

REVIEW PAPER

Plant phenology: a critical controller of soil resource acquisition

Eric A. Nord¹ and Jonathan P. Lynch^{2,*}

¹ Intercollege Program in Ecology, The Pennsylvania State University, 310 Tyson Building, University Park, PA 16802, USA

² Intercollege Program in Ecology and Department of Horticulture, The Pennsylvania State University, 221 Tyson Building, University Park, PA 16802, USA

Received 16 October 2008; Revised 4 January 2009; Accepted 16 January 2009

Abstract

Plant phenology, the timing of plant growth and development, is changing in response to global climate change. Changing temperature, soil moisture, nitrogen availability, light, and elevated CO₂ are all likely to affect plant phenology. Alteration of plant phenology by global climate change may alter the ability of plants to acquire soil resources (water and nutrients) by altering the timing and duration of the deployment of roots and leaves, which drive resource acquisition. The potential importance of phenologically-driven changes in soil resource acquisition for plant fitness and productivity have received little attention. General hypotheses are proposed for how plant acquisition of soil resources may be affected by the alteration of phenology. It is expected that the acquisition of mobile resources will be approximately proportional to total transpiration. Alteration of phenology that increases total transpiration should increase, while changes in phenology that reduce transpiration should decrease the acquisition of mobile resources. The acquisition of immobile resources will be approximately proportional to root length duration, thus changes in phenology that increase growth duration should increase the acquisition of immobile resources and vice versa. For both groups of resources, longer growing seasons would tend to increase resource acquisition, and shorter growing seasons would tend to decrease resource acquisition. In the case of resources that exhibit seasonal variability in availability, the synchrony of resource availability and acquisition capacity is important, and subject to disturbance by the alteration of phenology.

Key words: Global change, nutrients, phenology, soil resources, water.

Introduction

The observation of the timing of plant emergence and flowering is a long-standing feature of human societies. Both hunter/gatherer and pre-modern agricultural societies probably used plants as seasonal indicators, and there are recorded observations of plant phenology dating to the 8th century (for an overview of the history of the observation of phenology, see: <http://en.wikipedia.org/wiki/Phenology>). The modern discipline of phenology can be traced to the observations of Robert Marsham in Norfolk, England beginning in 1736 and reached a peak of interest in the first half of the 20th century (Sparks and Carey, 1995).

In recent decades, there has been a resurgence of interest in plant phenology, and changes in phenology are exten-

sively utilized as indicators of global change (Post *et al.*, 2001; Fitter and Fitter, 2002; Parmesan and Yohe, 2003; Badeck *et al.*, 2004; Menzel *et al.*, 2006). Phenology is a useful indicator because it integrates climate signals over a sustained period of time and is easily measured. Global climate change has increased the length of the growing season in temperate regions by as much as 12–18 d over the last two decades (Zhou *et al.*, 2001). This includes an earlier onset of the growing season (about 2.5 d per decade in Europe) (Menzel *et al.*, 2006), as well as an extension of the growing season in the autumn.

The timing of reproduction and maturity is a key component of fitness (Stearns, 1992), and a large body of

* To whom correspondence should be addressed. E-mail: jpl4@psu.edu

literature has addressed the optimal timing of reproduction in plants, considering time and resource limitations (Cohen, 1971, 1976; Iwasa, 2000). Fewer attempts have been made to understand or predict the effects of changes in phenology (either already observed or possible responses to continuing climate change) on plant fitness. Several studies have considered the possibility that global change may lead to changes in critical daylength for plants (Bradshaw and Holzapfel, 2001; Van Dijk and Hautekeete, 2007) or changes in geographic distribution (Walther *et al.*, 2005).

It is likely that global change-induced alteration of plant phenology will affect plant fitness by altering the age of reproduction. For example, a photoperiod-sensitive plant that germinates earlier as a result of earlier spring warming might experience a longer vegetative growth phase. Such alterations in phenology would impact plant growth and resource acquisition. Plant phenology, and timing of reproduction in particular, exhibit plastic responses to resource availability (Pigliucci *et al.*, 1995; Dorn *et al.*, 2000; Gungula *et al.*, 2003). Surprisingly, the question of how global change-induced alteration of plant phenology will affect plant fitness has received little attention. We are aware of only one study which has considered how changes in phenology might interact with global change to affect fitness. Lewis *et al.* (2003) manipulated age at flowering while plants were exposed to elevated CO₂. In this case, the degree to which vegetative growth was stimulated by elevated CO₂ was correlated with age at flowering.

Alteration of phenology is likely to have important effects on plant resource acquisition, but the nature of these effects is unknown. Our intent in the following is not an exhaustive review of the literature on the responses of plant phenology to global climate change. Several such reviews already exist (Jablonski *et al.*, 2002; Walther, 2004; Parmesan, 2006; Cleland *et al.*, 2007; Bertin, 2008). Neither is it intended to delineate all the possible ways in which resource acquisition may respond to plant phenology. Instead, it is intended to explore some of the potential effects of global change-induced alteration of plant phenology on the acquisition of soil resources by plants, based on the likely changes in phenology caused by climate change and the dynamics of key soil resources. Our hope is that the hypotheses presented here will stimulate further research and increase our ability to anticipate the effects of global change on plant growth and productivity.

Drivers of phenological change

Temperature

Warmer temperatures generally accelerate plant development (Zavaleta *et al.*, 2003; Badeck *et al.*, 2004), although responses can vary among groups of plants, for example, grasses and forbs (Cleland *et al.*, 2006). Phenological responses to warming may also vary at different stages of growth (Farnsworth *et al.*, 1995). This response may differ in distinct ecosystems. For example, the longer growing

season made possible by warming in an alpine system led to longer plant growth periods (Suzuki and Kudo, 1997).

Changes in temperature are likely to have indirect effects on water availability, both via changes in transpiration (Korner, 2006), and also perhaps via changes in precipitation, although this is likely to be more variable. It may also be important to distinguish between air and soil temperatures, as the two can have different effects on plant growth, and may vary asynchronously (Jonsdottir *et al.*, 2005). Soil temperature has profound effects on root growth and respiration. In perennials, root growth, mortality, and respiration are sensitive to soil temperature, with root respiration increasing by a factor of 1.5–3 for a 10 °C increase in temperature (Pregitzer *et al.*, 2000).

Finally, changes in temperature may affect nutrient availability. Mineralization rates generally increase with temperature, which would increase nutrient availability. However, temperature may indirectly affect nutrient availability by altering soil moisture or the input of organic matter to the soil. One study investigating the responses of arctic tundra systems to increased snowfall reported that peak N mineralization was shifted from midsummer to winter, presumably as soil temperature was increased and increased permafrost melting in the summer led to increased N immobilization in the summer (Borner *et al.*, 2008). Such shifts in resource availability are likely to cause changes in plant community structure.

Elevated CO₂

Elevated CO₂ generally stimulates leaf-level photosynthesis, which can (but may not necessarily) translate into faster growth (Korner, 2006). These responses can be species-specific (Asshoff *et al.*, 2006), and vegetative responses may not be correlated with reproductive responses (Leishman *et al.*, 1999; Jablonski *et al.*, 2002; Lewis *et al.*, 2003). The stimulation of growth or net primary production in mature forests in elevated CO₂ is often transient (Korner, 2006), but may still be important if compounded over time (Ward and Strain, 1999). The transient nature of this response may be caused by down-regulation of photosynthesis in elevated CO₂ (Rogers and Ellsworth, 2002; Bigras and Bertrand, 2006). In some cases, however, the stimulation of growth by elevated CO₂ has been sustained for many years (Moore *et al.*, 2006). Responses to elevated CO₂ may vary within a population, or even within an individual plant (Cavender-Bares *et al.*, 2000; Herrick and Thomas, 2003).

Elevated CO₂ accelerated development in *Oryza sativa* (Seneweera *et al.*, 1994), *Triticum aestivum* (McMaster *et al.*, 1999), and *Trifolium repens*, but not in *Lolium perenne* (Wagner *et al.*, 2001). In a study of the effects of elevated CO₂ on grassland communities, flowering was accelerated in forbs, but delayed in grasses (Cleland *et al.*, 2006). Elevated CO₂ accelerated leaf senescence in *Opulus trichocarpa* in low nutrient conditions (Sigurdsson, 2001). The effects of elevated CO₂ on tree phenology vary, but generally budburst is unchanged or delayed, while bud set is unchanged or accelerated (Ceulemans *et al.*, 1995;

Ceulemans, 1997). Elevated CO₂ prolonged the C gain period of leaves in shade plants more than in sun plants (Cavender-Bares *et al.*, 2000).

Elevated CO₂ interacts with other environmental factors in many complex ways. Elevated CO₂ reduced the stimulation of primary production in a grassland by other environmental changes (Cleland *et al.*, 2006), and accelerated development in *Capsicum annuum* if N and water were adequate (Penuelas *et al.*, 1995), but accelerated flowering in *Trifolium repens* even in deficient N (Wagner *et al.*, 2001). Elevated CO₂ increased the water use efficiency of *Calluna vulgaris* when N and P were sufficient (Whitehead *et al.*, 1997). In other studies, no interaction of CO₂ × nutrient availability on phenology was found (Franzaring *et al.*, 2008). The reduced transpiration made possible by elevated CO₂ may be an important indirect effect, and could prolong leaf phenology (Reich, 1995).

In a recent review, Korner suggests that changes in temperature and precipitation associated with global change are likely to have more impact on plant growth and productivity than the direct effects of elevated CO₂ (Korner, 2006). Unfortunately, changes in temperature and precipitation are more difficult to predict, and may be highly site specific. In an experiment with two tree species and contrasting soils, Spinnler *et al.* (2002) showed strong soil × CO₂ and species × soil interactions, highlighting the importance of soils and biodiversity in predicting responses to elevated CO₂. Another important response to elevated CO₂ may be changes in soils resulting, at least partially, from plant responses to CO₂. *Plantago lanceolata* grown with elevated CO₂ in soil that had developed in elevated CO₂ showed few biomass differences from those grown with ambient CO₂ in soil developed in ambient CO₂, although seed production was reduced in elevated CO₂. In both atmospheres, plants in soil from elevated CO₂ bolted earliest, and had largest leaves (Edwards *et al.*, 2003).

Water

Water availability is likely to change in many regions as precipitation increases in some areas and decreases in others (Christensen *et al.*, 2007). Of these, decreased water availability is more likely to affect phenology. Water deficits accelerate reproduction in many cases (Aronson *et al.*, 1992; Desclaux and Roumet, 1996), although this is not universally true, especially when reproduction is size-dependent, as water deficits reduce the growth rate (Blum, 1996). Early reproduction in water-deficit conditions can be adaptive, and reproduction can be accelerated by natural selection in relatively few generations (Franks *et al.*, 2007). Early reproduction is acknowledged to be a critical trait for drought tolerance in crops (Loss *et al.*, 1997; Fukai *et al.*, 1999; Quarrie *et al.*, 1999; Berger *et al.*, 2004, 2006; Gonzalez *et al.*, 2007). Water deficits may also accelerate senescence (Aronson *et al.*, 1992), although it has also been reported to promote gradual leaf fall, and so interfere with efficient N translocation (Delarco *et al.*, 1991).

The effect of water deficits on phenology and yield may also depend on whether they develop during the vegetative or reproductive phases of growth (Lilley and Fukai, 1994; Nam *et al.*, 2001). In some cases, phenological responses to water deficits disrupt reproduction. Severe water deficits in maize delay silking but not anthesis, with predictable yield reductions (Blum, 1996). Growth duration affects both plant size and water demand (Blum, 1996), but water demand also strongly affects the acquisition of nutrients acquired in bulk flow. Drought can also affect acquisition of diffusion-limited nutrients, as decreased soil water content increases tortuosity and decreases the effective diffusion rate (Barber, 1995). Water deficits generally reduce yield and may also make plants more responsive to elevated CO₂, by favouring reduced transpiration. Elevated CO₂ could therefore mimic increased water availability (Korner, 2006; Volk *et al.*, 2000).

Nitrogen

Burning of fossil fuels, as well as indirect effects from nitrogen fertilizer application, have led to increased atmospheric N, which leads to increased deposition of N on the land surface (Vitousek *et al.*, 1997). Nitrogen is the plant nutrient needed in largest quantities and also regulates plant growth. Addition of N generally increases plant growth rates and biomass (Marschner, 1995). Nitrogen as nitrate is highly soluble and mobile in the soil. Plants acquire nitrogen in the transpiration-driven bulk flow of soil solution to their roots (Barber, 1995). Nitrogen availability often varies throughout the season, both because there is often seasonality to the organic matter inputs to the soil and because of seasonality in the soil biota involved in nitrogen mineralization (Waldrop and Firestone, 2006). The transient nature of N availability is reflected in the rapid inducibility of N transporters in the roots. The machinery for this metabolically expensive activity is only constructed when it is needed, and it is constructed quickly. Not surprisingly, in some ecosystems phenology is coupled to N availability, with flushes of plant growth coinciding with pulses of N availability (Nomura and Kikuzawa, 2003; Tessier and Raynal, 2003). In low-N environments root growth is favoured over shoot growth, leading to an increased root:shoot ratio (Marschner, 1995).

Because N availability often declines throughout the growing season, there is little advantage for plants to delay maturity in conditions of N deficiency. Consequently, accelerated senescence of leaves is a typical symptom of N deficiency (Marschner, 1995). Nitrogen translocation associated with leaf senescence can be an important source of N for seeds (Aerts, 1996; Gobert *et al.*, 2005; Milla *et al.*, 2005), so leaf growth and C acquisition competes with seed demand for N (Lynch and White, 1992). Low N often favours early maturing genotypes (Kamoshita *et al.*, 1998) and N fertilization extends maturity (Shepherd *et al.*, 1987; Thies *et al.*, 1995). Nitrogen deposition also promoted early bud break in *Calluna vulgaris* (Power *et al.*, 2006). The trade-offs between N allocation to vegetative growth and

reproductive growth are consistent with the findings that the acclimation of wheat to elevated CO₂ and N stress depended on leaf age and developmental stage (Adam *et al.*, 2000).

Summary

Elevated CO₂, warming, and drought are all components of future climates, and all can accelerate development. In addition, warming is likely to shift the growing season in temperate, alpine, and arctic systems, as warmer conditions arrive earlier in the year. The responses of plant phenology to future climates will be species-specific, but three broad response scenarios can be delineated, the implications of which are developed below. Where plants rely on photoperiodic cues for reproduction and maturity, the earlier initiation of growth could result in an *extended* growing season. Where plants rely on autonomous cues and when reproduction and maturity are not accelerated, earlier initiation may simply lead to a *shifted* growing season. A third scenario is the *compressed* growing season, where acceleration of reproduction and maturity may be combined with an earlier initiation of growth.

In temperate, arctic, and alpine environments, where temperature is the main driver of plant seasonality, it is expected that the potential growing season may be lengthened both by earlier spring warming and later autumn cooling. The ability of plants to utilize this time will be highly dependent on precipitation and the seasonality of precipitation. In subtropical and tropical climates, precipitation is likely to be the primary driver of plant seasonality. In this work, the focus is on how altered phenology may affect resource acquisition in changing climates, and the alteration of growing season length is likely to be important, whether caused by changes in temperature or precipitation.

Phenology and soil resource availability

Our focus is the potential effects of altered plant phenology on the plant's acquisition of soil resources. However, the acquisition of resources depends both on the phenology of plants and the supply of the resource. Here, several ways in which resource availability may be affected by global change are briefly discussed. It is noted that increased transpiration caused by warming and decreased transpiration caused by elevated CO₂ may cancel out if changes are of a similar magnitude but transpiration effects could further change water availability if the magnitude of these effects is unequal. It is also noted that changes in water availability are likely to be quite site-specific and that altered water availability will affect the availability of other resources.

Water availability could be affected both directly, through changing precipitation, and indirectly, through changes in evaporation and transpiration caused by changes in temperature and in stomatal opening in response to elevated CO₂

(Korner, 2006). Changes in water availability and temperature, along with changes in plant senescence, could affect both the magnitude and timing of availability of nitrogen, phosphorus, and to a lesser extent, the other plant nutrients.

Changes in resource availability may be quite unpredictable. For example, in a tundra system, increased snow depth led to a later snow-free date, which shifted temporal N dynamics, with the peak of N mineralization shifting from early to mid-summer to winter (Borner *et al.*, 2008). In high-latitude tundra systems, warming stimulates N mineralization more than P mineralization, so P limitation may become more important in these systems (Aerts *et al.*, 2006). Such complex changes may be important, and highlight the need for continuing experiments with multiple climate change factors.

Phenology and soil resource acquisition

Plants depend on soil for the acquisition of water and 16 essential mineral nutrients. These nutrients are required in varying quantities, and differences in chemical properties mean that deficiencies of some are common while deficiencies of others are rare. We will focus our discussion on those which are most likely to be limiting. Rather than address all 17 resources, they are grouped into two categories based on mobility. Nutrients that are highly soluble and acquired in the transpiration-driven bulk flow of soil solution to the plant roots are considered to be mobile and those that are sparingly soluble and diffuse slowly to be immobile.

Mobile soil resources

Mobile resources include water, nitrogen (as nitrate), silicon, calcium, and magnesium. Nitrate concentration in soil solution has a strong seasonal pattern in many environments (Haynes, 1986), but the concentration of Si, Ca, and Mg should vary less. Three basic scenarios of resource availability are considered in this section, seasonal and unchanged (Fig. 1), seasonal and shifted (Fig. 2), and non-seasonal (Fig. 3), along with the three scenarios for plant phenology outlined above as they relate to the various mobile soil resources.

Water and nitrogen: Water and nitrogen are the mobile resources needed in the greatest quantities. Availability of water is likely to change in many ecosystems, as both the quantity and the timing of precipitation may change (Christensen *et al.*, 2007). Alteration of plant phenology should therefore affect water acquisition in a manner similar to Figs. 1 and 2 where water availability is seasonal, and similar to Fig. 3 where water availability varies little throughout the year. Nitrogen availability often exhibits strong seasonality, driven by the stimulation of mineralization by seasonality of temperature or moisture, so Figs. 1 and 2 will be more relevant to N acquisition.

Note that Fig. 2 considers only one of the many ways that resource availability could change. Climate change may

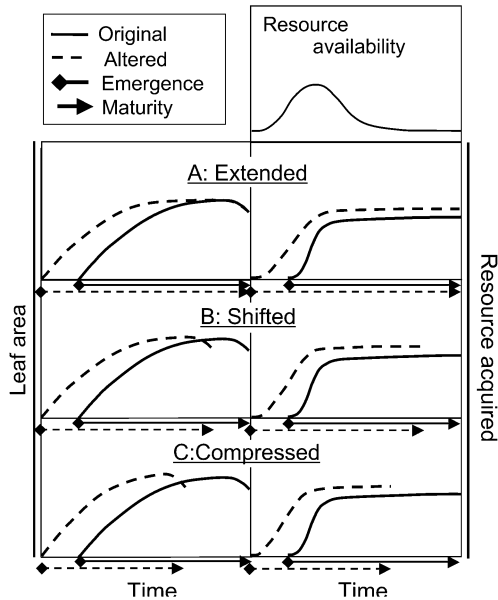


Fig. 1. Possible patterns of leaf area and resource acquisition (A–C) for a mobile resource with seasonal availability. Transpiration should be roughly proportional to leaf area duration (area under leaf area curves). Increased leaf area duration can lead to increased transpiration. This may allow increased acquisition if increased transpiration coincides with high nutrient availability. The increase in resource acquired may represent reduced leaching from the system, or reduced availability to other plants in the system. In these scenarios, early growth may be reduced if resource availability is insufficient, and increased transpiration may drive a more rapid decline of the resource.

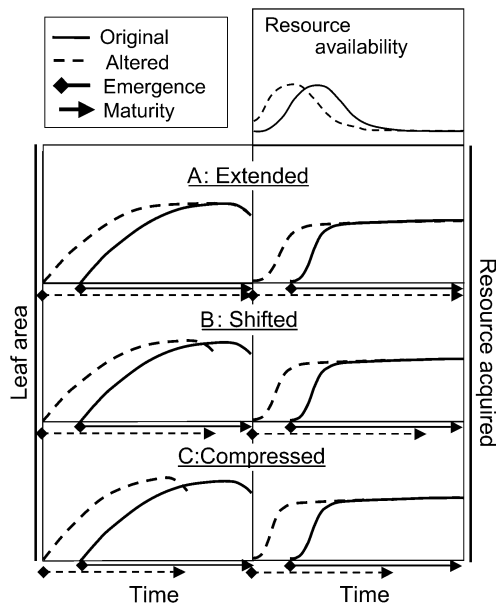


Fig. 2. Possible patterns of leaf area and resource acquisition (A–C) for a mobile resource with shifted seasonal availability. Here the shift in resource availability is similar to that in emergence. In this case, resource acquisition is little affected. Note that availability of the resource could change in many ways not considered here, both in amplitude and timing.

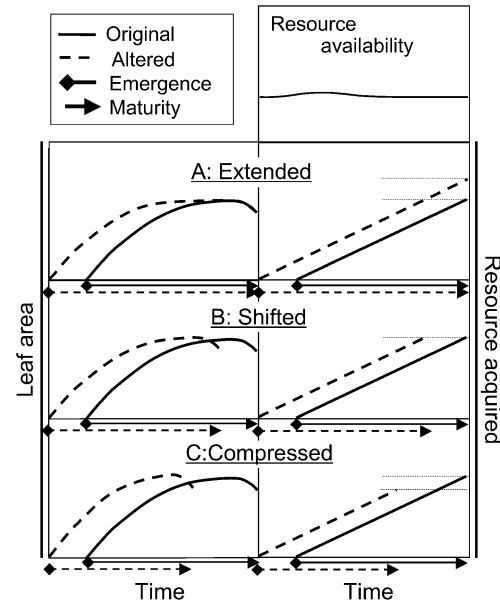


Fig. 3. Possible patterns of leaf area growth and resource acquisition (A–C) for a mobile resource with relatively constant availability. For the case of constant availability, transpiration later in the growing season affects resource acquisition, with extended phenology (A) likely to increase resource acquisition, and compressed phenology (C) likely to decrease resource acquisition.

alter the availability of water and nitrogen in complex ways. Both maximal and minimal availability, and timing of maxima and minima might change, and could, in principle, shift in either direction. Furthermore, bimodal patterns of resource availability may replace unimodal patterns. A comprehensive review of such shifts is beyond the scope of this review. Rather, the general synchrony between resource availability and acquisition is considered. Natural selection should tend to synchronize the resource acquisition capacity of plants to the resource availability in a given environment. Unless shifts in phenology caused by global change are quite similar to shifts in resource availability, reduced synchrony between supply and demand is probable. For the sake of brevity, our discussion is confined either to no shift in resource availability or to small shifts in resource availability that mirror shifts in phenology.

In Fig. 1, there is a possibility of increased acquisition of water and/or nitrogen, even with slower initial growth, when plant growth begins earlier in the season. This depends on the synchrony between availability of resource (water or N) and water uptake capacity (transpiration). Uptake is maximized by reaching maximal leaf area at approximately the same time as maximal resource availability. Resource acquisition may increase as a consequence of either alteration of plant phenology or alteration of timing of resource availability in one of two ways. Either maximal resource availability was not originally well synchronized with maximal transpiration, so that alteration of phenology improves synchrony of supply and demand, or maximal resource availability is sufficiently increased so that acquisition is increased also.

While water is classified as a mobile nutrient, there can be substantial spatial heterogeneity in the availability of water in the soil. In drought conditions, surface horizons in the soil may dry before deeper horizons. In such cases, the vertical distribution of roots is important, and phenology may be an important factor. Kirkegaard and Lilley (2007) reported that root depth and hence water acquisition in wheat was strongly influenced by vegetative growth duration and root penetration rate. Longer growth duration permitted access to deeper water resources.

Since both water and N availability regulate plant growth, the acquisition of these resources can impact the acquisition of other resources. For example, both water deficit and N deficiency can accelerate development, which could reduce the acquisition of immobile resources (Fig. 4C). Finally, note that compressed phenology (Figs. 1C, 2C) may be a common (and perhaps beneficial) response in regions where late-season drought becomes more common.

Silicon, calcium, and magnesium: These nutrients are mobile, but their availability is relatively constant throughout the growing season. Acquisition is controlled by mass flow, which is driven by transpiration, so acquisition should be roughly proportional to leaf area duration.

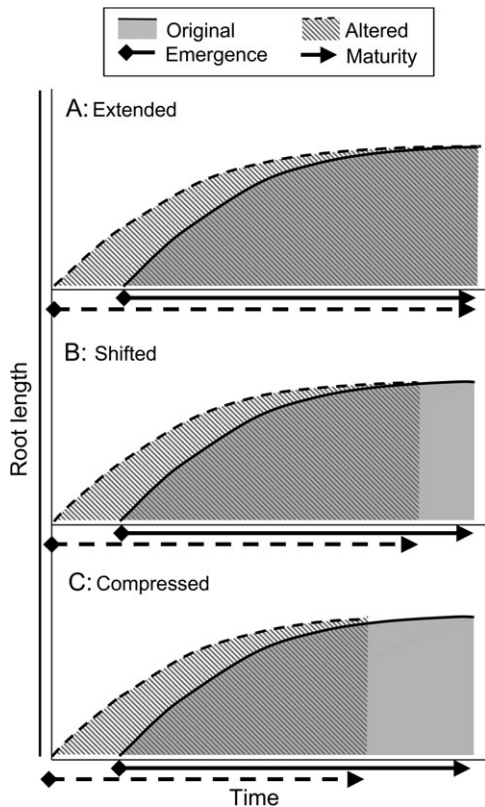


Fig. 4. Alteration of plant phenology may affect acquisition of immobile soil resources in several ways. (A) Reproduction and maturity respond to external cues that are not altered with the climate, for example, day-length. (B) Reproduction and maturity are not changed with respect to germination. (C) Reproduction and maturity are accelerated. In all three cases, root growth is stimulated, and nutrient availability is constant.

Where plant phenology is extended by global change, acquisition of these resources should increase (Fig. 3A). Shifting plant phenology should not affect the acquisition of these resources (Fig. 3B), but compression of plant phenology is likely to reduce the acquisition of these resources (Fig. 3C). This is especially true where plant maturity is responding to temperature since maturation is accelerated in a warmer climate. In particular, warmer nights would accelerate maturation with a lower total transpiration, which may result in the reduced acquisition of silicon, calcium, and magnesium. In the case of calcium, this reduced transpiration may not result in decreased acquisition. In soils where Ca availability is high, acquisition is limited by root uptake of Ca, and the rhizosphere may be enriched as a consequence of Ca transport by mass flow (Marschner, 1995). In this case, extended phenology (Fig. 3A) may lead to a greater concentration of Ca in the rhizosphere.

Immobile soil resources

Immobile soil resources reach plant roots by diffusion (Table 1). The principal immobile nutrients are phosphorus (P) and potassium (K). Ammonium (NH_4^+) is also a low-mobility resource. The micronutrient metals (iron, manganese, copper, and zinc) are also relatively immobile, especially in alkaline soils, where deficiency of these elements can occur.

Availability of immobile resources should be less variable than of mobile resources, as they are unlikely to leach, and are generally taken up slowly. In addition, many of these resources are highly buffered, so plant uptake has minimal effects on availability. As a consequence, the effects of phenological change on the acquisition of these resources should be somewhat more predictable than for mobile resources. Acquisition of immobile soil resources should be primarily influenced by root length duration, which is the

Table 1. Relative significance of root interception, mass flow, and diffusion in supplying corn with nutrient requirements from a fertile alfisol silt loam

Quantities in kg ha^{-1} (% of requirement in parentheses). Table adapted from Barber (1995). *Soil nutrient bioavailability: a mechanistic approach*. New York, USA: John Wiley & Sons, Inc. This material is reproduced with permission of John Wiley and Sons Inc.

Nutrient	Requirement for 9500 kg ha^{-1} grain	Approximate amount supplied by		
		Root interception (kg ha^{-1}) (%)	Mass Flow (kg ha^{-1}) (%)	Diffusion (kg ha^{-1}) (%)
Nitrogen	190	2 (11)	150 (79)	38 (20)
Phosphorus	40	1 (3)	2 (5)	37 (92)
Potassium	195	4 (2)	35 (18)	156 (80)
Calcium	40	60 (150)	150 (375)	0 (0)
Magnesium	45	15 (33)	100 (272)	0 (0)
Sulphur	22	1 (5)	65 (295)	0 (0)

integral of root length over time (Fig. 4, note shading under curves).

Phosphorus: Soil phosphorus availability is often suboptimal for plant growth (Lynch and Deikman, 1998) because of its extreme immobility in most soils (Barber, 1995) and because the phosphorus cycle is open-ended and tends toward depletion over time (Schlesinger, 1991). Plants display an array of adaptations to low phosphorus availability (low P) (Lynch and Brown, 2006). One frequently reported response to low P is delayed reproduction. Delayed reproduction increases root length duration which permits greater P acquisition, which permits greater reproduction (Fig. 5) (Nord and Lynch, 2008).

Other important responses to low P include root hairs (Ma *et al.*, 2001) and root exudates (Hinsinger, 2001). Root hairs increase P acquisition by increasing the radius of the depletion shell around the root and root exudates do so by increasing the rate of desorption of P from immobile pools. We are not aware of any work directly addressing the interaction of any of these responses with phenology. In general, we expect that the benefit of these P acquisition adaptations should be related to root length duration, and so to phenology.

Preliminary analysis by Jaramillo (unpublished data) shows that low P (defined as native soil P <12 ppm, based on soil suborders) affects over 50% of vegetated land, and over 50% of vegetated land is expected to experience a 3–6 °C increase in temperature (Fig. 6). This analysis, while preliminary, indicates the potential importance of low P in plant responses to future climates.

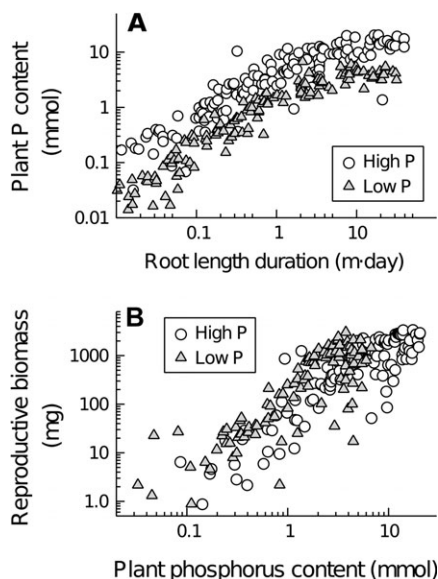


Fig. 5. The relationship of root-length duration and fecundity in seven genotypes of *Arabidopsis thaliana* grown in high- and low P. (A) Plant phosphorus content versus root-length duration. (B) Reproductive biomass versus plant phosphorus content. (From Nord and Lynch, 2008, and reproduced by kind permission of Wiley-Blackwell).

Ammonium and potassium: Ammonium and potassium are nearly immobile in soils, although they are slightly more mobile than phosphorus. Ammonium is an important nitrogen source in acidic soils, and where ammonium is the primary source of nitrogen, this may regulate growth. Nitrogen deficiency typically accelerates development (Marschner, 1995). In cases where ammonium is a major nitrogen source and is deficient, this may be maladaptive. Potassium is needed in substantial quantities, but does not regulate growth as nitrogen and phosphorus do, and so potassium deficiency is less likely to affect the phenology or growth of plants. Rather, deficient plants develop symptoms of the deficiency as potassium in the plant is diluted by continuing growth (Rubio *et al.*, 2003).

Iron, manganese, copper, and zinc: The mobility of these metal micronutrients is influenced by soil pH. In alkaline soils, they are relatively immobile, and plant growth and fecundity may be impaired. In acid soils, greater bioavailability can lead to Mn toxicity. The potential for accumulation of these metals to toxic levels may be more problematic where plant phenology is extended by global change (Fig. 4A). This is particularly true where bioavailability is enhanced by soil acidification.

Phenology and resource utilization

Although our focus is on resource acquisition, we note briefly that phenology also has effects on nutrient utilization by changing the duration of nutrients in plant tissue. Nutrient duration is simply the integral of tissue nutrient content over time, and is generally related with nutrient utility. For example, the utilization of leaf nitrogen for photosynthetic carbon gain was directly related to leaf duration in *Phaseolus vulgaris* (Lynch and Rodriguez, 1994), and leaf phosphorus duration was related to bolt biomass in *Arabidopsis thaliana* (Nord and Lynch, 2008). Although increased nutrient duration generally increases

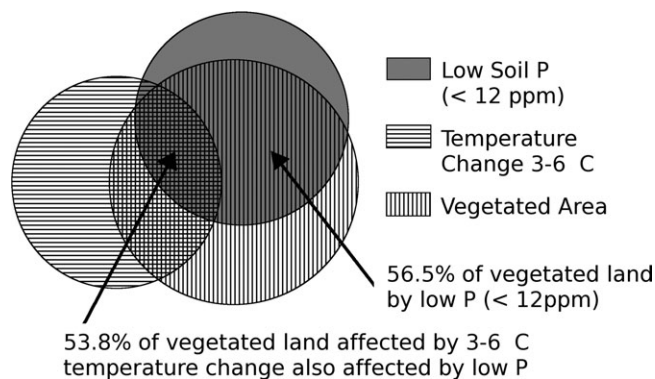


Fig. 6. Co-occurrence of low soil P, vegetative area, and estimated temperature change of 3–6 °C. Over 50% of vegetated land is affected by low P, as is over 50% of vegetated land at risk of 3–6 °C temperature change. (Adapted from R Jaramillo and JP Lynch, unpublished data.)

nutrient utilization, continued leaf accumulation of some elements can also lead to nutrient imbalances and toxicity, as in the case of Mn toxicity in trees of the eastern forest of North America (Lynch and St Clair, 2004).

Phenology may also affect resource utilization by altering the length of the reproductive phase. Earlier maturation without earlier reproduction reduces the length of the reproductive phase. This can have consequences for resource utilization. In a study with *Arabidopsis thaliana*, it was found that seed production in one genotype was reduced in elevated CO₂ because the reproductive phase was shortened (Nord, 2008). Seed-filling duration is known to influence yield in grain crops (Egli, 2004), and grain yields have been reported to decline when grain-filling duration is reduced by elevated temperature (Sofield *et al.*, 1977). These illustrate the importance of time for the conversion of acquired resources into seed.

Conclusion

Growing seasons in temperate regions are already beginning earlier, and many of the expected changes in climate are reported to accelerate development, although responses are species specific. Therefore a range of phenological patterns, from extended to compressed phenology is expected. In general, it is expected that acquisition of mobile resources will be roughly related to total transpiration, and acquisition of immobile resources to root length duration. In both cases, extended phenology would tend to increase resource acquisition, and compressed phenology would tend to decrease resource acquisition. Of course, future climates will differ from the present in multiple ways, especially when multiple global change variables are considered together, and the site-specific nature of changes in water availability further complicates the picture. Only a few of these cases have been considered here in an attempt to outline the most general cases.

Most of our discussion has been focused on annual plants. The responses of perennials are more complex, and they have not been explicitly considered here. However, in general terms, the effects of phenology on resource acquisition should be similar. Transpiration is the main driver for the acquisition of mobile resources and should still be related to leaf area duration. For immobile resources, root length duration is the main driver of acquisition. Perennials differ from annuals in that they can begin the growing season with a larger rooting volume, and that they can acquire resources during the dormant period, if they have sufficient reserves of carbohydrate. This could give perennials an advantage over annuals in the acquisition of immobile resources.

Unfortunately, there is insufficient understanding of how interactions between species may be altered by elevated CO₂, let alone by multiple changes in global change variables, so ecosystem responses to global change are difficult to predict (Karnosky, 2003). Different responses by different functional groups in a community may buffer

changes in community-level resource acquisition and net primary productivity (Cole *et al.*, 2008; Rich *et al.*, 2008) but could lead to changes in seasonal resource dynamics and nutrient cycling (Hooper and Vitousek, 1998). Range shifts due to changes in temperature and N availability may lead to changes in plant communities that are difficult to predict but, in general, faster-growing species should be favoured more than slower-growing ones, and vascular plants may be favoured over non-vascular plants (Aerts *et al.*, 2006). It is also likely that climate changes will permit new biological invasions, which can affect nutrient cycling and availability (Ehrenfeld, 2003). Ultimately, all of these changes could also affect availability and thus acquisition of resources in ways that are difficult to predict.

Several novel hypotheses concerning the effects of altered plant phenology on resource acquisition have been proposed. These highlight the need for continued investigation into plant responses to global change. Changes in resource acquisition as a result of global change-induced alteration of phenology are likely to be of special relevance for agriculture in the developing world, where smallholder, subsistence agriculture occurs on marginal lands, with low nutrient availability, and little access to fertilizers. These production systems are likely to be especially sensitive to either a decreased or an increased acquisition of soil resources by crop plants, so that small differences in resource acquisition may be reflected in yield or in crop quality.

References

- Adam NR, Wall GW, Kimball BA, *et al.* 2000. Acclimation response of spring wheat in a free-air CO₂ enrichment (FACE) atmosphere with variable soil nitrogen regimes. 1. Leaf position and phenology determine acclimation response. *Photosynthesis Research* **66**, 65–77.
- Aerts R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* **84**, 597–608.
- Aerts R, Cornelissen JHC, Dorrepaal E. 2006. Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. *Plant Ecology* **182**, 65–77.
- Aronson J, Kigel J, Shmida A, Klein J. 1992. Adaptive phenology of desert and mediterranean populations of annual plants grown with and without water-stress. *Oecologia* **89**, 17–26.
- Asshoff R, Zotz G, Korner C. 2006. Growth and phenology of mature temperate forest trees in elevated CO₂. *Global Change Biology* **12**, 848–861.
- Badeck FW, Bondeau A, Bottcher K, Doktor D, Lucht W, Schaber J, Sitch S. 2004. Responses of spring phenology to climate change. *New Phytologist* **162**, 295–309.
- Barber SA. 1995. *Soil nutrient bioavailability: a mechanistic approach*. New York, USA: John Wiley & Sons, Inc.
- Berger JD, Ali M, Basu PS, *et al.* 2006. Genotype by environment studies demonstrate the critical role of phenology in adaptation of chickpea (*Cicer arietinum* L.) to high and low yielding environments of India. *Field Crops Research* **98**, 230–244.

- Berger JD, Turner NC, Siddique KHM, Knights EJ, Brinsmead RB, Mock I, Edmondson C, Khan TN.** 2004. Genotype by environment studies across Australia reveal the importance of phenology for chickpea (*Cicer arietinum* L.) improvement. *Australian Journal of Agricultural Research* **55**, 1071–1084.
- Bertin RI.** 2008. Plant phenology and distribution in relation to recent climate change. *Journal of the Torrey Botanical Society* **135**, 126–146.
- Bigras FJ, Bertrand A.** 2006. Responses of *Picea mariana* to elevated CO₂ concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis, and growth. *Tree Physiology* **26**, 875–888.
- Blum A.** 1996. Crop responses to drought and the interpretation of adaptation. *Plant Growth Regulation* **20**, 135–148.
- Borner AP, Kielland K, Walker MD.** 2008. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan arctic Tundra. *Arctic, Antarctic and Alpine Research* **40**, 27–38.
- Bradshaw WE, Holzapfel CM.** 2001. Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences, USA* **98**, 14509–14511.
- Cavender-Bares J, Potts M, Zacharias E, Bazzaz FA.** 2000. Consequences of CO₂ and light interactions for leaf phenology, growth, and senescence in *Quercus rubra*. *Global Change Biology* **6**, 877–887.
- Ceulemans R.** 1997. Direct impacts of CO₂ and temperature on physiological processes in trees. In: Mohren GMJ, Kramer K, Sabate S, eds. *Impacts of global change on tree physiology and forest ecosystems*. Dordrecht, The Netherlands: Kluwer, 3–14.
- Ceulemans R, Jiang XN, Shao BY.** 1995. Effects of elevated atmospheric CO₂ on growth, biomass production and nitrogen allocation of two *Populus* clones. *Journal of Biogeography* **22**, 261–268.
- Christensen JH, Hewitson B, Busiuc A, et al.** 2007. Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. *Climate change 2007: the physical science basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK; New York, USA: Cambridge University Press.
- Cleland EE, Chiariello NR, Loarie SR, Mooney HA, Field CB.** 2006. Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences, USA* **103**, 13740–13744.
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD.** 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- Cohen D.** 1971. Maximizing final yield when growth is limited by time or by limiting resources. *Journal of Theoretical Biology* **33**, 299–307.
- Cohen D.** 1976. The optimal timing of reproduction. *American Naturalist* **110**, 801–807.
- Cole L, Buckland SM, Bardgett RD.** 2008. Influence of disturbance and nitrogen addition on plant and soil animal diversity in grassland. *Soil Biology and Biochemistry* **40**, 505–514.
- Delarco JM, Escudero A, Garrido MV.** 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. *Ecology* **72**, 701–708.
- Desclaux D, Roumet P.** 1996. Impact of drought stress on the phenology of two soybean (*Glycine max* L Merr) cultivars. *Field Crops Research* **46**, 61–70.
- Dorn LA, Pyle EH, Schmitt J.** 2000. Plasticity to light cues and resources in *Arabidopsis thaliana*: Testing for adaptive value and costs. *Evolution* **54**, 1982–1994.
- Edwards GR, Clark H, Newton PCD.** 2003. Soil development under elevated CO₂ affects plant growth responses to CO₂ enrichment. *Basic and Applied Ecology* **4**, 185–195.
- Egli DB.** 2004. Seed-fill duration and yield of grain crops. *Advances in Agronomy* **83**, 243–279.
- Ehrenfeld JG.** 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**, 503–523.
- Farnsworth EJ, NunezFarfan J, Careaga SA, Bazzaz FA.** 1995. Phenology and growth of three temperate forest life forms in response to artificial soil warming. *Journal of Ecology* **83**, 967–977.
- Fitter AH, Fitter RSR.** 2002. Rapid changes in flowering time in British plants. *Science* **296**, 1689–1691.
- Franks SJ, Sim S, Weis AE.** 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences, USA* **104**, 1278–1282.
- Franzaring J, Holz I, Fangmeier A.** 2008. Different responses of *Molinia caerulea* plants from their origins to CO₂ enrichment and nutrient supply. *Acta Oecologica-International Journal of Ecology* **33**, 176–187.
- Fukai S, Pantuwan G, Jongdee B, Cooper M.** 1999. Screening for drought resistance in rainfed lowland rice. *Field Crops Research* **64**, 61–74.
- Gobert S, Lejeune P, Lepoint G, Bouqueneau JM.** 2005. C, N, P concentrations and requirements of flowering *Posidonia oceanica* shoots. *Hydrobiologia* **533**, 253–259.
- Gonzalez A, Martin I, Ayerbe L.** 2007. Response of barley genotypes to terminal soil moisture stress: phenology, growth, and yield. *Australian Journal of Agricultural Research* **58**, 29–37.
- Gungula DT, Kling JG, Togun AO.** 2003. CERES-maize predictions of maize phenology under nitrogen-stressed conditions in Nigeria. *Agronomy Journal* **95**, 892–899.
- Haynes R.** 1986. Uptake and assimilation of mineral nitrogen by plants. In: Haynes RJ, Sherlock RR, eds. *Mineral nitrogen in the plant-soil system*. Orlando, FL, USA: Academic Press, 303–378.
- Herrick JD, Thomas RB.** 2003. Leaf senescence and late-season net photosynthesis of sun and shade leaves of overstory sweetgum (*Liquidambar styraciflua*) grown in elevated and ambient carbon dioxide concentrations. *Tree Physiology* **23**, 109–118.
- Hinsinger P.** 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* **237**, 173–195.
- Hooper DU, Vitousek PM.** 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**, 121–149.
- Iwasa Y.** 2000. Dynamic optimization of plant growth. *Evolutionary Ecology Research* **2**, 437–455.
- Jablonski LM, Wang XZ, Curtis PS.** 2002. Plant reproduction under elevated CO₂ conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* **156**, 9–26.

- Jonsdottir IS, Magnusson B, Gudmundsson J, Elmarsdottir A, Hjartarson H.** 2005. Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology* **11**, 553–563.
- Kamoshita A, Fukai S, Muchow RC, Cooper M.** 1998. *Sorghum* hybrid differences in grain yield and nitrogen concentration under low soil nitrogen availability. II. Hybrids with contrasting phenology. *Australian Journal of Agricultural Research* **49**, 1277–1286.
- Karnosky DF.** 2003. Impacts of elevated atmospheric CO₂ on forest trees and forest ecosystems: knowledge gaps. *Environment International* **29**, 161–169.
- Kirkegaard JA, Lilley JM.** 2007. Root penetration rate: a benchmark to identify soil and plant limitations to rooting depth in wheat. *Australian Journal of Experimental Agriculture* **47**, 590–602.
- Korner C.** 2006. Plant CO₂ responses: an issue of definition, time and resource supply. *New Phytologist* **172**, 393–411.
- Leishman MR, Sanbrooke KJ, Woodfin RM.** 1999. The effects of elevated CO₂ and light environment on growth and reproductive performance of four annual species. *New Phytologist* **144**, 455–462.
- Lewis JD, Wang XZ, Griffin KL, Tissue DT.** 2003. Age at flowering differentially affects vegetative and reproductive responses of a determinate annual plant to elevated carbon dioxide. *Oecologia* **135**, 194–201.
- Lilley JM, Fukai S.** 1994. Effect of timing and severity of water-deficit on 4 diverse rice cultivars. 3. Phenological development, crop growth and grain-yield. *Field Crops Research* **37**, 225–234.
- Loss SP, Siddique KHM, Martin LD.** 1997. Adaptation of faba bean (*Vicia faba* L.) to dryland Mediterranean-type environments. 2. Phenology, canopy development, radiation absorbtion and biomass partitioning. *Field Crops Research* **52**, 29–41.
- Lynch J, Deikman J, eds.** 1998. *Phosphorus in plant biology: regulatory roles in molecular, cellular, organismic, and ecosystem processes*. Rockville, MD: American Society of Plant Biologists.
- Lynch J, Rodriguez NS.** 1994. Photosynthetic nitrogen-use efficiency in relation to leaf longevity in common bean. *Crop Science* **34**, 1284–1290.
- Lynch J, White JW.** 1992. Shoot nitrogen dynamics in tropical common bean. *Crop Science* **32**, 392–397.
- Lynch JP, Brown KM.** 2006. Whole plant adaptations to low phosphorus availability. In: Huang B, ed. *Plant–environment interactions*. Boca Raton: CRC Press, 209–242.
- Lynch JP, St Clair SB.** 2004. Mineral stress: the missing link in understanding how global climate change will affect plants in real world soils. *Field Crops Research* **90**, 101–115.
- Ma Z, Walk TC, Marcus A, Lynch JP.** 2001. Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: a modeling approach. *Plant and Soil* **236**, 221–235.
- Marschner H.** 1995. *Mineral nutrition of higher plants*. London: Academic Press.
- McMaster GS, LeCain DR, Morgan JA, Aiguo L, Hendrix DL.** 1999. Elevated CO₂ increases wheat CER, leaf and tiller development, and shoot and root growth. *Journal of Agronomy and Crop Science* **183**, 119–128.
- Menzel A, Sparks TH, Estrella N, et al.** 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976.
- Milla R, Castro-Diez P, Maestro-Martinez M, Montserrat-Marti G.** 2005. Relationships between phenology and the remobilization of nitrogen, phosphorus and potassium in branches of eight Mediterranean evergreens. *New Phytologist* **168**, 167–178.
- Moore DJP, Aref S, Ho RM, Phippen JS, Hamilton JG, De Lucia EH.** 2006. Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment. *Global Change Biology* **12**, 1367–1377.
- Nam NH, Chauhan YS, Johansen C.** 2001. Effect of timing of drought stress on growth and grain yield of extra-short-duration pigeonpea lines. *Journal of Agricultural Science* **136**, 179–189.
- Nomura N, Kikuzawa K.** 2003. Productive phenology of tropical montane forests: fertilization experiments along a moisture gradient. *Ecological Research* **18**, 573–586.
- Nord E.** 2008. Patience is a virtue: delayed phenology is an adaptive response for plants in soils with low phosphorus availability. PhD thesis, The Pennsylvania State University. PA: University Park, 105.
- Nord E, Lynch J.** 2008. Delayed reproduction in *Arabidopsis thaliana* improves fitness in soil with suboptimal phosphorus availability. *Plant, Cell, and Environment* **31**, 1432–1441.
- Parmesan C.** 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* **37**, 637–669.
- Parmesan C, Yohe G.** 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Penuelas J, Biel C, Estiarte M.** 1995. Growth, biomass allocation, and phenology responses of pepper to elevated CO₂ concentrations and different water and nitrogen supply. *Photosynthetica* **31**, 91–99.
- Pigliucci M, Schlichting CD, Whitton J.** 1995. Reaction norms of *Arabidopsis*. 2. Response to stress and unordered environmental variation. *Functional Ecology* **9**, 537–547.
- Post E, Forchhammer MC, Stenseth NC, Callaghan TV.** 2001. The timing of life-history events in a changing climate. *Proceedings of the Royal Society of London Series B* **268**, 15–23.
- Power SA, Green ER, Barker CG, Bell JNB, Ashmore MR.** 2006. Ecosystem recovery: heathland response to a reduction in nitrogen deposition. *Global Change Biology* **12**, 1241–1252.
- Pregitzer KS, King JA, Burton AJ, Brown SE.** 2000. Responses of tree fine roots to temperature. *New Phytologist* **147**, 105–115.
- Quarrie SA, Stojanovic J, Pekic S.** 1999. Improving drought resistance in small-grained cereals: a case study, progress and prospects. *Plant Growth Regulation* **29**, 1–21.
- Reich PB.** 1995. Phenology of tropical forests: patterns, causes, and consequences. *Canadian Journal of Botany-Revue Canadienne De Botanique* **73**, 164–174.
- Rich PM, Breshears DD, White AB.** 2008. Phenology of mixed woody–herbaceous ecosystems following extreme events: net and differential responses. *Ecology* **89**, 342–352.

- Rogers A, Ellsworth DS.** 2002. Photosynthetic acclimation of *Pinus taeda* (loblolly pine) to long-term growth in elevated $p\text{CO}_2$ (FACE). *Plant, Cell and Environment* **25**, 851–858.
- Rubio G, Zhu JM, Lynch JP.** 2003. A critical test of the two prevailing theories of plant response to nutrient availability. *American Journal of Botany* **90**, 143–152.
- Schlesinger WH.** 1991. *Biogeochemistry: an analysis of global change*. San Diego: Academic Press.
- Seneweera S, Milham P, Conroy J.** 1994. Influence of elevated CO_2 and phosphorus-nutrition on the growth and yield of a short-duration rice (*Oryza sativa* L. cv. Jarrah). *Australian Journal of Plant Physiology* **21**, 281–292.
- Shepherd KD, Cooper PJM, Allan AY, Drennan DSH, Keatinge JDH.** 1987. Growth, water-use and yield of barley in Mediterranean-type environments. *Journal of Agricultural Science* **108**, 365–378.
- Sigurdsson BD.** 2001. Elevated $[\text{CO}_2]$ and nutrient status modified leaf phenology and growth rhythm of young *Populus trichocarpa* trees in a 3-year field study. *Trees: Structure and Function* **15**, 403–413.
- Sofield I, Evans LT, Cook MG, Wardlaw IF.** 1977. Factors influencing rate and duration of grain filling in wheat. *Australian Journal of Plant Physiology* **4**, 785–797.
- Sparks TH, Carey PD.** 1995. The responses of species to climate over two centuries: an analysis of the Marham phenological record, 1736–1947. *Journal of Ecology* **83**, 321–329.
- Spinnler D, Egli P, Körner C.** 2002. Four-year growth dynamics of beech–spruce model ecosystems under CO_2 enrichment on two different forest soils. *Trees: Structure and Function* **16**, 423–436.
- Stearns S.** 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Suzuki S, Kudo G.** 1997. Short-term effects of simulated environmental change on phenology, leaf traits, and shoot growth of alpine plants on a temperate mountain, northern Japan. *Global Change Biology* **3**, 108–115.
- Tessier JT, Raynal DJ.** 2003. Vernal nitrogen and phosphorus retention by forest understory vegetation and soil microbes. *Plant and Soil* **256**, 443–453.
- Thies JE, Singleton PW, Bohlool BB.** 1995. Phenology, growth, and yield of field-grown soybean and bush bean as a function of varying modes of N-nutrition. *Soil Biology and Biochemistry* **27**, 575–583.
- Van Dijk H, Hautekeete N.** 2007. Long day plants and the response to global warming: rapid evolutionary change in day length sensitivity is possible in wild beet. *Journal of Evolutionary Biology* **20**, 349–357.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG.** 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**, 737–750.
- Volk M, Niklaus P, Körner C.** 2000. Soil moisture effects determine CO_2 responses of grassland species. *Oecologia* **125**, 380–388.
- Wagner J, Luscher A, Hillebrand C, Kobald B, Spitaler N, Larcher W.** 2001. Sexual reproduction of *Lolium perenne* L. and *Trifolium repens* L. under free air CO_2 enrichment (FACE) at two levels of nitrogen application. *Plant, Cell and Environment* **24**, 957–965.
- Waldrop MP, Firestone MK.** 2006. Seasonal dynamics of microbial community composition and function in oak canopy and open grassland soils. *Microbial Ecology* **52**, 470–479.
- Walther GR.** 2004. Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics* **6**, 169–185.
- Walther GR, Berger S, Sykes MT.** 2005. An ecological ‘footprint’ of climate change. *Proceedings of the Royal Society of London Series B* **272**, 1427–1432.
- Ward JK, Strain BR.** 1999. Elevated CO_2 studies: past, present and future. *Tree Physiology* **19**, 211–220.
- Whitehead SJ, Caporn SJM, Press MC.** 1997. Effects of elevated CO_2 , nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytologist* **135**, 201–211.
- Zavaleta ES, Shaw MR, Chiariello NR, Thomas BD, Cleland EE, Field CB, Mooney HA.** 2003. Grassland responses to three years of elevated temperature, CO_2 , precipitation, and N deposition. *Ecological Monographs* **73**, 585–604.
- Zhou LM, Tucker CJ, Kaufmann RK, Slayback D, Shabanov NV, Myneni RB.** 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research-Atmospheres* **106**, 20069–20083.