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\textsubscript{2} and climate change. In this viewpoint article, we begin to explore the impacts of elevated CO\textsubscript{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\textsubscript{2}.

Additional keywords: arbuscular mycorrhizas, cyanogenesis, elevated CO\textsubscript{2}, food security, nitrogen, secondary metabolism.

Introduction

Plant nutrient demand, acquisition and utilisation are all altered by changes in atmospheric CO\textsubscript{2} concentrations. In the context of looming fertiliser shortages (Cordell \textit{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\textsubscript{2} (eCO\textsubscript{2}) on two specific aspects of plant nutrients that have traditionally been considered separately: acquisition and utilisation.

First, we consider the impacts of eCO\textsubscript{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\textsubscript{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\textsubscript{2}.

Impacts of eCO\textsubscript{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\textsubscript{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\textsubscript{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\textsubscript{2} world, and forms a reference point for this section.

Nutrient acquisition by AM under eCO\textsubscript{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\textsubscript{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 \textit{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 \textit{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. Daep\textit{p} \textit{et al}. 2001) and P supply (e.g. Campbell and Sage 2006) in determining the response of plants to eCO\textsubscript{2}, it is essential that we understand how the acquisition of nutrients by AM is likely to be affected by eCO\textsubscript{2}.

It is well established that growth of C\textsubscript{3} plants usually increases under eCO\textsubscript{2}, primarily because the current daytime atmospheric CO\textsubscript{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\textsubscript{3} plant growth under eCO\textsubscript{2} is dependent on access to sufficient nutrients. In a meta-analysis of the growth...
responses of herbaceous and woody species to eCO2, for example, the eCO2 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 eCO2 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 eCO2; indeed, P limitation may be more critical in some systems (Edwards et al. 2005). Phosphorus constraints on the response to eCO2 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 eCO2 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 eCO2 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 eCO2, 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 eCO2 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 eCO2 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 eCO2, 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 eCO2 are

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**Fig. 1.** Potential links between eCO2, agricultural management, AM and plant nutrient acquisition. NB: Emphasis is on nutrient uptake and supply to (C3) plants, not C supply to the fungi. (1) Environmental factors aside from eCO2, 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.
likely to come where the relative contributions of both root and fungal uptake are considered, as has been done under ambient CO₂ conditions (Smith et al. 2004).

As indicated previously, equally important although much less well understood, are the impacts of eCO₂ 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 CO₂ and eCO₂. Arbuscular mycorrhizal fungi (AMF) can acquire N both as NO₃⁻ and NH₄⁺, and transfer it to plants (Ames et al. 1983; Johansen et al. 1993). Uptake of N in its more mobile form NO₃⁻ by AMF is likely to be important in agricultural soils, where NO₃⁻ 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 NO₃⁻ 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 NH₄⁺ and NO₃⁻, it has been shown that they can take up and deliver to the plant up 10 times as much N when supplied as NH₄⁺ (Tanaka and Yano 2005). Provision of N as NH₄⁺ could become increasingly important in the future, as recent studies indicate that eCO₂ inhibits NO₃⁻ assimilation in leaves (Bloom et al. 2010).

Any improvements in plant N nutrition resulting from the formation of AM at eCO₂ 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 eCO₂ concentrations (Gamper et al. 2005). Similarly, in a study on tomatoes (Solanum lycopersicum L.), positive mycorrhizal effects on plant N content were greater under eCO₂ than under ambient CO₂ conditions, although differences were small (Cavagnaro et al. 2007). Chen et al. (2007) found that the effects of mycorrhizal colonisation on N uptake under eCO₂ were species-specific, with N uptake enhanced by colonisation under eCO₂ 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 eCO₂; there is a need for further dedicated investigations in this area. The assessment of plant nutritional changes due to AM under eCO₂ 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 eCO₂ (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 photosynthetic supply to roots under eCO₂ 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 eCO₂ to date (Treseder 2004; Hu et al. 2006; Lukac et al. 2010). By contrast, while most studies under eCO₂ 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; Olssrud et al. 2010). It is important to recognise that considering AM responses to eCO₂ 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 eCO₂ 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 eCO₂ 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 eCO₂ on the AMF as the fungal biomass response to eCO₂ 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 eCO₂ 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 eCO₂ (Kironomos et al. 1998); however, given their rapid rates of turnover, this is perhaps not unexpected. The impacts of eCO₂ 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 eCO₂ 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 eCO₂ 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 eCO2 response of plant species from different functional groups (e.g. C3, C4, legumes, and woody or herbaceous) there is a need to study the responses of a wide variety of plant–fungal combinations under eCO2 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 eCO2 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 nutritive value of a plant as food depends on their relative proportions (Gleadow and Woodrow 2002; Lindroth 2010). When plants are grown under eCO2, 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 eCO2 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 eCO2 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 CO2 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 eCO2 effects on CCSMs (Lindroth 2010), leaves of plants grown at eCO2 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 eCO2 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 eCO2 on N-based defences have received little research attention (Gleadow et al. 2009c; Lindroth 2010). Given the lower concentration of tissue N in C3 plants grown at eCO2, it was originally hypothesised that the concentration of NCSMs would be lower under eCO2 (Lambers 1993). Experimentally, however, the concentration of NCSMs has been found to be higher in many plants grown under eCO2 either on a mass basis (Ziska et al. 2005; Matros et al. 2006; Bidart-Bouzat and Imeh-Nathaniel 2008; Gleadow et al. 2009a, 2009b) or relative to plant protein (e.g. Gleadow et al. 1998, 2009a, 2009c), 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 C3 plants grown at eCO2 (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. 2009a, 2009b). Thus, many plants, especially those investing in N-based defences, may become more toxic to herbivores under eCO2 (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 C4 plants under eCO2 have, to date, not been investigated, although C4 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. 2009c). However, changes in plant water use, soil water and nutrient availability (Dijkstra et al. 2010), and AM associations under eCO2 may affect nutrient content and allocation in C4 plants.

Any increase in NCSMs in staple crops is an important but, until recently, little considered response of plants to eCO2 (Gleadow et al. 2009b). 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).
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 eCO2 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 micro-nutrients (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 eCO2 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 CO2 supply (Gleadow et al. 2009a; Gleadow and Woodrow 2000). This highlights the need for an integrated approach that not only considers the impacts of eCO2 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 eCO2 on AM. We predict that these associations will play an increasingly important role in a high CO2 world, especially when considered in light of increasing scarcity of synthetic fertilisers and increased demand for nutrients as (C3) plants become less C-limited. Second, we turned our attention to the impacts of eCO2 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
defence in the context of a high CO2 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 eCO2 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 eCO2 (Cotrufo et al. 1998). Since the rate of herbivory can be increased under eCO2 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 eCO2 conditions.

**Hypothesis 2**

Plants (C3) grown under eCO2 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).
Rationale

As atmospheric CO₂ concentrations increase, C₃ 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 eCO₂ 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 eCO₂.

Conclusion

In this viewpoint article, we have explored the impacts of eCO₂ 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 C₃ plants is typically increased under eCO₂, 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 eCO₂ 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 disciplinary boundaries.

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References


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