Plant nutrient acquisition and utilisation in a high carbon dioxide world

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Abstract. Producing enough food to meet the needs of an increasing global population is one of the greatest challenges we currently face. The issue of food security is further complicated by impacts of elevated CO_2 and climate change. In this viewpoint article, we begin to explore the impacts of elevated CO_2 on two specific aspects of plant nutrition and resource allocation that have traditionally been considered separately. First, we focus on arbuscular mycorrhizas, which play a major role in plant nutrient acquisition. We then turn our attention to the allocation of resources (specifically N and C) *in planta*, with an emphasis on the secondary metabolites involved in plant defence against herbivores. In doing so, we seek to encourage a more integrated approach to investigation of all aspects of plant responses to eCO_2.

Additional keywords: arbuscular mycorrhizas, cyanogenesis, elevated CO_2, food security, nitrogen, secondary metabolism.

Introduction

Plant nutrient demand, acquisition and utilisation are all altered by changes in atmospheric CO_2 concentrations. In the context of looming fertiliser shortages (Cordell *et al*. 2009) and increasing global demand for food (Rosegrant and Cline 2003), we need to understand how all facets of plant nutrient dynamics will respond to a changing climate. In this viewpoint article, we focus on the impacts of elevated atmospheric CO_2 (eCO_2) on two specific aspects of plant nutrients that have traditionally been considered separately: acquisition and utilisation.

First, we consider the impacts of eCO_2 on the formation and functioning of arbuscular mycorrhizas (AM), which play a major role in plant nutrient acquisition. Second, we discuss the impacts of eCO_2 on plant allocation of resources (specifically N and C) to secondary metabolites involved in defence against herbivores. Finally, we begin to explore how these two quite different aspects of plant biology may be linked, and conclude with several readily testable hypotheses with a view to stimulating further work in this area. In so doing, we seek to better understand where our own areas of research can inform one another and to encourage a more integrated approach to investigating all aspects of plant responses to eCO_2.

Impacts of eCO_2 on arbuscular mycorrhizas

In this first section, we outline the benefits to plants of forming AM, in terms of nutrient acquisition, and discuss the impact of eCO_2 on acquisition of nutrients by AM and on C supply to the fungi. We also discuss how AM may be relatively more important with rising atmospheric CO_2. The simple model in Fig. 1 summarises the potential role of AM in nutrient supply and as a C sink in a high CO_2 world, and forms a reference point for this section.

Nutrient acquisition by AM under eCO_2

Arbuscular mycorrhizal associations are formed by the majority of terrestrial plants, including most crop species, with a specialised group of soil fungi. They play important roles in plant nutrition by providing access to soil-derived nutrients not necessarily otherwise accessible to roots (Smith and Read 2008). To date, the majority of research, both under ambient and eCO_2 conditions, has focussed on the role of AM in plant P nutrition. This is not surprising, given that in some crops, up to 100% of plant P can be delivered via the AM fungal pathway (Smith *et al*. 2004). However, AM also play an important, albeit less well studied, role in the acquisition of other essential nutrients, including N, Zn and others (Cavagnaro 2008). With global P supply expected to peak in coming decades (Cordell *et al*. 2009), we predict that the AM contribution to plant P nutrition in agricultural systems will become increasingly important. Furthermore, given the importance of both N (e.g. Daepp *et al*. 2001) and P supply (e.g. Campbell and Sage 2006) in determining the response of plants to eCO_2, it is essential that we understand how the acquisition of nutrients by AM is likely to be affected by eCO_2.

It is well established that growth of C_3 plants usually increases under eCO_2, primarily because the current daytime atmospheric CO_2 concentration (approximately 380 ppm; IPCC 2007) is still suboptimal for Rubisco, the enzyme that catalyses carbon fixation (Stitt and Krapp 1999; Ainsworth and Rogers 2007). Critically, this increase in C_3 plant growth under eCO_2 is dependent on access to sufficient nutrients. In a meta-analysis of the growth

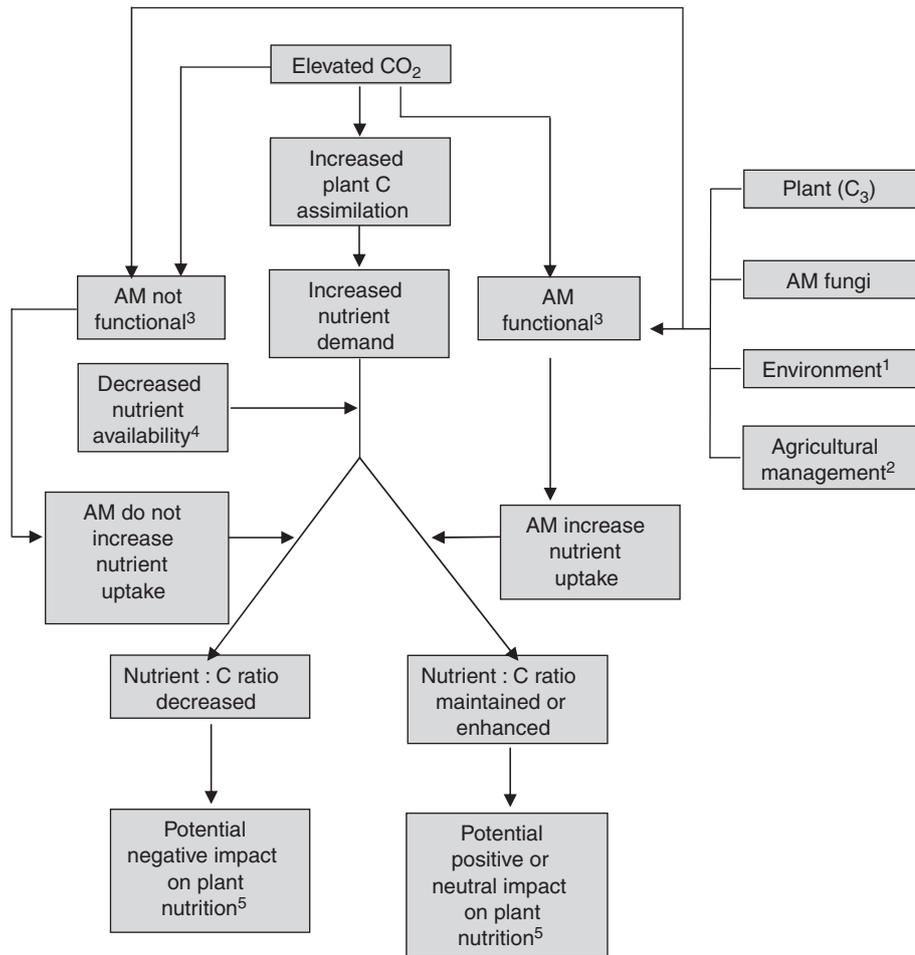**Fig. 1.**   Potential links between eCO$_2$, agricultural management, AM and plant nutrient acquisition. NB: Emphasis is on nutrient uptake and supply to (C$_3$) plants, not C supply to the fungi. (1) Environmental factors aside from eCO$_2$, e.g. edaphic, temperature, etc. (2) Tillage, nutrient management, crop rotations (including fallow). (3) AM function in this example refers to increased nutrient uptake and delivery to the plant. (4) Looming P shortage, limited access due to increased cost. (5) Impact on crop yields, nutrient content or both.

responses of herbaceous and woody species to eCO$_2$, for example, the eCO$_2$ stimulation of aboveground biomass by +20.1% was more than halved to +8.8% when nitrogen supply was limited (de Graaff *et al.* 2006). A range of other studies across grasses, crops and other functional groups report similar nutrient (N) constraints on the magnitude of the eCO$_2$ response (e.g. Wand *et al.* 1999; Nowak *et al.* 2004; Reich *et al.* 2006; Jackson *et al.* 2008). Phosphorus supply can also limit the stimulation of photosynthesis and growth by eCO$_2$; indeed, P limitation may be more critical in some systems (Edwards *et al.* 2005). Phosphorus constraints on the response to eCO$_2$ have been reported in trees and grasses (Conroy *et al.* 1992; Stöcklin *et al.* 1998), and have been widely reported among legumes (Grünzweig and Körner 2003; Edwards *et al.* 2005; Rogers *et al.* 2009), many of which form AM.

Due to greater plant biomass and carbohydrate accumulation, plants grown at eCO$_2$ almost always have lower concentrations of nutrients such as P and N (Treseder and Allen 2000; Jifon *et al.*

2002). Lower concentrations of P in the tissues of plants when grown under eCO$_2$ have been shown to be alleviated, to varying extents, by the formation of AM in some, but not all, cases (Gavito *et al.* 2002; Gavito *et al.* 2003; Cavagnaro *et al.* 2007). For example, plant P concentrations of non-mycorrhizal black locust seedlings (*Robinia pseudoacacia* L.) declined by 50% under eCO$_2$, whereas in mycorrhizal seedlings, the decline in P concentration was 22% (Olesniewicz and Thomas 1999). In a study of two *Citrus* spp., AM colonisation under eCO$_2$ stimulated plant growth and P acquisition in the more mycorrhizal-dependent of the species but not in the other (Syvertsen and Graham 1999). The effect of eCO$_2$ on AM colonisation and plant P nutrition may also vary over time (Rouhier and Read 1998; Staddon *et al.* 1999). Interestingly, in a study in *Pisum sativum* L. under eCO$_2$, the greater shoot P content and concentration of plants with AM compared with non-mycorrhizal plants could not be attributed to hyphal P uptake (Gavito *et al.* 2002). We suggest that important insights into AM and P nutrition under eCO$_2$ are

likely to come where the relative contributions of both root and fungal uptake are considered, as has been done under ambient CO_2 conditions (Smith *et al.* 2004).

As indicated previously, equally important although much less well understood, are the impacts of eCO_2 on plant acquisition of other nutrients such as N via the AM pathway. There have been fewer studies on AM-mediated N uptake both under ambient CO_2 and eCO_2. Arbuscular mycorrhizal fungi (AMF) can acquire N both as NO_3^- and NH_4^+, and transfer it to plants (Ames *et al.* 1983; Johansen *et al.* 1993). Uptake of N in its more mobile form NO_3^- by AMF is likely to be important in agricultural soils, where NO_3^- is often the dominant form of N in the soil (Bloom *et al.* 2010), but will also be important in dry soils, as limited water can interfere with NO_3^- supply to the roots (via mass flow) (Smith *et al.* 1985; Tobar *et al.* 1994; Allen *et al.* 2003). While AMF can take up both NH_4^+ and NO_3^-, it has been shown that they can take up and deliver to the plant up 10 times as much N when supplied as NH_4^+ (Tanaka and Yano 2005). Provision of N as NH_4^+ could become increasingly important in the future, as recent studies indicate that eCO_2 inhibits NO_3^- assimilation in leaves (Bloom *et al.* 2010).

Any improvements in plant N nutrition resulting from the formation of AM at eCO_2 are likely to be important, but to date only a handful of studies have investigated this directly. In one study, AMF were found to improve plant N acquisition, after a period of selection of the fungal community over several generations under eCO_2 concentrations (Gamper *et al.* 2005). Similarly, in a study on tomatoes (*Solanum lycopersicum* L.), positive mycorrhizal effects on plant N content were greater under eCO_2 than under ambient CO_2 conditions, although differences were small (Cavagnaro *et al.* 2007). Chen *et al.* (2007) found that the effects of mycorrhizal colonisation on N uptake under eCO_2 were species-specific, with N uptake enhanced by colonisation under eCO_2 in *Plantago lanceolata* L., but not in *Festuca arundinacea* Schreb. These three examples serve to highlight the potential for AMF to improve plant N acquisition under eCO_2; there is a need for further dedicated investigations in this area. The assessment of plant nutritional changes due to AM under eCO_2 may be complicated to some extent by the different ways in which plant nutrient status is reported, e.g. total nutrient content per plant or total nutrient uptake versus nutrient concentration. While total nutrient uptake may reflect AM function and be more commonly reported in the AM literature, tissue nutrient concentrations may be more important for plant nutritional value. In addition, most studies of the role of AM in plant nutrition focus on changes in nutrient concentrations (or contents); they rarely consider the fate of those nutrients *in planta*. In particular, the fate of acquired N has not been investigated in studies of AM, despite the implications for food security (see below).

Demand for C resources by AM

Producing and supporting AM comes at a cost to plants because C is required to both establish and maintain the association with the fungi. It has been hypothesised that the relative cost of forming AM is likely to decrease at eCO_2 (Treseder and Allen 2000; Jifon *et al.* 2002). This is essentially because the fungi rely solely upon the plant for their C supply; thus any increase in C assimilation and photosynthate supply to roots under eCO_2 is predicted to reduce

the relative cost of the association to the plant (Lovelock *et al.* 1997). Consistent with this, the majority of studies in which AMF biomass is measured (e.g. as extra-radical hyphal length per g soil) report either significant increases in AMF biomass or a neutral response, with no reported decreases AM biomass under eCO_2 to date (Treseder 2004; Hu *et al.* 2006; Lukac *et al.* 2010). By contrast, while most studies under eCO_2 similarly report either no change or increases in the most common measure of AM formation, the percent root colonised by AMF (Hartwig *et al.* 2002; Lukac *et al.* 2003; Gamper *et al.* 2004; Treseder 2004; Hu *et al.* 2006), decreases in percent root colonisation have also been reported (Rillig and Allen 1999; Olsrud *et al.* 2010). It is important to recognise that considering AM responses to eCO_2 in terms of AM colonisation of roots alone is likely to be an oversimplification, since the extent of colonisation is a function of both fungal and root growth (Alberton *et al.* 2005; Smith and Read 2008). Consequently, when the well-established stimulatory effects of eCO_2 on root growth are taken into account, differences in colonisation are often eliminated (Alberton *et al.* 2005). Further, changes in percent root colonisation may not be the best measure of mycorrhizal response to eCO_2 as percent root colonisation (1) does not necessarily correlate with nutrient transfer to the plant (Smith and Read 2008), (2) may underestimate the stimulatory effect of eCO_2 on the AMF as the fungal biomass response to eCO_2 is typically greater than any increase in root colonisation (Staddon *et al.* 2004; Treseder 2004; Hu *et al.* 2006), and (3) may be found not to change, despite significant eCO_2 effects on a range of other measures of AM such as the intensity of colonisation (i.e. hyphal number per root length) or the frequency and abundance of arbuscules and vesicles (Rillig *et al.* 1998; Gamper *et al.* 2004).

AM have both intra- and extra-radical phases of colonisation. The intra-radical phase involves fungal penetration of the root epidermis, and growth between and within the cortical cells, where arbuscules and hyphal coils, across which nutrients are transferred, are formed (Smith and Read 2008). Since nutrients are transferred from the fungi to the plant across the arbuscular interface, impacts on arbuscule production may be more informative than impacts on total colonisation. Arbuscules themselves exhibit variable responses to eCO_2 (Klironomos *et al.* 1998); however, given their rapid rates of turnover, this is perhaps not unexpected. The impacts of eCO_2 on the extra-radical phase of colonisation, which involves the growth of the fungi into the soil beyond the roots, will also be important (Rillig 2004; Collins-Johnson *et al.* 2005), especially where function is also taken into account. For example, in one study, an increase in hyphal production under eCO_2 did not result in an increase in P uptake (Sanders *et al.* 1998).

Further studies done at finer spatial scales (Cavagnaro *et al.* 2001; Dickson 2004) and using multiple time points (Garcia *et al.* 2008) will be important in determining the impact of eCO_2 on both the intra- and extra-radical phases of colonisation. Ideally, we should move beyond simple counts of percent root colonisation (Alberton *et al.* 2005) and embrace the information afforded by (1) advanced microscopic techniques to give measurements of changes in the area of symbiotic interface (Bago *et al.* 1998; Dickson and Kolesik 1999), (2) visualisation of metabolically active and inactive fungal biomass (Dickson and Smith 2001; van Aarle *et al.* 2005), and (3) genomic and

proteomic analyses of nutrient transport processes (Glassop *et al.* 2005; González-Guerrero *et al.* 2005, 2007). All these methods, which are more costly and time-consuming than quantification of the percentage of the root length colonised by the fungi, would also need to be verified against both the rate of nutrient acquisition and impact on plant growth and development. Given that AM exhibit a considerable functional diversity in terms of their impacts on plant growth and nutrition (Smith *et al.* 2004; Cavagnaro *et al.* 2005), and the diversity in the eCO$_2$ response of plant species from different functional groups (e.g. C$_3$, C$_4$, legumes, and woody or herbaceous) there is a need to study the responses of a wide variety of plant–fungal combinations under eCO$_2$ and differing nutrient supply (Alberton *et al.* 2005; Collins-Johnson *et al.* 2005), using this wider spectrum of techniques. This, however, is only half of the story; once nutrients have been acquired, it is equally as important to consider their fate *in planta*.

Impacts of eCO$_2$ on the nutritive value of plants and chemical defence

In this second section, we move our attention to the fate of nutrients (especially N) once they have been taken up or delivered to plants. Once plants acquire nutrients, irrespective of the mechanisms involved, they are incorporated into a wide array of primary and secondary metabolites, including nucleic acids, amino acids and secondary metabolites. Many secondary metabolites play an important role in defence, acting to protect plants from losing valuable biomass and nutrients to herbivores, including humans (Agrawal and Fishbein 2006). Any change in allocation in resources between the different metabolites within the plant is important to us because the nutritional value of a plant as food depends on their relative proportions (Gleadow and Woodrow 2002; Lindroth 2010). When plants are grown under eCO$_2$, the abundance of carbohydrates and the reduced demand for leaf N by the photosynthetic apparatus (Stitt and Krapp 1999) allows plants to invest in both resource acquisition (i.e. roots) and defence (Lambers 1993; Coley *et al.* 2002). Changes in not only N content and allocation under eCO$_2$ but also in P, P : C ratios and C : N : P ratios may also affect plant yield and nutritional status (Loladze 2002). Thus, the impacts of eCO$_2$ on plant stoichiometry are expected to change the economics of the plant defence equation and, therefore, their nutritional value (Lambers 1993; Coley *et al.* 2002; Bidart-Bouzat and Imeh-Nathaniel 2008). Consistent with the view of Bennett *et al.* (2006), we propose that the formation of AM may further alter the economics of this equation through their provisioning of mineral nutrients to plants.

The economic trade-off between investment in primary production and defence depends on the availability of input resources (including C : N ratios), the efficiency of the metabolic apparatus, the developmental stage of the plant and the value of the particular organ for growth and reproduction (see Fig. 2; Gleadow and Woodrow 2000; Boege and Marquis 2005; Cornelissen *et al.* 2008; Haugen *et al.* 2008). Chemical defences are often classified as C- and N-containing secondary metabolites (CCSMs and NCSMs) (Rhoades 1979). CCSMs (e.g. phenolics and tannins) act by reducing the digestibility of plant tissue (Agrawal and Fishbein 2006). While few studies have examined the effect of AM on foliar secondary metabolites,

one study under ambient CO$_2$ found that AM colonisation of *Plantago lanceolata* increased concentrations of C-based defences (Gange and West 1994), suggesting that AM can affect changes in CCSMs. Despite species specificity in the eCO$_2$ effects on CCSMs (Lindroth 2010), leaves of plants grown at eCO$_2$ tend to contain higher concentrations of some CCSMs (particularly tannins and some phenolics, but not terpenoids) in proportion to the higher C : N ratio (Lincoln *et al.* 1993; Lawler *et al.* 1997; Coley *et al.* 2002; Agrawal and Fishbein 2006). The increased synthesis of CCSMs may be particularly pronounced in plants that are also N-limited, consistent with the higher C : N ratio (Peñuelas and Estiarte 1998). The formation of AM may further alter this balance (C : N) under eCO$_2$ through demand for C and supply of N.

NCSMs (e.g. cyanogenic glycosides, glucosinolates, alkaloids) are usually toxic and act in lower concentrations than CCSMs (Gleadow and Woodrow 2002). In general, the effects of eCO$_2$ on N-based defences have received little research attention (Gleadow *et al.* 2009*c*; Lindroth 2010). Given the lower concentration of tissue N in C$_3$ plants grown at eCO$_2$, it was originally hypothesised that the concentration of NCSMs would be lower under eCO$_2$ (Lambers 1993). Experimentally, however, the concentration of NCSMs has been found to be higher in many plants grown under eCO$_2$ either on a mass basis (Ziska *et al.* 2005; Matros *et al.* 2006; Bidart-Bouzat and Imeh-Nathaniel 2008; Gleadow *et al.* 2009*a*, 2009*b*) or relative to plant protein (e.g. Gleadow *et al.* 1998, 2009*a*, 2009*c*), although there are exceptions (see Bazin *et al.* 2002; Bidart-Bouzat and Imeh-Nathaniel 2008). This response appears to be linked to the higher nitrogen use efficiency (NUE) of C$_3$ plants grown at eCO$_2$ (Drake *et al.* 1997; Ainsworth and Long 2005), which effectively 'frees' N from the primary metabolism to be incorporated into secondary metabolites (see Fig. 2; Gleadow *et al.* 2009*a*, 2009*b*). Thus, many plants, especially those investing in N-based defences, may become more toxic to herbivores under eCO$_2$ (see Fig. 2). The impact of AM on this N allocation *in planta* has, to our knowledge, not been reported in the scientific literature. Changes in N-based defences in C$_4$ plants under eCO$_2$ have, to date, not been investigated, although C$_4$ plants are not expected to show such a reallocation of resources, as NUE is not affected to the same degree (Ghannoum *et al.* 1997; Gleadow *et al.* 2009*c*). However, changes in plant water use, soil water and nutrient availability (Dijkstra *et al.* 2010), and AM associations under eCO$_2$ may affect nutrient content and allocation in C$_4$ plants.

Any increase in NCSMs in staple crops is an important but, until recently, little considered response of plants to eCO$_2$ (Gleadow *et al.* 2009*b*). The group of NCSMs with which we are most familiar is the cyanogenic glycosides, which break down when cyanogenic plant tissue is macerated to release hydrogen cyanide and either an aldehyde or a ketone (Zagrobelny Bak *et al.* 2008). Because over half of all crop plants have at least some parts that are cyanogenic (Jones 1998), we consider N allocation to cyanogenesis especially important in the context of food security. The capacity of herbivores to convert toxic cyanide (HCN) to the less toxic thiocyanate (SCN) is known to be dependent on the overall dose and rate of ingestion, and the availability of sulfur-rich proteins (Westley 1988; Cardoso *et al.* 1998; Gleadow and Woodrow 2002).
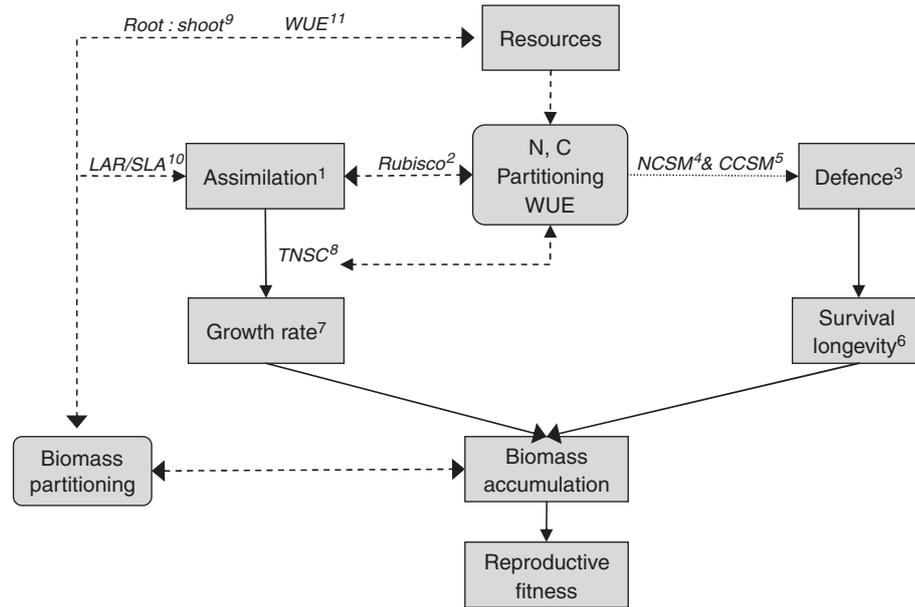
Fig. 2. Resource allocation within plants. Plant morphology, biochemistry and the efficiency of the physiological processes are integrated with nutrient supply and partitioning. Any change in resource supply or resource-use efficiency affects the partitioning of resources and the defence–growth equilibrium. (1) Assimilation rate is controlled by the size and effectiveness of the photosynthetic machinery, especially (2) Rubisco, as it accounts for ~25% of leaf N. A smaller but variable proportion of resources are allocated to the (3) synthesis of (C- or N-based) defensive secondary compounds, here classified on whether they contain (4) nitrogen (NCSM) or (5) not (CCSM). (6) Defended plants are assumed to have greater longevity, but at the cost of (7) high growth rates. (8) Plants grown at elevated atmospheric [CO$_2$] accumulate more total non-structural carbohydrates, which inhibit Rubisco synthesis. Low nutrient supply and elevated atmospheric [CO$_2$] is associated with (9) greater root growth (root : shoot ratio), and (10) decreased leaf area ratio and specific leaf area. (11) These, in turn, affect the ability of plants to acquire water and transpiration rates (WUE).

The ability of animals, including humans, to tolerate toxins and other anti-feedants in food is dependent on the toxin concentration, the availability of other food and importantly, total protein intake. Leaves of plants grown at eCO$_2$ almost always have less leaf protein on a per mass basis (Cotrufo *et al*. 1998). Since almost all of the N in the leaves in cereal crops is translocated to grain during senescence (Martre *et al*. 2003), low leaf protein is expected to impact grain protein as well. Indeed, studies in wheat (*Triticum aestivum* L.) and rapeseed (*Brassica napus* L.) report significant declines in total protein and essential amino acids, as well as a range of macro- and micronutrients (Högy and Fangmeier 2008; Högy *et al*. 2009, 2010). The protein concentration in wheat, barley (*Hordeum vulgare* L.) and rice (*Oryza sativa* L.) is forecast to be 10–15% lower in plants by 2030, reducing the nutritional value (Taub *et al*. 2008; Wieser *et al*. 2008; Gregory *et al*. 2009; Erbs *et al*. 2010), and affecting properties such as the amino acid balance and bread-making quality (Kimball *et al*. 2001; Wieser *et al*. 2008). Herbivores generally compensate for the lower plant protein concentration under eCO$_2$ by eating more (Lindroth *et al*. 1993; Agrell *et al*. 2006; Schädler *et al*. 2007; Stiling and Cornelissen 2007). Significantly, some studies indicate that this compensatory feeding may not be possible in species containing NCSMs (Schädler *et al*. 2007).

In the future, herbivores, including humans, may well face the twofold problem of decreased protein and increased defence chemicals in their diets. The defence–protein balance is closely linked to plant N status, which, in turn, is dependent on nutrient (be it via the root or AMF uptake pathways) and CO$_2$ supply (Gleadow *et al*. 2009*a*; Gleadow and Woodrow 2000). This highlights the need for an integrated approach that not only considers the impacts of eCO$_2$ on plant mineral nutrient status and the mechanisms by which plants acquire those nutrients, but also the flow-on effects on plant primary and secondary metabolism.

Integration, hypotheses and conclusions

In this viewpoint article, we have deliberately turned our attention to two quite different aspects of plant nutrition. First, we considered the impacts of eCO$_2$ on AM. We predict that these associations will play an increasingly important role in a high CO$_2$ world, especially when considered in light of increasing scarcity of synthetic fertilisers and increased demand for nutrients as (C$_3$) plants become less C-limited. Second, we turned our attention to the impacts of eCO$_2$ on the fate of nutrients *in planta*, with an emphasis on secondary metabolites with a role in plant defence. These compounds highlight the importance of considering not only the concentration of nutrients in plant tissues (as is typically measured in studies of AM, with some exceptions), but also the forms in which they are present. It is for these reasons that we have turned our attention to the nexus between AM and plant chemical
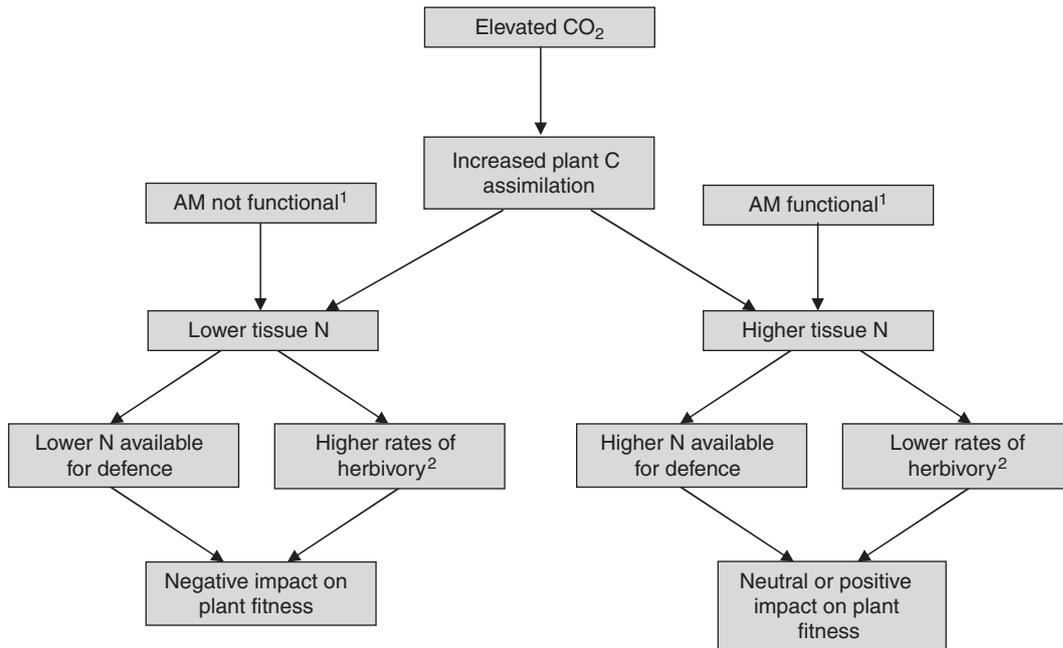
Fig. 3. Hypothesised links between eCO$_2$, plant (C$_3$) N nutrition, AM and plant defences. (1) AM function in this example refers to increased nutrient uptake and delivery to the plant. (2) Decreased tissue N leads to increased rates of herbivory as herbivores consume more plant tissue to satisfy their dietary N requirements.

defence in the context of a high CO$_2$ world. While the potential overlap between the two distinct aspects of plant nutrition we consider here are clear, there has been essentially no investigation of such links. Thus, in this final section, we present several hypotheses related to these issues. In doing so, our aim is to stimulate further research in this area.

Hypothesis 1

The formation of AM will lead to improved plant N nutrition under eCO$_2$ and thence to increased supply of N to N-based defence compounds (see Fig. 3).

Rationale

Mycorrhizal uptake of N (Tanaka and Yano 2005) can help alleviate the N deficiency (under low soil N conditions) typically observed under eCO$_2$ (Cotrufo *et al*. 1998). Since the rate of herbivory can be increased increase under eCO$_2$ as herbivores need to increase their consumption of plant tissue to meet their dietary requirements (Veteli *et al*. 2002), plants which allocate more N to defence compounds will be at a competitive advantage. Consequently, the capacity of AM to increase plant supply of nutrients (including N) will be of increased benefit to plants (see Fig. 3). To test this hypothesis, there is a need for studies of AM impacts on plant N nutrition and the production of N-based defence compounds under eCO$_2$ conditions.

Hypothesis 2

Plants (C$_3$) grown under eCO$_2$ are less C-limited and thus, the capacity of plants to meet the demand for C by AMF and C-based defence compounds is increased (see Fig. 4).
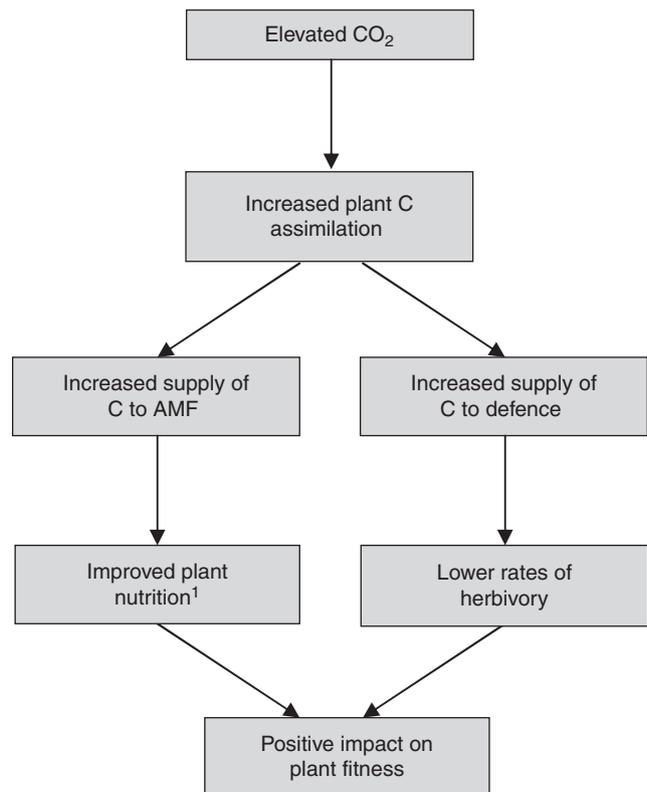

Fig. 4. Hypothesised links between eCO$_2$, C assimilation, AM and (C$_3$) plant defences. (1) AM function in this example refers to increased nutrient uptake and delivery to the plant.

Rationale

As atmospheric CO$_2$ concentrations increase, C$_3$ photosynthesis will be less C-limited. As a consequence, more C will be available to support both the synthesis of C-based defence compounds, and also the establishment and maintenance of AM (Bennett *et al.* 2006). However, with the increased rates of herbivory under eCO$_2$ due to compensatory feeding (Schädler *et al.* 2007), there may be no net benefit. Again, there is a need for dedicated studies in which the competing demands for C by AMF and C-based defence compounds are assessed under eCO$_2$.

Conclusion

In this viewpoint article, we have explored the impacts of eCO$_2$ on aspects of plant biology that are typically considered in isolation from one another. Many different but equally important complex interactions between different aspects of plant biology exist, and are also in need of consideration in unison rather than isolation. The growth of C$_3$ plants is typically increased under eCO$_2$, but it is likely that this will only be realised where N and P supply (and other nutrients) to plants is adequate. With much of the world's population having limited access to costly fertilisers, the potential yield increases that eCO$_2$ make possible may not be fully realised. Moreover, changes in the nutritional status of plants in the future could negatively impact on subsistence farmers who have fewer options available to them. We contend that if we are to discover how plants (especially food plants) will respond to environmental change, the plant sciences need to take an integrated approach to the study of plant responses to the environment, and one that is not constrained by discipline boundaries.

Acknowledgements

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