultural Science*, 22, 371–377.

Lempereur, M., Martin-StPaul, N.K., Damesin, C., Joffre, R., Ourcival, J.M., Rocheteau, A. et al. (2015) Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: implications for assessing forest productivity under climate change. *The New Phytologist*, 207, 579–590.

Linderholm, H.W., Walther, A. & Chen, D. (2008) Twentieth-century trends in the thermal growing season in the greater Baltic area. *Climate Change*, 87, 405–419.

Liu, F., Wang, C. & Wang, X. (2021) Can vegetation index track the interannual variation in gross primary production of temperate deciduous forests? *Ecological Processes*, 10, 51.

Liu, H., Wang, H., Li, N., Shao, J., Zhiu, X., van Groeningen, K.J. et al. (2022) Phenological mismatches between above- and belowground plant responses to climate warming. *Nature Climate Change*, 12, 97–102.

Liu, Q., Piao, S., Janssens, I.A., Fu, Y., Peng, S., Lian, X. et al. (2018) Extension of the growing season increases vegetation exposure to frost. *Nature Communications*, 9, 426.

Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, 25, 735–742.

Lundell, R., Hänninen, H., Saarinen, T., Åström, H. & Zhang, R. (2020) Beyond rest and quiescence (endodormancy and ecodormancy): a novel model for quantifying plant–environment interaction in bud dormancy release. *Plant, Cell & Environment*, 43, 40–54.

Lupi, C., Rossi, S., Vieira, J., Morin, H. & Deslauriers, A. (2014) Assessment of xylem phenology: a first attempt to verify its accuracy and precision. *Tree Physiology*, 34, 87–93.

Ma, H., Mo, L., Crowther, T.W., Maynard, D.S. & Zohner, C.M. (2021) The global distribution and environmental drivers of aboveground versus belowground plant biomass. *Nature Ecology and Evolution*, 5, 1110–1122.

Ma, X., Zhu, X., Xie, Q., Jin, J., Zhou, Y., Luo, Y. et al. (2022) Monitoring nature's calendar from space: emerging topics in land surface phenology and associated opportunities for science applications. *Global Change Biology*, 28, 7186–7204.

Maysonnave, J., Delpierre, N., Jourdan, C.F.M., Cornut, I., Bazot, S., Vincent, G. et al. (2022) Contribution of deep soil layers to the transpiration of a temperate deciduous forest: implications for the modelling of productivity. *Science of the Total Environment*, 838, 155981.

McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D. et al. (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *The New Phytologist*, 207, 505–518.

Meusburger, K., Trotsiuk, V., Schmidt-Walter, P., Baltensweiler, A., Brun, P., Bernhard, F. et al. (2022) Soil–plant interactions modulated water availability of swiss forests during the 2015 and 2018 droughts. *Global Change Biology*, 28, 5928–5944.

Michaletz, S.T., Kerkhoff, A.J. & Enquist, B.J. (2017) Drivers of terrestrial plant production across broad geographical gradients. *Global Ecology and Biogeography*, 27, 166–174.

Möhl, P., von Büren, R.S. & Hiltbrunner, E. (2022) Growth of alpine grassland will start and stop earlier under climate warming.

Nature Communications, 13, 7398. Available from: https://doi.org/10.1038/s41467-022-35194-5

Monson, R.K., Turnipseed, A.A., Sparks, J.P., Harley, P.C., Scott-Denton, L.E., Sparks, K. et al. (2002) Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology*, 8, 459–478.

Moser, L., Fonti, P., Büntgen, U., Esper, J., Luterbacher, J., Franzen, J. et al. (2010) Timing and duration of European larch growing season along altitudinal gradients in the swiss Alps. *Tree Physiology*, 30, 225–233.

Muller, B., Pantin, F., Genard, M., Turc, O., Freixes, S., Piques, M. et al. (2011) Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, 62, 1715–1729.

Müller, H.N. (1981) Messungen zur Beziehung Klimafaktoren—Jahrringwachstum von Nadelbaumarten verschiedener waldgrenznaher Standorte. *Mitt Forstl Bundesversuchsanst, Wien*, 142, 327–355.

Nagelmüller, S., Yates, S. & Walter, A. (2018) Diel leaf growth of rapeseed at critically low temperature under winter field conditions. *Functional Plant Biology*, 45, 1110–1118.

Norby, R.J., Hartz-Rubin, J.S. & Verbrugge, M.J. (2003) Phenological responses in maple to experimental atmospheric warming and CO_2 enrichment. *Global Change Biology*, 9, 1792–1801.

Obeso, J.R. (2002) The costs of reproduction in plants. *The New Phytologist*, 155, 321–348.

Oldfather, M.F. & Ackerly, D.D. (2019) Microclimate and demography interact to shape stable population dynamics across the range of an alpine plant. *The New Phytologist*, 222, 193–205.

Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E.S., Høgda, K.-A., Karlsen, S.R. et al. (2016) Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environmental Research Letters*, 11, 084001.

Paulsen, J. & Körner, C. (2014) A climate-based model to predict potential treeline position around the globe. *Alpine Botany*, 124, 1–12.

Peichl, M., Martinez-Garcia, E., Fransson, J.E.S., Wallerman, J., Laudon, H., Lundmark, T. et al. (2023) Landscape-variability of the carbon balance across managed boreal forests. *Global Change Biology*, 29, 1119–1132.

Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J.W., Frank, D.C., Schaub, M. et al. (2021) Turgor – a limiting factor for radial growth in mature conifers along an elevational gradient. *The New Phytologist*, 229, 213–229.

Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S. et al. (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, 451, 49–52.

Piao, S., Liu, Q., Chen, A., Janssens, I.A., Fu, Y., Dai, J. et al. (2019) Plant phenology and global climate change: current progresses and challenges. *Global Change Biology*, 25, 1922–1940.

Prescott, C.E., Grayston, S.J., Helmisaari, H.S., Kaštovská, E., Körner, C., Lambers, H. et al. (2020) Surplus carbon drives allocation and plant–soil interactions. *Trends in Ecology & Evolution*, 35, 1110–1118.

Puchałka, R., Klisz, M., Koniakin, S., Czortek, P., Dylewski, Ł., Paź-Dyderska, S. et al. (2022) Citizen science helps predictions of climate change impact on flowering phenology: a study on *Anemone nemorosa*. *Agricultural and Forest Meteorology*, 325, 109133.

Rammig, A., Jonas, T., Zimmermann, N.E. & Rixen, C. (2010) Changes in alpine plant growth under future climate conditions. *Biogeosciences*, 7, 2013–2024.

Reekie, E.G. (1997) Trade-offs between reproduction and growth influence time of reproduction. In: Bazzaz, F.A. & Grace, J.

(Eds.) *Plant resource allocation*. San Diego: Academic Press, pp. 191–209.

Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N. et al. (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3227–3246.

Rossi, S., Anfodillo, T., Cufar, K., Cuny, H.E., Deslauriers, A., Fonti, P. et al. (2013) A meta-analysis of cambium phenology and growth: linear and non-linear patterns in conifers of the northern hemisphere. *Annals of Botany*, 112, 1911–1920.

Rossi, S., Deslauriers, A., Anfodillo, T. & Carraro, V. (2007) Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, 152, 1–12.

Rubinstein, E. (1924) Beziehungen zwischen dem Klima und dem Pflanzenreiche. *Meteorologische Zeitschrift*, 41, 15–17.

Russelle, M.P., Wilhelm, W.W., Olson, R.A. & Power, J.F. (1984) Growth analysis based on degree days. *Crop Science*, 24, 28–32.

Sarris, D., Siegwolf, R. & Körner, C. (2013) Inter- and intra-annual stable carbon and oxygen isotope signals in response to drought in Mediterranean pines. *Agricultural Meteorology*, 168, 59–68.

Saugier, B., Roy, J. & Mooney, H.A. (2001) Estimations of Global Terrestrial Productivity. In: *Terrestrial global productivity*. London: Academic Press.

Savage, J.A. & Cavender-Bares, J. (2013) Phenological cues drive an apparent trade-off between freezing tolerance and growth in the family Salicaceae. *Ecology*, 94, 1708–1717.

Scartazza, A., Sbrana, C., D'Andrea, E., Matteucci, G., Rezaie, N. & Lauteri, M. (2023) Above- and belowground interplay: canopy CO_2 uptake, carbon and nitrogen allocation and isotope fractionation along the plant-ectomycorrhiza continuum. *Plant, Cell & Environment*, 46, 889–900.

Scherrer, D. & Körner, C. (2009) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, 16, 2602–2613.

Scherrer, D. & Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 38, 406–416.

Schiestl-Aalto, P., Nikinmaa, E. & Makela, A. (2013) Duration of shoot elongation in scots pine varies within the crown and between years. *Annals of Botany*, 112, 1181–1191.

Scholz, K., Hammerle, A., Hiltbrunner, E. & Wohlfahrt, G. (2018) Analyzing the effects of growing season length on the net ecosystem production of an alpine grassland using model-data fusion. *Ecosystems*, 21, 982–999.

Schulze, E.-D., Beck, E., Buchmann, N., Clemens, S., Müller-Hohenstein, K. & Scherer-Lorenzen, M. (2019) *Plant Ecology (2nd ed.) Chapter 16*. Heidelberg: Springer-Nature.

Sestak, Z., Catsky, J. & Jarvis, P.G. (1971) *Plant photosynthetic production. Manual of methods.* The Hague: Junk N.V. Publishers.

Shekar, A., Buchmann, N. & Gharun, M. (2022) How well do recently reconstructed solar induced fluorescence datasets model gross primary production? *Remote Sensing of Environment*, 283, 113282.

Sloan, V.L., Fletcher, B.J. & Phoenix, G.K. (2016) Contrasting synchrony in root and leaf phenology across multiple sub-Arctic plant communities. *Journal of Ecology*, 104, 239–248.

Steinaker, D.F. & Wilson, S.D. (2008) Phenology of fine roots and leaves in forest and grassland. *Journal of Ecology*, 96, 1222–1229.

Steinaker, D.F., Wilson, S.D. & Peltzer, D.A. (2010) Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology*, 16, 2241–2251.

Stocker, B.D., Tumber-Dávila, S.J., Konings, A.G., Anderson, M.C., Hain, C. & Jackson, R.B. (2023) Global patterns of water storage in the rooting zone of vegetation. *Nature Geoscience*, 16, 250–256.

Sutinen, S., Partanen, J., Viherä-Aarnio, A. & Häkkinen, R. (2012) Development and growth of primordial shoots in Norway spruce

buds before visible bud burst in relation to time and temperature in the field. *Tree Physiology*, 32, 987–997.

Tang, J.W., Körner, C., Muraoka, H., Piao, S.L., Shen, M.G., Thackeray, S.J. et al. (2016) Emerging opportunities and challenges in phenology: a review. *Ecosphere*, 7, e01436.

Tardieu, F. (2013) Plant response to environmental conditions: assessing potential production, water demand, and negative effects of water deficit. *Frontiers in Physiology*, 4, 17.

Valeriano, C., Gutierrez, E., Colangelo, M., Gazol, A., Sanchez-Salguero, R., Tumajer, I. et al. (2023) Seasonal precipitation and continentality drive bimodal growth in Mediterranean forests. *Dendrochronologie*, 78, 126057.

Vegis, A. (1964) Dormancy in higher plants. *Annual Review of Plant Physiology*, 15, 185–224.

Verma, M., Friedl, M.A., Richardson, A.D., Kiely, G., Cescatti, A., Law, B.E. et al. (2014) Remote sensing of annual terrestrial primary productivity from MODIS: an assessment using the FLUXNET La Thuile data set. *Biogeosciences*, 11, 2185–2200.

Vitasse, Y., Rebetez, M., Filippa, G., Cremonese, E., Klein, G. & Rixen, C. (2017) 'Hearing' alpine plants growing after snowmelt: ultrasonic snow sensors provide long-term series of alpine plant phenology. *International Journal of Biometeorology*, 61, 349–361.

Vorkauf, M., Kahmen, A., Körner, C. & Hiltbrunner, E. (2021) Flowering phenology in alpine grassland strongly responds to shifts in snowmelt but weakly to summer drought. *Alpine Botany*, 131, 73–88.

Vorkauf, M., Marty, C., Kahmen, A. & Hiltbrunner, E. (2021) Past and future snowmelt trends in the swiss Alps: the role of temperature and snowpack. *Climatic Change*, 165, 44–62.

Wang, H.J., Wu, C.Y., Ciais, P., Penuelas, J., Dai, J.H., Fu, Y.S. et al. (2020) Overestimation of the effect of climatic warming on spring phenology due to misrepresentation of chilling. *Nature Communications*, 11, 1–9.

Wang, J.Y. (1960) A critique of the heat unit approach to plant-response studies. *Ecology*, 41, 785–790.

Warren, J.M., Hanson, P.J., Iversen, C.M., Kumar, J., Walker, A.P. & Wullschleger, S.D. (2015) Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations. *The New Phytologist*, 205, 59–78.

Würth, M.K.R., Pelaez-Riedl, S., Wright, S.J. & Körner, C. (2005) Non-structural carbohydrate pools in a tropical forest. *Oecologia*, 143, 11–24.

Yang, H., Yang, X., Heskel, M., Sun, S. & Tang, J. (2017) Seasonal variations of leaf and canopy properties tracked by ground-based NDVI imagery in a temperate forest. *Scientific Reports*, 7, 1267.

Yates, S., Jaškunė, K., Liebisch, F., Nagelmüller, S., Kirchgessner, N., Kölliker, R. et al. (2019) Phenotyping a dynamic trait: leaf growth of perennial ryegrass under water limiting conditions. *Frontiers in Plant Science*, 10, 344.

Zohner, C.M., Mo, L., Pugh, T.A.M., Bastin, J.F. & Crowther, T.W. (2020) Interactive climate factors restrict future increases in spring productivity of temperate and boreal trees. *Global Change Biology*, 26, 4042–4055.

Zweifel, R., Sterck, F., Braun, S., Buchmann, N., Eugster, W., Gessler, A. et al. (2021) Why trees grow at night. *The New Phytologist*, 231, 2174–2185.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.