Elevated [CO$_2$] and forest vegetation: more a water issue than a carbon issue?

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Abstract. Studies of responses of forest vegetation to steadily increasing atmospheric concentrations of CO$_2$ have focussed strongly on the potential of trees to absorb extra carbon; the effects of elevated [CO$_2$] on plant–soil water relations via decreased stomatal conductance and increased ambient temperature have received less attention, but may be significant in the long term at the ecosystem level. CO$_2$ augmentation experiments with young trees demonstrate small increases in aboveground carbon content, but these increases tend to diminish as trees get older. By contrast, several experiments suggest continued decreases in transpiration and increased soil water content under these conditions. In tropical forests, the major cause of increases in aboveground biomass observed in the recent past is not necessarily elevated [CO$_2$]. Undoubtedly, the potential of monitoring trees in forest dynamics plots to deduce CO$_2$-specific alterations in forest structure and standing biomass will unfold in the decades to come. The comprehensive understanding of responses of forest vegetation to elevated [CO$_2$] in the Anthropocene will depend upon the inclusion of detailed measurements of soil water pools and water fluxes through the soil–plant–atmosphere continuum in future tree CO$_2$ augmentation experiments and forest dynamics plot studies.

Additional keywords: climate change, carbon sequestration, evapotranspiration, FACE (free air CO$_2$ enrichment), water use efficiency.

Introduction

Carbon and water physiology are intrinsically linked in plants because of the inevitable loss of water vapour from leaves when stomata open to allow for the uptake of CO$_2$ from the atmosphere. The annual gross uptake of ~120×10^9 tonnes of C from the atmosphere by vegetation worldwide is coupled with transpiration of ~32.1×10^{12} tonnes of H$_2$O (Hetherington and Woodward 2003), an amount equivalent to 1.2 times the volume of the largest continental lake on earth, Lake Baikal (Siberia). At a global level, plants lose, on average, 180 molecules of water for each molecule of CO$_2$ fixed.

Since the middle of the 19th century, when the [CO$_2$] of the atmosphere was ~$280\ \mu$mol mol^{-1}, atmospheric [CO$_2$] has risen by almost 40% (Hofmann *et al*. 2009), a manifestation of how an expanding human population has generated energy and used land. The best documented short-term responses of plants to rising [CO$_2$] are increases in the rate of photosynthetic CO$_2$ uptake and decreases in both stomatal conductance and transpirational water loss. As these responses generally result in the assimilation of more carbon at a given rate of transpiration, a consistent observed response of plants to elevated [CO$_2$] is an increase in plant water use efficiency (WUE), the amount of C gained per unit of water lost.

An issue of fundamental importance to how ecosystems might function in the future is whether or not increased WUE under elevated [CO$_2$] results in a significant reduction of water extraction from the soil (Morgan *et al*. 2004). In principle, if biomass did increase in response to elevated [CO$_2$], the absolute consumption of water may also increase despite enhanced WUE. In some forest types, such as tropical dry forests, growth may be enhanced indirectly through prolonged exposure to soil water if soil moisture is depleted more slowly. It is unclear to what degree the interactions between elevated [CO$_2$], CO$_2$ gain, transpiration and WUE that are evident at the leaf or plant level translate to the stand and ecosystem levels, particularly in forests, although CO$_2$ effects on WUE are expected to diminish when scaling up from the leaf to the ecosystem (Field *et al*. 1995; Meinzer *et al*. 1997).

We explore here the idea that the effects of increasing [CO$_2$] on ecosystem carbon storage may be of lesser overall significance to ecosystem structure and functioning than changes in plant water use and availability. The basis for this hypothesis is that the initial stimulation of photosynthesis and growth following CO$_2$ fertilisation often does not persist, or does not result in permanent increases in biomass, whereas the decrease in stomatal conductance and transpiration often does persist (Medlyn *et al*. 1999, 2001). Because forests are the predominant terrestrial component of the global carbon cycle, we focus on CO$_2$ and water exchange information available for trees exposed to experimentally and naturally augmented [CO$_2$] and on studies of the dynamics of tropical forests over the past few decades.

Increased carbon storage in vegetation under elevated [CO$_2$]?

No CO$_2$-augmentation experiment has tracked the biomass and phenology of trees throughout their life time. Several temperate northern hemisphere tree species have been grown at elevated [CO$_2$] for brief portions of their life cycles in free air CO$_2$ enrichment (FACE) experiments (Körner *et al.* 2005; Norby *et al.* 2006; Scarascia-Mugnozza *et al.* 2006; Schlesinger *et al.* 2006). In four studies in which saplings and young trees up to 25 years old were exposed to elevated [CO$_2$], generally ~550 µmol mol^{-1}, increases in aboveground biomass were observed (Fig. 1). Although the stimulation of growth rate was substantial in very young trees, it was small in older trees (Norby *et al.* 2001, 2005; Oren *et al.* 2001; Hamilton *et al.* 2002; Calfapietra *et al.* 2003; King *et al.* 2005; Finzi *et al.* 2006; McCarthy *et al.* 2010). The biomass data of Fig. 1 do not contradict the results of an analysis of net primary productivity (NPP) of the same four FACE studies which concludes 'that the response of forest NPP to elevated [CO$_2$] is highly conserved across a broad range of productivity, with a stimulation at the median of $23 \pm 2\%$' (Norby *et al.* 2005). This is because NPP does not necessarily equate to changes in carbon storage: it represents the amount of organic carbon entering an ecosystem but does not address the fate of that carbon (Norby *et al.* 2005; Körner 2009). Furthermore, the calculation of NPP includes estimates of annual carbon increments of wood, leaf, coarse root and fine root biomasses and considers litterfall and fine root turnover. Quantification of some of these parameters is not easy (Clark *et al.* 2001*a*, 2001*b*) and confidence levels may be moderate. In the context of this paper, we prefer to use simple biomass data in discussing possible forest responses to enhanced [CO$_2$].

Increased stem biomass accumulation was not detected in ten 80–120 year old, not yet mature, 35 m tall deciduous trees exposed to elevated [CO$_2$] for 4 years in Switzerland (Körner
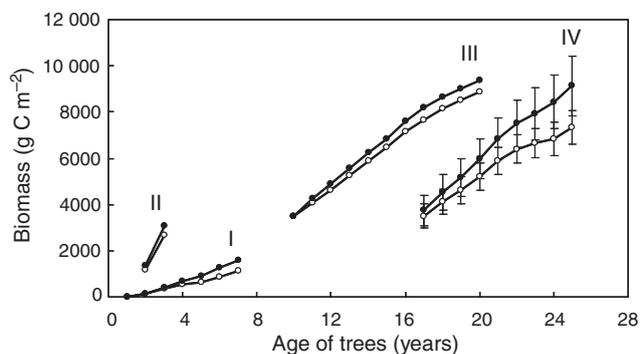
et al. 2005). An extension of these studies over longer time periods and a broadening to other forest types is clearly warranted. The greater responsiveness in younger than in older plants confirms open-top and growth chamber studies with seedlings and saplings, especially when soils are nutrient rich (Lovelock *et al.* 1998; Medlyn *et al.* 1999; Norby *et al.* 1999; Winter *et al.* 2000, 2001*a*; Nowak *et al.* 2004). In a 4.5 year open-top chamber study of birch (*Betula pendula* Roth), Rey and Jarvis (1997) concluded that the 66% increase in final tree biomass associated with elevated [CO$_2$] resulted largely from accelerated development during the first year of CO$_2$ enrichment.

Evidence for long-term responses of plants to elevated [CO$_2$] has also been sought from trees that live in proximity to natural CO$_2$ springs. In Italy, 30-year-old coppiced Mediterranean oaks (*Quercus ilex* L.) growing near two CO$_2$ vents exhibited a 12% increase in radial stem width that was ascribed to increased tree ring growth rates when plants were young (Hättenschwiler *et al.* 1997; Idso 1999). Such an increase was not observed in two other studies at one of the sites that examined tree rings of *Q. ilex* and four other tree species (Tognetti *et al.* 2000; Saurer *et al.* 2003). If stem biomass differences do exist between trees growing near the CO$_2$ vents and trees growing under ambient CO$_2$ at this relatively nutrient poor site, they are close to the limits of detection (Körner and Miglietta 1994).

In the absence of direct measurements of the effects of rising [CO$_2$] on tropical forests (Stork *et al.* 2007; Körner 2009), largely because of the technical challenges and costs associated with large-scale, long-term CO$_2$ augmentation, periodic inventories of biomass in forest plots have been used to infer possible forest responses to elevated [CO$_2$]. At a global level, the average aboveground tree biomass in tropical forests of ~200 tonnes C ha^{-1} appears to be increasing (Fig. 2), although recent approximations of 0.24 (Chave *et al.* 2008*a*) and 0.49 tonnes C ha^{-1} year^{-1} (Lewis *et al.* 2009*a*) demonstrate uncertainty as to the rate. At a continental level, estimates of biomass accrual are higher for Amazonia (0.62 tonnes C ha^{-1}

Fig. 1. Aboveground biomass or wood of four temperate northern hemisphere forest tree species grown under free air CO$_2$ enrichment (FACE) conditions at ambient (○) and elevated [CO$_2$] (~550 µmol mol^{-1}; ●). The four species are (I) *Populus tremuloides* (trembling aspen) (values are biomass of stem-wood for 1998–2003; King *et al.* 2005); (II) *Populus nigra* (values are aboveground biomass for 2000–2001; Calfapietra *et al.* 2003); (III) *Liquidambar styraciflua* (sweetgum) (values for stem wood for 1997–2007; Norby *et al.* 2001, 2008); (IV) *Pinus taeda* (loblolly pine) (values of biomass ±1 s.e. of stems and branches for 1996–2004 are those by McCarthy *et al.* 2010). Where necessary, carbon contents were calculated from biomass by assuming carbon was 50% of mass.
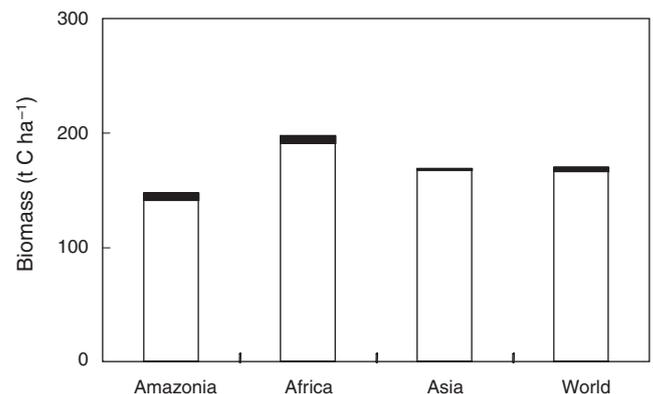

Fig. 2. An estimate of aboveground carbon in living biomass in tropical forests in 2000. The solid section represents the accumulation of carbon between 1991 and 2000 inclusive (data from Baker *et al.* 2004; Chave *et al.* 2008*a*; Phillips *et al.* 2008; Lewis *et al.* 2009*a*). During the 10-year interval the global average [CO$_2$] in the atmosphere increased from ~355 to ~368 µmol mol^{-1}. 'World' carbon value is the mean of values reported by Chave *et al.* (2008*a*) (0.24 tonnes ha^{-1} year^{-1}) and Lewis *et al.* (2009*a*) (0.49 tonnes ha^{-1} year^{-1}).

year^{-1}; Baker *et al*. 2004; Phillips *et al*. 2008) and Africa (0.63 tonnes C ha^{-1} year^{-1}; Lewis *et al*. 2009*a*) than for Asia (0.15 tonnes C ha^{-1} year^{-1}; Chave *et al*. 2008*a*). These global and continental-scale averages mask considerable heterogeneity in forest biomass dynamics and in their interpretation. For example, increases in biomass were not observed in 18 of 79 plots surveyed in Africa, in 13 of 59 plots surveyed in Amazonia, or in 2 of 5 plots surveyed in Asia. In the very carefully studied 50 ha plot on Barro Colorado Island, Republic of Panama, tree biomass did not change between 1985 and 2005 (Chave *et al*. 2008*a*).

The extent to which these recent average increases in tropical forest biomass can be attributed to CO_2 fertilisation is by no means clear. Despite robust debate on how one deciphers the composition and dynamics of the vegetation in the plots, it is broadly agreed that the successional state of forests in plots affects biomass accumulation and, therefore, estimations of possible contributions of [CO_2] to biomass change (Lewis *et al*. 2004, 2006, 2009*b*; Laurance *et al*. 2005; Nelson 2005; Wright 2005, 2006; Phillips *et al*. 2008; Muller-Landau 2009). Even in old growth forests, the majority of the area is expected to gradually accumulate biomass most of the time due to recovery from past gap-forming events (Feeley *et al*. 2007*a*). A selection of inventory sites with a bias towards younger areas of forest will therefore overestimate the rate of non-CO_2 related biomass accumulation for the forest as a whole. Conversely, disturbance events may be overrepresented if the selection of inventory sites is biased towards older areas of forest. On the basis of increasing dominance of slow-growing species, Chave *et al*. (2008*a*) posited that nine of the ten 50 ha study plots in their global analysis of old-growth forests could have been recovering from past disturbance and thus their movement towards a higher carbon storage state may be unrelated to rising [CO_2]. A similar conclusion was reached for plots in Central Amazonia when the effects of increases in net primary productivity on carbon storage were modelled for known and expected changes in [CO_2] between 1850 and 2100 (Chambers and Silver 2004; Chambers *et al*. 2004). The model predicted that changes in [CO_2] could explain an increase of only 0.05 tonnes C ha^{-1} year^{-1} between 1980 and 2020, a value approximately one order of magnitude less than has been reported (Baker *et al*. 2004; Phillips *et al*. 2008). It was concluded that changes in biomass reported for central Amazonia were not generally being driven by increasing [CO_2].

There is, thus, little evidence that CO_2 fertilisation *per se* will drastically alter biomass in temperate or tropical forests, although increases in biomass have been inferred (Lewis *et al*. 2009*b*; McMahon *et al*. 2010, for temperate forests). One would have to postulate changes in size and age distribution of trees for the latter to have implications for carbon storage (Körner 2009) rather than tree turnover. Temperate trees experimentally exposed to [CO_2] roughly 200 µmol mol^{-1} above ambient appear to accumulate more aboveground biomass when young, but, as in grassland species (Reich *et al*. 2006), the initial growth stimulation is likely transitory as nutrients and the capacity of plants to use extra carbon (sink capacity) become increasingly limiting (Oren *et al*. 2001; Finzi *et al*. 2006; Hungate *et al*. 2006; Norby and Iverson 2006), although enhanced rates of soil organic matter decomposition may temporarily provide extra nitrogen (Lichter

et al. 2008). Thus, the biomass of mature stands of temperate trees grown throughout their life time under elevated [CO_2] may not be markedly higher than present levels. The biomass of tropical forests appears to be increasing on average, but the estimates of the global rate of increase vary 2-fold and scientific opinion differs as to what fraction of the recent change, if any, is a direct response to [CO_2] (Körner 2009; Lewis *et al*. 2009*b*).

Persistent reduction in transpiration under elevated [CO_2]?

While evidence for substantial CO_2-associated increases in biomass of forests in natural or close to natural situations is underwhelming, is there clear evidence for a persistent reduction in transpiration under elevated [CO_2]? It has been suggested that an outcome of decreased transpiration may already be visible as a worldwide increase of water runoff into continental rivers (Labat *et al*. 2004; Gedney *et al*. 2006; Betts *et al*. 2007; see Huntington 2008 for a contrary review) and that long-term river records may be used to monitor CO_2 effects on the terrestrial carbon sink although, at the global scale, plant signals may be strongly confounded by land-use changes such as deforestation (Piao *et al*. 2007). At the local scale of a temperate deciduous forest in Switzerland, Leuzinger and Körner (2010) concluded that the key drivers for runoff are the temporal distribution of rainfall and the water storage capacity of the soil, whereas increased runoff under future [CO_2] due to direct plant physiological CO_2 effects will be small.

The coupling of elevated [CO_2] and reduced stomatal conductance to water vapour transfer between leaves and the atmosphere, now often described as 'physiological forcing', features prominently in canopy and energy exchange models (Sellers *et al*. 1996; Betts *et al*. 2007; Boucher *et al*. 2009) but the penetration of the water-associated effects of elevated [CO_2] into other indirect and scale-dependent processes, particularly soil processes, has not been considered comprehensively (Huntingford *et al*. 2008; Sitch *et al*. 2008). Since a reduction in transpiration should result in an increase in soil moisture, any biotic or abiotic process that is affected by changes in soil moisture is expected to be sensitive to elevated [CO_2]. In addition to evaporation from the soil, such processes include surface-water runoff, soil–water infiltration, movement of water between soil water reservoirs, litter decomposition, the composition of microbial communities, nutrient mineralisation and soil formation. Moreover, plants adjust physiologically and developmentally to soil water availability, adjustments that may ultimately affect ecosystem species composition, i.e. biodiversity.

Examining the sensitivity of stomatal conductance to elevated [CO_2], the general trends are that (i) grasses are more responsive than forbs, which are more responsive than trees, and (ii) broadleaf trees are more responsive than conifers (Saxe *et al*. 1998; Medlyn *et al*. 2001). In well-watered agricultural crops, including grasses, grown at between 500 and 700 µmol mol^{-1} CO_2, stomatal conductance is reduced by 20–40%, with no clear evidence for differences between C_3 and C_4 species (Ainsworth and Long 2005; Leakey *et al*. 2009). Such reductions in stomatal conductance are associated with reduced evapotranspiration, reduced soil moisture depletion

and amelioration of drought stress (Kimball *et al.* 2002; Nowak *et al.* 2004). Studies of trees have yielded less coherent indications of the importance of stomatal responses to elevated [CO$_2$] at the tree canopy scale. Curtis (1996) could not detect a consistent reduction in stomatal conductance in 41 tree species, Curtis and Wang (1998) reported a non-significant reduction of 11% in 48 tree species, Field *et al.* (1995) an average 23% decrease in 23 tree species and Medlyn *et al.* (2001) reported a significant 21% reduction in 13 European forest tree species. These surveys included an array of CO$_2$ augmentation techniques (open-top chambers, glasshouses, growth chambers and branch bags) and pot- and field-grown plants, many of which were juveniles (Norby *et al.* 1999). In some studies the effects of growth enclosure and CO$_2$ delivery technique on stomatal conductance can be as large as the responses to the CO$_2$ treatment (Seiler *et al.* 2009).

The evidence in trees for or against temporal acclimation of stomatal conductance to elevated [CO$_2$] is also equivocal (Gunderson and Wullschleger 1994). Medlyn *et al.* (2001) concluded that if acclimation occurs, its magnitude is generally small. Nonetheless, there are indications that species differences occur and that older trees exhibit smaller CO$_2$-related decreases in stomatal conductance than do younger trees.

The variation in response of stomatal conductance of trees to ~550 µmol mol^{-1} CO$_2$ is highlighted in FACE experiments. In three studies, significant reductions in stomatal conductance were observed and in two they were not. Twelve-year-old *Liquidambar styraciflua* L. grown for 2 years at elevated [CO$_2$] (Wullschleger and Norby 2001; Wullschleger *et al.* 2002) and 4-year-old *Acer saccharum* Marshall and *Populus tremuloides* Michx. grown for their entire 4 years at elevated [CO$_2$] exhibited pronounced decreases in stomatal conductance (Karnosky *et al.* 2003; Sharma *et al.* 2003, but see Uddling *et al.* 2009). For *L. styraciflua*, a 23% reduction in stomatal conductance averaged over the growing season translated into a 13% reduction in sap flow, a 14% reduction in canopy transpiration and an increase in the annual integrated WUE of the stand from 1.5 to 1.9 g aboveground dry mass kg^{-1} H$_2$O (Wullschleger and Norby 2001; Wullschleger *et al.* 2002). The extra water stored in the upper 20 cm of soil was sufficient to increase soil water potential by +0.3 MPa. Similarly, a CO$_2$-associated decrease in seasonal water consumption of up to 10% was observed in 80–120 year old *Carpinus betulus* L. and *Fagus sylvatica* L. in a Swiss deciduous forest (Keel *et al.* 2007; Leuzinger and Körner 2007). During rainless periods, soil moisture at 10 cm depth decreased at a slower rate under high-CO$_2$ treated trees than under control trees. For *L. styraciflua*, although CO$_2$ effects on stomatal conductance were observed in the FACE experiment, it was argued that the attenuation of the leaf effect at higher scales did not statistically support the incorporation of reductions of forest water use into larger-scale models (Wullschleger *et al.* 2002). Nevertheless, for the *L. styraciflua* forest it was estimated that annual evapotranspiration was reduced by 7% (Wullschleger *et al.* 2002), a not unsubstantial amount when extrapolated across landscapes.

CO$_2$-associated partial stomatal closure was not statistically significant in *Populus alba* L., *Populus nigra* L. or *Populus* × *euramericana* (=*P. deltoides* W. Bartram ex Marshall × *P. nigra* L.) throughout the 3 year rotation cycle of a FACE experiment in Tuscany, Italy, although a trend of reduction in conductance of between 16 and 35% was observed (Tricker *et al.* 2005; Scarascia-Mugnozza *et al.* 2006). In FACE-grown *Pinus taeda* L. there was no CO$_2$ treatment effect on stomatal conductance, time-integrated ambient to substomatal ratio of [CO$_2$] (an indicator of WUE), soil moisture, needle water potentials or tissue osmotic pressures (Ellsworth 1999).

Well defined responses of stomatal conductance, transpiration and soil water storage to elevated [CO$_2$] occurred in a scrub-oak woodland system (mainly *Quercus myrtifolia* Willd. and *Quercus geminata* Small) in an 11 year open-top chamber study during which plants recovered from fire (Seiler *et al.* 2009). Stomatal conductance and transpiration were reduced (Hungate *et al.* 2002) and water content in the upper soil layer increased. Since the shrubs drew most of their water from the water table, a major response to elevated [CO$_2$] was diminished water uptake at depth, a response expected to have hydrological effects at the landscape scale (cf. Gedney *et al.* 2006). Another twist to the CO$_2$–H$_2$O story is that, while in the two scrub-oak species the CO$_2$-induced reduction of whole-tree water flux (sap flow) was associated with reduced transpiration per unit leaf area, in two Mediterranean oak species growing near CO$_2$ springs in Italy (*Q. ilex* and *Quercus pubescens* Willd.) a CO$_2$-related reduction in whole-tree water flux was accompanied by reduced leaf area per plant (Tognetti *et al.* 1998, 1999).

Quantification of CO$_2$-driven reductions in stomatal conductance requires sampling integrated over long periods because the CO$_2$ response may be overridden by other effectors of stomatal conductance such as light intensity, vapour pressure deficit (VPD) and temperature. As a result, CO$_2$-associated reductions in stomatal conductance may not be continually detected, especially if based on instantaneous spot measurements of individual leaves. FACE experiments that illustrate this phenomenon include the *L. styraciflua* system in which CO$_2$-mediated changes in conductance were observed on 7 out of every 11 days before 1300 hours (Wullschleger *et al.* 2002), and the Swiss system in which significant CO$_2$-effects were observed for *Carpinus betulus* L. only on an average of 2 out of 15 days (Keel *et al.* 2007).

In tropical forests no changes in water fluxes have as yet been associated with effects of rising atmospheric [CO$_2$] on stomatal opening, but there has been minimal experimental exploration of the topic. The potential effect of rising atmospheric [CO$_2$] on water exchange in tropical forests has been generally accorded 'small impact' status because it is assumed that increases in leaf area index (LAI) and atmospheric boundary layer feedbacks attenuate the expression of changes in leaf transpiration and WUE at stand and ecosystem scales. However, although LAI tends to increase in expanding forests, as forests mature LAI may no longer increase or may be reduced at elevated [CO$_2$] (Tognetti *et al.* 1998, 1999; Norby *et al.* 2006). Boundary layer feedbacks do tend to increase transpiratory water loss, because when stomata reduce their apertures in response to elevated [CO$_2$], leaf temperatures increase and the resulting increase in leaf-to-air VPD promotes transpiration (Kimball and Bernacchi 2006). Increases in VPD also tend to reinforce stomatal closure, which, at least partially, compensates the leaf temperature effect (Zotz *et al.* 1995; Doughty and Goulden 2008). Water savings tend to be greater in aerodynamically rough

ecosystems (e.g. highly diverse tropical forest canopies) than in aerodynamically smooth crop and tree plantation canopies (Field *et al*. 1995). Assuming a mean coupling coefficient of 0.5 in a tropical forest canopy, a reduction of stomatal conductance by 20% in response to elevated [CO_2] would lead to a reduction in transpiration by 10%, all other factors being equal (Meinzer *et al*. 1997).

In an open-top chamber study with seedlings of a tropical pioneer tree, *Ficus insipida* Willd., growing in a forest clearing in the Republic of Panama, the amount of water transpired per g dry mass accumulated decreased by 27–35% in response to elevated CO_2, irrespective of whether plants were fertilised or not (Winter *et al*. 2001*b*). In treatments in which biomass accumulation increased at elevated [CO_2], absolute water expenditure at elevated [CO_2] was greater or similar to that at ambient levels, despite the increased WUE at elevated [CO_2]. When soil conditions did not allow for increased growth at elevated [CO_2], the absolute water expenditure of plants was lower at elevated than at ambient [CO_2]. Thus, if tropical forest ecosystems, because of limitations such as soil nutrients, would not attain a markedly greater standing aboveground biomass per unit ground area than today, the major effect of enhanced CO_2 could well be a significant reduction in forest transpiration, potentially affecting rainfall patterns and soil water availability, particularly for plants in the forest understorey (Winter *et al*. 2001*b*).

The potential of CO_2-stimulated decreases in transpiration to affect tropical rainforests may have been underappreciated because of a perception that saving water is ecologically more important in biomes clearly limited by water than in the humid tropics (Nowak *et al*. 2004). However, water supply is by no means always abundant in tropical rainforests and may become less so in the future (Malhi *et al*. 2009). Roughly half of the evergreen forests of the Amazon Basin experience dry seasons of at least 3 months duration with less than 0.5 mm day^{-1} (Nepstad *et al*. 1994) and most climate models predict increasingly El Niño-like climate conditions and reduced rainfall over eastern Amazonia (Trenberth and Hoar 1997; Yeh *et al*. 2009). Rainfall exclusion experiments have demonstrated that at two Amazonian sites the resilience to drought of forests depends upon soil type and depth, which affect soil water storage and whether or not roots are tapping the water table (Nepstad *et al*. 2002; Sotta *et al*. 2007; Brando *et al*. 2008). CO_2-associated reductions in transpiration should conserve soil moisture and increase the resilience of forests to drought. It is because such tree–soil–water interactions are complex and variable that Amazonian ecosystem models require further testing against water flux data particularly with respect to their assumptions concerning hydraulic limitations of belowground water pools, plant rooting depths and the long-distance horizontal movement of water (Rolim *et al*. 2005; Fisher *et al*. 2007; Huntingford *et al*. 2008).

Some plants, such as shallow-rooted plants in the forest understorey (Engelbrecht *et al*. 2007) and epiphytes, may be more sensitive to changes in water supply than others and may particularly benefit from CO_2-related increases in WUE.

The links between elevated [CO_2], water use and water availability and the resulting effects on forest structure, function and diversity are, thus, manifold and their resolution

requires appropriately sophisticated analyses. Direct plant–CO_2 interactions affect transpiration, plant water status, soil moisture accumulation and related hydrological processes. Interactions between CO_2 and radiation (now frequently referred to as 'radiative forcing') affect plants through increases in temperature, seasonality of climate, precipitation patterns, frequency and intensity of storms, cloud formation and soil moisture; all-in-all, changes that will ultimately alter the water status of ecosystems. The temporal dynamics of altered soil water status and thresholds of water availability within which physiological processes are affected depend overwhelmingly upon rainfall patterns. Water savings are expected to significantly affect soil moisture, increase nutrient mineralisation and stimulate tree growth in forests that experience infrequent rainfall and seasonal drought.

Conclusions

Broadleaf and coniferous trees exposed for several years to elevated [CO_2] exhibit reasonably small increases of aboveground biomass (Fig. 1). It is arguable whether such increases are of sufficient magnitude to significantly affect ecosystem structure or function. Whether tropical forests experiencing [CO_2] increases at current rates are accumulating biomass as a direct effect of CO_2 fertilisation is open to interpretation (Wright 2005; Lewis *et al*. 2009*b*; Muller-Landau 2009). In forest plots it is difficult to disentangle direct effects of elevated [CO_2] on aboveground carbon content from the consequences of forest dynamic processes. In some forests more rapid forest turn-over times are indicated and increasing proportions of light-loving faster-growing trees are plausible responses to both elevated [CO_2] and post-disturbance processes (Laurance *et al*. 2004, 2005). In other forests, carbon is either accumulating or decreasing in late successional trees (Feeley *et al*. 2007*b*; Chave *et al*. 2008*a*, 2008*b*), suggesting that non-CO_2-related processes are driving changes in biomass (Wright 2005).

The evidence that elevated [CO_2] suppression of transpiration may significantly change ecosystem structure and function in forests is also meagre, although in four of five tree FACE systems, all in temperate landscapes, and in a subtropical scrub-oak woodland system, soils were more moist beneath trees exposed to elevated [CO_2], providing evidence for a reduction in plant water use. No such information is available for tropical forest dynamics plots. Current plot research mainly quantifies changes of carbon pools and species diversity but these studies have not been paired with measurements of hydrological pools and fluxes. The ability of current generation climate-biosphere models to convincingly predict the consequential effects of elevated [CO_2] on stomatal conductance is also impeded by their simplified representation of vegetation and soil-water processes (Betts *et al*. 2007; Huntington 2008; Sitch *et al*. 2008; Boucher *et al*. 2009). An improved systems understanding of forest water relations in the face of rising [CO_2] is still required, particularly in tropical forests (Stork *et al*. 2007). At the tree level, studies need to go beyond instantaneous spot-measurements of leaf conductance. Long-term estimates of the rates at which water is extracted from the soil, the influences of environment upon these rates and the depth from which water is extracted are required. At the soil level, long-

term measurements of surface water runoff, soil water pool sizes and fluxes are necessary. Quantification of soil water pools and water movement at suitable scales may well be best addressed through classical gravimetric lysimetry in CO$_2$ enrichment experiments and, at a landscape level, through watershed monitoring, with arrays of buried sensors that estimate soil water storage and the direction of water movement, and studies which employ emerging geological lysimetric technologies based on deeply buried piezoelectric pressure sensors that detect changes in the weight of up to several hectares of land.

Water supply looms as a critical issue in a future high [CO$_2$] Amazonia if predictions are correct that productivity will be reduced in response to increased temperatures, increases in seasonality of rainfall and more frequent drought (Betts *et al.* 2004; Phillips *et al.* 2009). Nonetheless, it is feasible that water saved by reduced transpiration may prolong the availability of critical water resources. Such microclimatically generated inertia operating in tandem with long tree life spans, slow rates of community turnover and a diverse range of species and functional types, may provide resilience (so-called demographic and ecosystem inertia), albeit possibly only temporarily, to potential drought-influenced changes in forest and even biome structures predicted by forest 'dieback' and 'tipping' analyses (Lewis 2006; Malhi *et al.* 2009).

The detection of CO$_2$-specific natural forest responses to increases of ~2 μmol mol^{-1} CO$_2$ year^{-1} (Hofmann *et al.* 2009) in climatically 'noisy' environments is difficult in the short term. The potential of forest plot networks to provide definitive evidence of such CO$_2$ effects on forest and ecosystem processes will unfold, but it may require 50–100 years before trends can be assigned to individual factors, although, even then, uncertainty associated with the lack of an adequate control will remain. Predictions of increasing climatic seasonality and drought, and concerns about the future of tropical forests, reinforce the connection between water and enhanced [CO$_2$] and emphasise the necessity for a better understanding of soil water conditions and water fluxes through the soil-plant-atmosphere continuum in the years to come.

Acknowledgements

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