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## Plant Traits and Production Rates from CO2 Starvation to Saturation

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# Summary

Throughout the history of plant life on Earth levels of the essential plant resource  $\text{CO}_2$  have varied from a high 3000 ppm in the early Devonian ( $\sim 400$  Myr ago) to a low 180 ppm during the Pleistocene glacials ( $\sim 20$  Kyr ago). For the past 10 Myr to 20 Kyr ago the  $\text{CO}_2$  concentration has been broadly around this 180 ppm low point, less than half of today's level. Over the past two centuries atmospheric  $\text{CO}_2$  levels have risen from 280 ppm just before the Industrial Revolution to currently  $\sim 400$  ppm. Furthermore, over the coming century  $\text{CO}_2$  levels are expected to rise even more to around 800 ppm if no special action is taken. Plants have not experienced such a high level for over 40 Myr and are thus rapidly moving from a long period of low  $\text{CO}_2$  availability to a period of very high  $\text{CO}_2$  availability.

In light of this rapid change the aims of this thesis were (1) to better understand plant functioning at  $\text{CO}_2$  concentrations representing those of the recent geological past and (2) to improve our understanding of plants' role in the terrestrial carbon cycle in the past, present and future. Such understanding may help us to interpret whether and how traits underpinning plants' long-term adaptations to a low  $\text{CO}_2$  atmosphere may have left a legacy on their responsiveness to future higher levels.

Compared to the large body of work on the response of plant species to high  $\text{CO}_2$  comparatively little is known on how plants respond to low  $\text{CO}_2$  representing conditions of the past. In an attempt to begin to fill this knowledge gap, in chapter 2, I performed a meta-analysis based on available literature reporting results from low  $\text{CO}_2$  growth experiments; which consisted of 34 studies with 54 species in total. I quantified how plant traits vary at reduced  $\text{CO}_2$  levels and whether  $\text{C}_3$  versus  $\text{C}_4$  and woody versus herbaceous plant species respond differently. At low  $\text{CO}_2$  as in the past, plant functioning changed drastically. Low  $\text{CO}_2$  reduced net photosynthesis by 38% ( $A_{\text{net}}$ ), increased stomatal conductance by 60% (enabling stomata to open more to capture more precious  $\text{CO}_2$ ) and decreased intrinsic water use efficiency by 48%. Total plant dry biomass decreased by 47% while specific leaf area (SLA; leaf area per mass) increased by 17%; i.e. leaves became thinner or less dense, maximizing light-capturing area with minimal investment of the scarce element carbon. While the meta-analysis yielded interesting results on plants' responses to low  $\text{CO}_2$ , a clear picture of how the morphological and physiological traits related to carbon uptake are adjusted by  $\text{CO}_2$  in concert was still lacking. This is why I went for a multi-species experimental approach in chapters 3-5, where I obtained robust new data by screening wide-ranging herbaceous and woody plants for a broad range of relevant traits across a range of relevant  $\text{CO}_2$  concentrations representing past, present and near-future atmospheres.

Evolutionary adaptation to variation in resource supply has resulted in plant strategies that are based on trade-offs in functional traits. In chapter 3 I investigated, for the first time across multiple species, if such trade-offs were also apparent in growth and morphology responses to  $\text{CO}_2$  concentration. I grew young plants of similar ontogenetic phase of up to 28  $\text{C}_3$  species (16 forbs, 6 woody and 6 grasses) in climate chambers at 160 ppm, 450 ppm and 750 ppm  $\text{CO}_2$ . I determined total biomass, biomass allocation between different parts, specific leaf area (SLA), leaf area ratio (LAR; total leaf area per total plant mass) and relative growth rate (RGR), thereby doubling the globally available data on these plant responses to low  $\text{CO}_2$ . Fast growers when measured at ambient  $\text{CO}_2$  had the greatest reduction in RGR at low  $\text{CO}_2$  as they lost the benefits of a fast-growth morphology (decoupling of RGR and LAR). Despite these shifts, species ranking based on biomass and RGR was unaffected by

CO<sub>2</sub>. Thus, winners continued to win, regardless of CO<sub>2</sub>. Unlike for other plant resources I did not find any trade-offs in morphological and growth responses to CO<sub>2</sub>, i.e. changes in morphological traits appeared decoupled from changes in growth at low or high CO<sub>2</sub>.

In chapter 4 I asked whether adjustments of physiological traits could underpin faster growth from low to high CO<sub>2</sub> and how these responses varied among plant types. 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 in species from habitats where resources are poor and traits related to fast turnover in species from habitats where resources are plentiful. On the same species set as for chapter 3 I measured leaf gas exchange parameters (including photosynthetic rates), chemical composition (especially leaf nitrogen, with supports maximum photosynthetic rates) and stomatal traits related to the proportion of leaf surface area open to gas exchange. Plants drastically increased SLA by at low CO<sub>2</sub> so that despite lower carbon gain per area, carbon gain per unit mass was not reduced as much. Contrary to the responses to availability of other resources, plant traits along the LES when compared among species are adjusted towards the “fast” end of the spectrum (high SLA, high nitrogen content and higher photosynthesis per unit mass) at low CO<sub>2</sub> and towards the “slow” end with increasing CO<sub>2</sub>. This suggests that CO<sub>2</sub> increases from the past to the future are allowing plant species globally to combine faster growth with more robust, resource conservative leaves.

Due to anthropogenic climate change periods of low water availability are expected to increase in frequency and or severity in large parts of the world. In chapter 5 I determined how drought affects CO<sub>2</sub> responses and if there were trade-offs in responsiveness to CO<sub>2</sub> and drought. I subjected a subset of seven C<sub>3</sub> annuals from chapters 3 and 4 to two levels of reduced soil water availability (SWA). Compared to well-watered conditions the relative effect of drought was the same at all CO<sub>2</sub> conditions. Plant size was therefore a key element in the absolute response to SWA decrease. Thus, in absolute terms the larger, faster growing species were more affected by drought at high CO<sub>2</sub>. Biomass allocation was not affected by drought, but these species invested relatively less in belowground tissue at low CO<sub>2</sub>. These findings suggest that, when plants grow faster and larger at future high CO<sub>2</sub> conditions, the effects of drought may become more noticeable with potentially large effects for highly productive plant species.

With rising CO<sub>2</sub> leading to shifts in climate and given the very rapid rise from a low CO<sub>2</sub> atmosphere to an elevated CO<sub>2</sub> atmosphere, understanding how plants respond and adapt to this changing environment is crucial. Future research on plants' responses to CO<sub>2</sub> should therefore focus on the effect of a long evolutionary history at low CO<sub>2</sub> on the response to elevated CO<sub>2</sub> and other environmental resources. Trait correlation networks can be used to find trade-offs in response to multiple environmental factors. More long term field experiments should be done comparing CO<sub>2</sub> and other resources to test the effect on community composition. By studying plant functioning and evolutionary history at conditions already different from today due to ongoing climate change, the extent to which plants are capable of adjusting to changing conditions can become apparent. With this knowledge long term predictions can be made that can aid in mitigation and adaptation to climate change. Understanding the past thus aids in predicting the future.

