



Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Research article

Increases in CO₂ from past low to future high levels result in “slower” strategies on the leaf economic spectrum

Andries A. Temme^{a,*}, Jin Chun Liu^{a,b}, Jurgen van Hal^a, Will K. Cornwell^{a,c},
Johannes (Hans) H.C. Cornelissen^a, Rien Aerts^a

^a Department of Ecological Science, VU University, De Boelelaan 1085, 1081HV Amsterdam, The Netherlands

^b Key Laboratory of Eco-environment in Three Gorges Reservoir Region, School of Life Science, Southwest University, Beibei, Chongqing 400715, China

^c Ecology and Evolution Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Kensington 2052, Sydney, Australia



ARTICLE INFO

Keywords:

Leaf economic spectrum

Low CO₂

Plant traits

Growth

Photosynthesis

ABSTRACT

Depending on resource availability plants exhibit a specific suite of traits. At the interspecific level these traits follow the leaf economic spectrum (LES), traits related to slow turnover when resources are poor and fast turnover when resources are plentiful. Limited data shows that within species, CO₂ availability, low in the recent geologic past, high in the near future, has led to plants shifting their trait levels on the LES towards faster traits. We asked whether adjustments of physiological traits could underpin faster growth from low to high CO₂ and how these responses varied among plant functional types. We analysed the trait response of seedlings of up to 28 C3 plant species grown at low (160 ppm), near-ambient (450 ppm), and high (750 ppm) CO₂. We measured growth, specific leaf area (SLA), leaf gas exchange, chemical composition and stomatal traits. On average photosynthesis was reduced by 59% at low CO₂ and increased by 14% at high CO₂ compared to ambient CO₂. Respiration decreased by 21% at low CO₂ and increased by 39% at high CO₂. Nitrogen content (N) per mass increased by 50% at low CO₂ and decreased by 9% at high CO₂. Plants drastically increased SLA at low CO₂ so that despite lower carbon gain per area, carbon gain per unit mass was not reduced as much. Contrary to the responses to other resources, plant traits along the LES are adjusted towards the “fast” end of the spectrum (higher SLA, higher N) at low CO₂ and towards the “slow” end (lower SLA, lower N) with increasing CO₂. For a limited number of species photosynthesis per unit mass showed the same, increase at low CO₂. From a resource economics perspective plants thus adjust the cost for growth towards the availability of carbon and the rate of assimilation: at lower CO₂ the carbon costs decrease due to decreased respiration and lower leaf mass per area (higher SLA thinner leaves). At higher CO₂ the carbon costs increase due to increased respiration and higher leaf mass per area (lower SLA thicker leaves). This suggests that CO₂ increases from the past to the future are allowing plant species globally to combine faster growth with more robust, resource conservative leaves.

1. Introduction

When plant growth is limited by the availability of one resource, economic theory dictates that in successful individuals the capacity to acquire other more plentiful resources should be limited; this is because it does not pay to have excess capacity in one area when resources in another cannot keep up (Bloom and Mooney, 1985; Chapin et al., 1987). Thus, the Leaf Economic Spectrum (LES) predicts that habitats of poor resource availability host plant species that exhibit a concerted predictable suite of traits that can be linked to slow matter cycling (slow leaf turnover, low nutrient content, thick tough leaves of low specific leaf area (SLA), slow growth), while habitats where resources are plentiful host species linked to fast cycling (high leaf turnover, high

nutrient content, thin “throw away” leaves of high SLA, fast growth) (Lambers and Poorter, 1992; Wright et al., 2004; Reich, 2014; Niinemets, 2015).

The availability of carbon, as an important growth-limiting resource, has greatly increased from a Pleistocene low (~180 ppm CO₂) (Hönisch et al., 2009) to current levels (~400 ppm) and will increase even more moving to high levels (possibly even >> 800 ppm) towards the end of this century (Ciais et al., 2013). From a carbon centric point of view growth rate of plants is dependent on plant morphology related to carbon uptake and plant physiology related to carbon processing (Evans, 1972; Lambers and Poorter, 1992). Up to date, different studies have assessed how plants adjust traits to carbon availability (Gerhart and Ward, 2010; Temme et al., 2013, others), as well as how the

* Corresponding author.

E-mail address: aatemme@gmail.com (A.A. Temme).

<https://doi.org/10.1016/j.ppees.2017.11.003>

Received 8 September 2016; Received in revised form 3 November 2017; Accepted 8 November 2017

Available online 11 November 2017

1433-8319/ © 2017 Elsevier GmbH. All rights reserved.

direction of these adjustments relates to variation in growth rate (Temme et al., 2015).

With current global change featuring rising CO₂ and increasing temperatures, most research in this field has focused on plants' response to high CO₂ (Gerhart and Ward, 2010; Temme et al., 2013). However, the effects of high CO₂ also the effects of low CO₂, as common for the past 10 Ma before the Industrial Revolution, should be considered in order to obtain a full picture of plants' responsiveness to CO₂. Plant physiology is strongly adjusted by CO₂ concentrations from transient to evolutionary time-scales (Medlyn and McMurtrie, 2005) with potential legacy effects of evolution in a low CO₂ atmosphere (Sage and Coleman, 2001; Zhu et al., 2004). Experiments have shown that plant trait responses to low CO₂ are far greater in magnitude than those to high CO₂ (Hattenschwiler and Korner, 2000; Quirk et al., 2013; Temme et al., 2013, 2015). However, unlike for other resources it has been found that, among plant species, there does not appear to be a trade-off in traits relating to carbon acquisition from Pleistocene low to future high CO₂ concentration, i.e. no species appears particularly suited to either low or high CO₂ (Temme et al., 2015). This is likely caused by carbon availability in open vegetation varying only little in space and only slowly and gradually in time until the Industrial Revolution (Hönisch et al., 2009). Carbon dioxide can be a selective agent on plant functioning, as indicated for instance by the repeated evolutionary appearance of C₄ plants with carbon-concentrating mechanisms for photosynthesis (Edwards et al., 2010; Christin and Osborne, 2014) as well as by the dominance of C₃ plants in the Holocene (Huang et al., 2006). However, we do not know whether the very rapid increase in CO₂ concentration since pre-industrial low levels and into the near future could show a similar trait CO₂ responsiveness to those in the Holocene (Sage and Coleman, 2001; Franks et al., 2013).

In a multispecies study on plant responses to a range from low to high CO₂ we confirmed that among species, at ambient CO₂ conditions, high SLA is linked with fast growth (Temme et al., 2015), as in previous studies (Lambers and Poorter, 1992; Cornelissen et al., 1996; Reich, 2014). However, contrary to what one would expect within species, low (past) carbon availability resulted in a “faster” morphology (high SLA) compared to that at ambient CO₂ but was at the same time associated with slower growth. Correspondingly, higher (future) carbon availability resulted in a “slower” morphology (lower SLA) but also faster growth than at ambient CO₂. Together, these responses go so far as to result in a decoupling of growth rate response from morphology response from low to high CO₂ (Temme et al., 2015). However, how CO₂ from past low to future high affects physiological traits (gas exchange traits, stomatal traits, respiration, and chemical composition) and how leaf morphological and those physiological traits along the LES combine to affect growth performance of plants at a range of low to high CO₂ has remained an open question so far (Medlyn and McMurtrie, 2005; Smith et al., 2012; Sack et al., 2013).

Experiments manipulating atmospheric CO₂ levels have shown a consistent adjustment in physiological traits within species. Low CO₂ strongly reduces photosynthetic rates and increases stomatal conductance and transpiration (Gerhart and Ward, 2010; Temme et al., 2013) whereas high CO₂ increases photosynthetic rate and decreases stomatal conductance and transpiration to a far lesser extent (Ainsworth and Rogers, 2007; Norby and Zak, 2011). At low and high CO₂, relative to ambient CO₂, plants' leaf area ratio (leaf area per plant mass, LAR) is strongly adjusted, following the response of one of its components, SLA (Temme et al., 2013, 2015). Plants drastically increase LAR at low CO₂ and decrease it at high CO₂. Under unchanged unit leaf rate (plant biomass production rate per unit leaf area, ULR) this would be expected to lead to faster growth at low CO₂ and slower growth at high CO₂, as relative growth rate (RGR) is the product of LAR and ULR (Lambers and Poorter, 1992). However, in reality quite the opposite happens because ULR, which is related to photosynthetic rates, is itself also affected by CO₂ availability (Poorter and Navas, 2003). Thus CO₂ starvation leads to reduced growth (Temme et al., 2015) and

excess CO₂ enhances growth (Poorter and Navas, 2003; Ainsworth and Rogers, 2007; Norby and Zak, 2011). This would imply stronger shifts in ULR in response to CO₂ that are only partially compensated for by altered leaf morphology and/or allocation (SLA, LAR).

Gas exchange and chemical composition are the key traits underlying biomass production per unit leaf rate (Evans and Poorter, 2001; Poorter et al., 2014). Important in plants' physiological response to CO₂ are the stomata as the entry point of CO₂ into the leaf. Over past geological cycles of shifts in CO₂, stomata have been relatively small and numerous during periods of low CO₂ (promoting high maximum stomatal conductance) and large but low in density during periods of high CO₂ (low maximum stomatal conductance) (Woodward, 1987; Franks and Beerling, 2009; de Boer et al., 2012). A higher stomatal conductance allows for greater carbon uptake at low CO₂ levels whereas at high CO₂ a developmentally lower maximum stomatal conductance allows for greater fine-tuning of stomatal conductance (Drake et al., 2013).

Besides by gas exchange leaf chemical composition is strongly altered by CO₂, with greater nitrogen content at low CO₂ (Temme et al., 2013). This may reflect greater investment into RuBisCO in order to facilitate the drawdown of CO₂ in photosynthesis via a stronger diffusion gradient. On the other hand the increase of nitrogen at low CO₂ might also be due to luxury consumption of nitrogen by small carbon-starved plants (Chapin, 1980). At higher CO₂, generally, nitrogen content is reduced (Ainsworth and Rogers, 2007). This reduction could be due to increased carbohydrate accumulation and/or redistribution of nitrogen towards other growth limiting steps (Díaz et al., 1993). Alternatively, closure of stomata to reduce transpiration at higher CO₂ limits the water flux through the roots, thereby possibly reducing N uptake (Taub and Wang, 2008). A comprehensive understanding of the linkages between gas exchange, stomatal traits, chemical composition and growth performance across the range from low to high CO₂ is still missing however, especially because empirical data on plant responses to low CO₂ are still scarce (Gerhart and Ward, 2010; Franks et al., 2013; Temme et al., 2013).

How the concerted trait shifts of individual species in response to CO₂ levels affects community composition requires broad generalizations. Scaling up individual species' responses to ecosystems is generally done by classifying species by functional type (Chapin et al., 1996). Whether and how different plant functional types (PFT), notably grasses, forbs and woody species, respond to CO₂ will provide a basis for (back-)predicting potential shifts in community composition from the low CO₂ past to the high CO₂ near future (Prentice and Harrison, 2009). Importantly in this context, dynamic global vegetation models that are coupled to global circulation models to predict biogeochemical cycling and climate at different CO₂ regimes, use similar functional types and traits (Sitch et al., 2008; Verheijen et al., 2015a,b). In relation to carbon availability different PFTs show different responses in traits to low CO₂ (Temme et al., 2013, 2015) versus high CO₂ (Poorter and Navas, 2003; Ainsworth and Rogers, 2007; Norby and Zak, 2011) but, again, information on physiological responses to low CO₂ is still minimal and based on a very small number of species (Temme et al., 2013).

With humanity increasingly altering the carbon cycle at an unprecedented rate through fossil fuel emissions and land use change, understanding plants' response to future conditions becomes increasingly important. Given plants' >>> 10Ma year evolution in a low CO₂ atmosphere, understanding how plants function at low CO₂ could shed light on how plants will respond to future high CO₂ environments. We therefore asked ourselves the following questions:

- How are leaf physiological traits related to plant carbon uptake affected by CO₂ from past low to future high levels and are there consistent differences in the response among plant functional types?
- How do the changes in leaf morphological traits in response to low versus high CO₂ serve to underpin the changes in plant physiology

Download English Version:

<https://daneshyari.com/en/article/8849536>

Download Persian Version:

<https://daneshyari.com/article/8849536>

[Daneshyari.com](https://daneshyari.com)