Plant Traits and Production Rates from CO2 Starvation to Saturation

Temme, A.A.

2016

document version
Publisher's PDF, also known as Version of record

Link to publication in VU Research Portal

citation for published version (APA)
Temme, A. A. (2016). *Plant Traits and Production Rates from CO2 Starvation to Saturation*. [, Vrije Universiteit Amsterdam]. CPI-Koninklijke Wöhrmann.

Chapter 1

General Introduction

Rising CO$_2$: from the low past to the high future

Carbon is an essential resource for plant growth. To live and grow terrestrial plants take up carbon in the form of CO$_2$, where it diffuses into the leaf through the stomata. Subsequently, in the chloroplasts, it is converted into the sugars necessary for maintaining plant metabolism and contributing to plant growth. Throughout the history of plant life on Earth CO$_2$ levels have varied from a high 3000 ppm in the early Devonian ($\sim$ 400 Myr ago) (Royer 2006) to a low 180 ppm during the Pleistocene glacials ($\sim$20 Kyr ago) (Petit *et al.* 1999). For the past 10 Myr to 20 Kyr ago the CO$_2$ concentration has been broadly around this 180 ppm low point, only half of today's level. Today's levels are higher due to fossil fuel emissions and land use change since the Industrial Revolution. Since then, over the past two centuries atmospheric CO$_2$ levels have risen from 280 ppm just before the Industrial Revolution to currently $\sim$400 ppm (IPCC 2015). Furthermore, over the coming century CO$_2$ levels have been expected to rise even more to around 800 ppm (Meinshausen *et al.* 2011) **(Fig 1.1)** although measures to be taken based on the recent global agreement to reduce climate warming this century to 1.5 to 2 °C only (Paris Summit, 12 December 2015) may lead to a lesser increase in CO$_2$. Even under a scenario of strongly reduced carbon emissions, plants have not experienced such a high level for over 40 Myr (Franks *et al.* 2014). Plants are thus rapidly moving from a long period of low CO$_2$ availability to a period of high CO$_2$ availability.

Given the rapid rise to a high CO$_2$ atmosphere, it is easy to understand why considerable research has been done on how plants respond to elevated CO$_2$. Initially, growth chamber studies on the effect of high CO$_2$ in crop species showed a strong fertilization effect of elevated CO$_2$ (Jablonski, Wang & Curtis 2002). Based on this it was predicted that elevated CO$_2$ would lead to plants growing larger with higher crop yields (Jablonski *et al.* 2002). More recently, studies have been undertaken from small individual plant containers to open top enclosures, larger growth chambers and greenhouses and all the way to forest canopy level Free-air Carbon dioxide Enrichment (FACE) plots. FACE plots are especially useful as they allow for assessing the effect of elevated CO$_2$ in a more natural setting. Interestingly, more recent research employing FACE plots has found that the CO$_2$ fertilization effect is far lower when other resources are more limiting than in crop settings (Ainsworth & Long 2005, Ainsworth & Rogers 2007, Norby & Zak 2011). This shows that responses of plants to elevated CO$_2$ are difficult to scale up from greenhouses and growth chambers to the field where other environmental factors can constrain the response of plants to CO$_2$ (Ainsworth *et al.* 2013, Parmesan & Hanley 2015).

Compared to the tremendous research effort to understand plant responses to high CO$_2$ relatively little is known on plants' responses to low CO$_2$ representing atmospheres of the past (Gerhart & Ward 2010). Based on data from the pollen record and modelling efforts we know that global vegetation was markedly different during the low CO$_2$ Pleistocene glacials. While a multitude of factors are different between the Pleistocene glacial world and today, the effect CO$_2$ concentration had on plant physiology is an important aspect driving modelled differences (Prentice, Harrison & Bartlein 2011). Experiments have shown that a low CO$_2$ environment leads to plants growing slower, delaying onset of flowering and with reduced seed numbers and seed mass (Gerhart & Ward 2010). Furthermore, biomass allocation to belowground tissues is strongly reduced at low CO$_2$, which may have had a large

impact on the carbon cycle by substantially slowing chemical weathering rates (Beerling *et al.* 2012). Moreover, experimental evolution studies have shown that low CO_2 is a stronger selective agent than high CO_2 (Ward *et al.* 2000). As the enzyme kinetics of the photosynthesis enzyme RuBisCO are fine-tuned to 200ppm CO_2 (Zhu, Portis & Long 2004) this indicates the potential for legacy effects of plants' recent evolution in a low CO_2 atmosphere. While we have to be careful to infer evolutionary adaptation based on phenotypic responses to different CO_2 levels (Onoda, Hirose & Hikosaka 2009) exploring plant responses to low CO_2 can thus help in our understanding of responses to future high CO_2 (Tissue & Lewis 2012).

CO_2 effects on plant types and plant traits

With over 350000 plant species on Earth ("The Plant List") it is necessary to find common patterns among species in order to make general predictions on plant responses to environmental factors. This search for commonality can be achieved via the plant functional type (PFT) concept (Chapin *et al.* 1996). In PFT's plant species are grouped by similarities in their morphology and physiology **(Fig 1.1)**. As a result of different growth form strategies and physiological mechanisms, plant functional types could show contrasting responses to shifts in CO_2 concentration. For example, investing a lot of C in non-photosynthetic woody stem tissue at low CO_2 might lead to woody species being outcompeted by grasses or forbs that can invest more in carbon acquiring leaf tissue (Bond and Midgley 2012). Conversely, at high CO_2 their greater CO_2 stimulation (Ainsworth and Long 2005) might lead them to outcompete grasses and forbs. Different PFT's may thus show different responses to low and elevated CO_2 with the potential for shifts in dominant vegetation.

Next to the broad categorizations of species into PFT's it can be useful to compare species for variation within the set of relevant traits a species exhibits (Violle *et al.* 2007). Not only should species traits be compared in given environmental settings, but also for how they respond to different environmental drivers (Pieruschka & Poorter 2012). Plant traits or properties such as photosynthetic rate, specific leaf area, biomass allocation to leaves, roots and stems, stomatal conductance, seed number can be categorized into several categories depending on their effect on plant fitness, growth and their effect on the environment. Thus when plants adjust trait levels in response to CO_2 this will have effect on their fitness, growth rates and on their environment.

Plant functional types are a useful tool in classifying species and allow for broader generalizations to a larger number of species, for instance in dynamic global vegetation models (Sitch *et al.* 2008, McMahon *et al.* 2011). However, plant functional types are generally fixed for the specific traits they express. Far from being fixed however, plant traits can both vary between species within PFT's and be flexible in response to environmental conditions; and influence those conditions in turn. Differences in the direction and magnitude of trait responses to CO_2 between species could thus also lead to shifts in competitive interactions between species (Ali *et al.* 2015). Recent inclusion of variable traits instead of fixed PFT's in a global vegetation model had profound effects on model outcomes in terms of global vegetation distribution and climate parameters (Verheijen *et al.* 2015a). Thus a key next step in improving vegetation models is to quantify the plasticity of different traits in relation to changing CO_2.

In the carbon centric point of view (Evans 1972), plant growth can be understood as being comprised of a morphological and a physiological component. Plants can exhibit ranges of values for morphological traits related to fast growth (e.g. high leafiness, thin leaves) and for physiological traits related to fast growth (e.g. high nitrogen content, high photosynthetic rates) (Poorter & Garnier 2007). These morphological and physiological traits are generally coordinated within species so that they fall along a coordinated interspecific spectrum of traits related to slow and fast growth called the Leaf Economic Spectrum (LES) or Plant Economic Spectrum (PES) (Wright *et al.* 2004, Freschet, Aerts & Cornelissen 2012, Reich 2014). Depending on resource availability, plants interspecifically adopt a slow suite of traits (morphological and physiological traits related to slow growth) at poor resource conditions or a fast suite of traits (morphological and physiological traits related to fast growth) at rich resource conditions. As CO_2 availability directly influences traits along the LES or PES, viewing the effect of CO_2 in this resource economics framework can inform us about whether and how CO_2 forces shifts of species position along the LES and their capacity to tolerate poor resource conditions.

Species shifts in trait level at different CO_2 concentrations reflects trait plasticity at short time scales (Nicotra *et al.* 2010) but at longer timescales adaptive evolutionary changes can also result in shifts in trait level (Medlyn & McMurtrie 2005). Plants' long history in low CO_2 and the rapid transition to high CO_2 could indicate the potential for legacy effects of evolution in a low CO_2 world (Sage & Coleman 2001). Traits favourable in a low CO_2 atmosphere (RuBisCo activity and efficiency, high N investment in photosynthesis, thin leaves) (Loreto *et al.* 1992, Sage 1994) are not as beneficial in a high CO_2 atmosphere when nutrient and water uptake are increasingly more limiting to growth (Ward *et al.* 1999, Reich *et al.* 2006, Campbell & Sage 2006). Thus traits resulting from plants' evolutionary history at low CO_2 could constrain their response to the rapid rise towards high CO_2.

CO_2 effects on the terrestrial carbon cycle

Plants take up carbon from the atmosphere through photosynthesis, after which it is either respired again to sustain plant metabolism, invested into tissues for new carbon assimilation or incorporated into biomass. As plants senesce and die this carbon stored in biomass is transferred to the soil where it is part of the pool of soil organic carbon and is potentially metabolised by decomposers. The rates of these active processes and passive 'after-life' effects have large impacts on the terrestrial carbon cycle (Austin & Zanne 2015). Climate models have to take into account how plants influence the terrestrial carbon cycle in order to determine how fossil fuel emissions and land use change will change global and local climate over the coming years (IPCC). Thus how CO_2 levels impact plant traits that involve biogeochemical cycling, both on the biomass production side and on the biomass loss side (herbivory, decomposition, fire), is a key component in successfully projecting the global carbon cycle and future climate.

The role of plants in the terrestrial carbon cycle via carbon assimilation, respiration, biomass accumulation and decomposition is affected by the availability of CO_2. Plants have low photosynthesis at low CO_2 and increasing CO_2 leads to higher photosynthetic rates following a saturating curve (Franks *et al.* 2013). Interestingly, for transpiration the opposite

is true, as plants need to be water spenders at low CO_2 due to the high stomatal aperture under those conditions and become increasingly water conservative at high CO_2 (Voelker et al. 2015) as the stomata can be closed further or more often. The effect of CO_2 on plant respiration is more difficult to determine as it is highly dependent on other factors such as temperature. Greater investment in photosynthetic machinery at low CO_2 could lead to higher respiration rates at the same temperature (Sage & Coleman 2001). The reduced photosynthetic rates at low CO_2 lead to severely reduced biomass accumulation of plants which, in turn, leads to much lower carbon storage in standing biomass (Prentice & Harrison 2009). Decomposition rates however, are not strongly impacted by elevated CO_2 (Norby et al. 2001, Hungate et al. 2013). Lastly, the relative performance of plant species under different CO_2 concentrations can lead to shifts in the dominance of trees versus grasses (Bond & Midgley 2012). This may in turn have severe consequences for C storage in a region due to the different C storage dynamics of tree versus grass-dominated ecosystem types. Thus there exists an important feedback between atmospheric CO_2 and plant traits that in turn influence that same CO_2 concentration.

CO_2 and other resources

While carbon is an important resource generally comprising a large proportion of plant biomass, plants are also dependent on several other resources for growth such as light, nutrients and water. Because of this there is disagreement about the validity of taking a carbon centric point of view in analysing plant growth (Fatichi, Leuzinger & Körner 2013, Körner 2015). However, traits that are involved in carbon uptake do have a large explanatory power in understanding differences in plant growth (Lambers & Poorter 1992, Poorter & Garnier 2007) and in understanding the effect of CO_2 on plant performance (Poorter & Nagel 2000, Poorter & Navas 2003, Poorter et al. 2012b). Furthermore, there is evidence for trade-offs between growth responses to CO_2 and to other resources, such as phosphorus and nitrogen availability which may dampen the fertilization effect of CO_2 (Campbell & Sage 2006, Lewis, Ward & Tissue 2010). Also, increasing CO_2 may improve plants' tolerance of drought (Quirk et al. 2013, Jin et al. 2014, Kelly et al. 2015). Thus when researching the effect of CO_2 on plant performance, the carbon centric point of view is worthwhile but interactions with other environmental factors should be taken into account.

Fluxes of water and CO_2 are closely linked through the stomata in the leaf. As stomata are opened to allow CO_2 to enter the leaf, water is lost through transpiration. Far from being wasteful this transpiration drives the transport of nutrients from the roots to the leaves. Nevertheless, should water availability decrease due to drought then plants need to close their stomata to prevent xylem cavitation and turgor loss. If the drought then persists it is the lack of water that kills the plant, not the lack of carbon assimilation (Hartmann et al. 2013, O'Grady et al. 2013). At low CO_2 plants have to open their stomata more to keep internal CO_2 concentration in the leaf high. With rising CO_2 plants could thus be increasingly water conservative as they are able to keep their stomata more closed (Voelker et al. 2015). However research has shown that the complete story is more complex with plants having differing responses to drought at low CO_2 (Ward et al. 1999, Quirk et al. 2013) and at high CO_2 (Medeiros & Ward 2013). As droughts were more common in the past (Yung et al. 1996, Lambert et al. 2008) and are expected to increase again in frequency and intensity in

the future (IPCC 2015), understanding the effect of past and future droughts on plant traits in a given CO_2 environment aids in understanding the interactions of water availability with the carbon cycle and climate.

Research aims and questions

From a long period of low CO_2 availability plants are rapidly moving towards life in a high CO_2 atmosphere. Humanity is increasingly altering the global climate by high levels of fossil fuel emissions and land use change. To make correct projections on the world's future vegetation distribution and climate it is important to take into account the interactions between vegetation, climate and atmosphere. While considerable research has been done in understanding plants' response to elevated CO_2, far less is known on plants' response to low CO_2 as has been common for a large part of the past 10 Myr (Royer 2006, Franks *et al.* 2014). Therefore I come to the following aims and questions:

» To better understand plant functioning at CO_2 concentrations representing those of the recent geological past

» To improve our understanding of plants' role in the terrestrial carbon cycle in the past, present and future

Thereto, I tried to answer the following research questions:

» How are the morphological and physiological traits of plants affected by CO_2 from past Pleistocene low to future high concentrations?

» Are there differences in response to CO_2 from past low to future high concentrations between woody, forb and grass plant types?

» Are there interactive effects between water availability and CO_2 availability on plant functioning?

To answer these questions I chose to screen a wide range of species representing wide-ranging C_3 plant strategies and growth forms, for their morphological, physiological and growth responses to variation both in CO_2 and water availability. I have divided this research into four parts, consisting of a literature meta-analysis of responses to CO_2 and three experimental chapters that are outlined in figure 1.1. Each part comprises a chapter in this thesis and these chapters are followed by a general discussion in which I return to the broader aims presented here.

Chapter 2: Meta-analysis reveals profound responses of plant traits to past glacial CO_2

In order to determine knowledge gaps and assess the extent of the research that has been done in determining the effect of past low CO_2 on plant functioning, I have surveyed the literature for quantitative data for a range of species and analysed plants' responses in a meta-analysis. From this meta-analysis we are able to determine some generality of plants' response to CO_2 and make a preliminary assessment of the magnitude of response to low versus elevated CO_2.
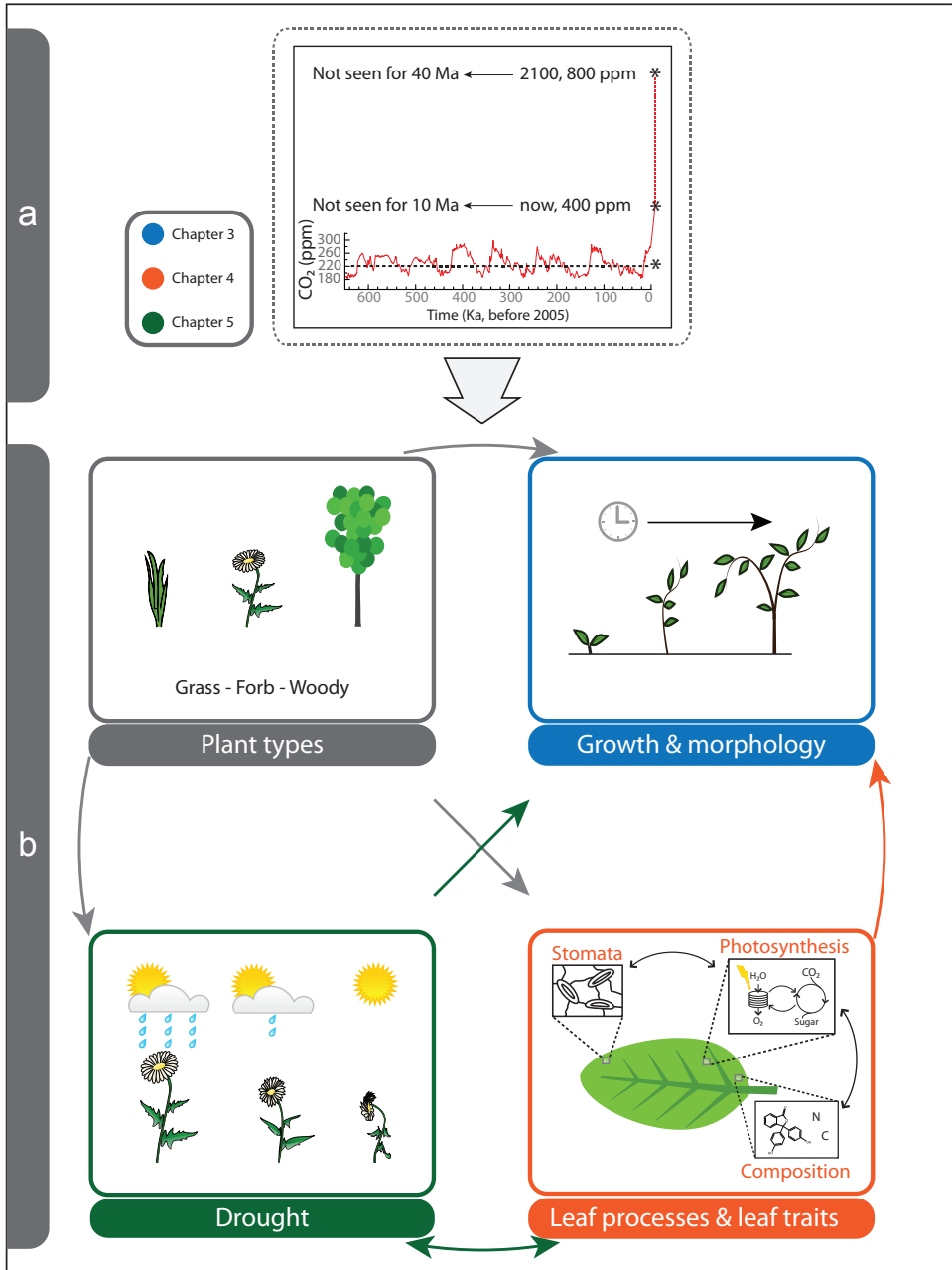
Figure 1.1 Schematic representation of the connections among the different components of the experimental work in this thesis. **(a)** CO_2 concentration, low in the recent past, currently already high and rising even further in the near future, influences plants. (graph modified from IPCC 2007, (Royer 2006)). **(b)** Chapter 3 (blue): CO_2 influences on growth and morphology of plants. Chapter 4 (orange): CO_2 influences on leaf processes and leaf traits and how they impact growth and morphology of plants. Chapter 5 (green): Interaction of CO_2 and drought and how both factors influence leaf processes and growth. All chapters (grey): Different plant types can show varying responses to CO_2 and respond differently in their growth, morphology and leaf processes.

Chapter 3: Winners always win: growth of a wide range of plant species from low to future high CO_2

In this first experimental chapter I address the morphological and growth response of up to 28 C_3 species at past low CO_2 (160 ppm), current ambient CO_2 (450 ppm) and future high CO_2 (750 ppm). I also address the relative differences between woody, grass and forb functional types and the effect of a 'fast growth morphology' on relative growth rates in relation to CO_2.

Chapter 4: Increases in CO_2 from past low to future elevated levels result in 'slower' strategies on the leaf economic spectrum

In this chapter I address the effects of CO_2 on plant physiology, chemical composition and stomatal characteristics. I determine the concerted adjustments in leaf traits plants employ to maintain high per-mass photosynthesis and view the effects CO_2 has on traits along the 'slow-fast axis' of the leaf or plant economic spectrum.

Chapter 5: Hungry and thirsty: interactive effects of low to high carbon and water availability on plant performance in 7 C_3 annuals

For a subset of 8 species I determine if there are interactive effects between drought and CO_2 and if there are trade-offs between drought tolerance and CO_2 responsiveness. I assess how differences in plant size due to CO_2 availability affect the sensitivity to reduced precipitation at three levels of water availability.

Chapter 6: General discussion

In the discussion I synthesise the results of the previous chapters on plant traits and plant types. I discuss the potential effect of plant trait adjustments due to CO_2 on the terrestrial carbon cycle and I discuss our findings in the context of the wider paleo-ecological record. I also discuss the importance of plastic response versus evolutionary adaptation to environmental conditions. Lastly I give some avenues for future research.

Experimental set-up for chapters 3-5

Whereas high CO_2 can be achieved by adding CO_2 to the environment from flasks or CO_2 generators, removing CO_2 is technically more challenging. Early studies have used plants CO_2 uptake as a method of reducing CO_2 in long connected tube compartments (Mayeux *et al.* 1993, Polley *et al.* 1993). More recent studies have reduced CO_2 by bubbling air through highly concentrated soda-lime solutions (Kgope, Bond & Midgley 2010) or by forcing pressurised air through a molecular sieve (Ripley, Cunniff & Osborne 2013). Compared to greenhouses and climate chambers the open Free Air Carbon Dioxide Enrichment (FACE) plots allow for testing the effect of elevated CO_2 in a natural real-world setting. For lowering CO_2 the rapid diffusion of CO_2 through the air makes an open FACE-like approach unfeasible. To keep CO_2 concentration low in such an open area, a continuous stream of low CO_2 air would have to be blasted into the plot at hurricane speeds (C. Osborne personal comment). Therefore, while FACE plots may be an excellent way to test the effects of elevated

CO_2, in this study where low CO_2 is an important aspect I have used controlled climate chambers where CO_2 is reduced by forcing air through a molecular sieve. The experimental work was performed in growth chambers at three different CO_2 concentrations (160 ppm, 450 ppm and 750 ppm CO_2).