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Location: Book Stacks

Item #:

Journal Title: Terrestrial Global
Productivity

Article Author:

Article Title: Water, Nitrogen, Rising
atmospheric CO2 and Terrestrial
Productivity

Volume:

Issue:

Month/Year: 2001

Pages:

Imprint:

TransactionNumber: 499354



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STATUS: NAU Undergrad
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Water, Nitrogen, Rising Atmospheric CO₂, and Terrestrial Productivity

Denis Loustau, Bruce Hungate, and Bert G. Drake

I. Introduction

The functioning of plants in terrestrial ecosystems must satisfy different constraints imposed by the physical environment. The prevention of embolism and conservation of internal water constrain stomatal behavior and leaf area indices that plants may sustain. Plant height and canopy structure are controlled by water and nutrients through carbon allocation between roots and leaves. The amount of available nutrients strongly influences net primary production, largely by determining the amount of photosynthetic enzymes, and in turn leaf area, that may be achieved in a given ecosystem. The impacts of stomatal function, leaf area index, and photosynthetic capacity on the net primary production of terrestrial ecosystems vary according to canopy roughness. Increasing atmospheric CO₂ concentration (C_a) usually stimulates carbon uptake and carbon distribution belowground, though the magnitude of these responses varies among ecosystems. Translating increased carbon uptake at the leaf and canopy levels to long-term carbon storage is not straightforward, and, so far there is little experimental verification of a CO₂-driven expansion of carbon pools with long-term storage potential. Nevertheless, evidence to date suggests that carbon uptake by the terrestrial biosphere will increase in concert with rising C_a .

The importance of water and nutrient regimes for net primary production (NPP) and net ecosystem production (NEP) has long been recognized for agricultural crops. A simple plot of annual net primary production vs. rainfall illustrates the dependency of NPP on rainfall for a wide range of agricultural and natural ecosystems (Fig. 7-1), the dependency being stronger for the drier ecosystems than for the more humid ones. A variety of surveys

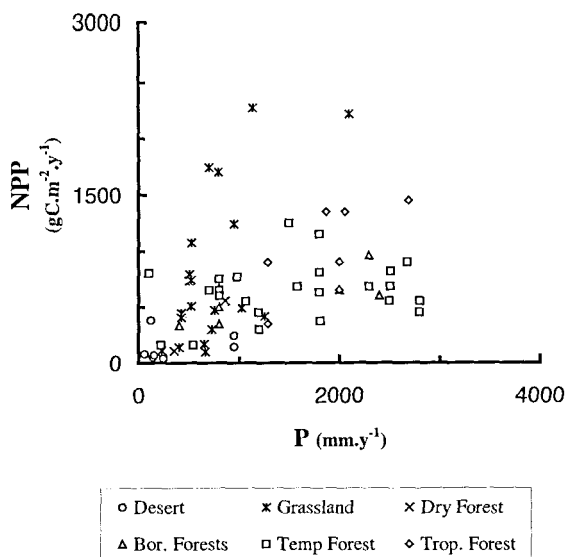


Figure 7-1 Annual net primary production (NPP) and rainfall for a range of terrestrial ecosystems. Data were taken from: Baldocchi and Vogel (1996), Baldocchi *et al.* (1997), Black *et al.* (1996), Breda and Granier (1996), Fan *et al.* (1995), Grace *et al.* (1995), Greco and Baldocchi (1996), Grier *et al.* (1992), Goulden *et al.* (1996), Harrington *et al.* (1995), Kelliher *et al.* (1993), Knapp *et al.* (1993), Long *et al.* (1989), Nizinski and Saugier (1989), Pook (1985), Redmann (1978), Runyon *et al.* (1995), Ryan *et al.* (1994), Schulze (1982), Schulze *et al.* (1996), Valentini *et al.* (1996), Vermetten *et al.* (1994), Waring *et al.* (1995), and Wofsy *et al.* (1993).

and experiments allow a quantitative estimation of the impact of water and nutrient limitations on the NPP and NEP in terrestrial ecosystems. Fertilization and irrigation experiments clearly show the extent to which NPP is limited by water and nutrients in agricultural crops, forests (Linder, 1987), and grasslands (Date, 1973). The role of nitrogen deposition in the enhancement of forest production across northern Europe shows that nutrient limitation affects forest NPP at large scales (Kauppi *et al.*, 1992), though excessive N deposition can reduce NPP in forests by causing soil acidification and losses of base cations (Johnson *et al.*, 1994; Aber *et al.*, 1998). Dendroclimatological studies have demonstrated that the history of drought experienced by various species of temperate trees accounts for some of the annual variation in carbon accumulation by secondary growth in a number of forests (e.g., Becker, 1989; Federer *et al.*, 1989; Becker *et al.*, 1994). A close correlation has been shown between the water balance of forest stands, annual secondary growth, and the carbon isotope ratio in annual ring series of different temperate species (Dupouey *et al.*, 1993; Bert *et al.*, 1997). A number of field experiments show that elevated atmospheric concentration

in CO_2 (C_a) stimulates photosynthesis at the leaf and canopy levels (Drake *et al.*, 1997); the degree of stimulation appears to be higher under limiting water conditions and, in some cases, to be lower when nutrient supply is low.

The aim of this chapter is to analyze the effects of water, nitrogen, and C_a on net primary and net ecosystem production of terrestrial ecosystems. In terrestrial ecosystems, carbon photosynthetic assimilation requires absorption of light and CO_2 and thus exposure of leaves to the atmospheric environment. Associated with the entry of CO_2 into the leaf is an output flux of water vapor from the internal (vapor-saturated) leaf tissues to the air, and loss of plant water. As explained further in Section II,A, plants need to maintain their water content within a relatively narrow range, corresponding to water potentials ranging roughly from 0 to -5 MPa. The presence of plants on the land surface demonstrates that plants can successfully conserve water in their internal tissues across a wide range of external water regimes. This implies that plants can replace lost water and adjust their transpiration to water availability. In addition, photochemical energy conversion and biochemical fixation of carbon result from a combination of various enzymatic activities, all demanding a certain amount of nitrogen, phosphorus, and other nutrients. Terrestrial plants must therefore simultaneously satisfy the different constraints imposed by water relations and nutrient requirements. These constraints are exerted on different components of NPP, including leaf area, stomatal function, photosynthetic capacity, and canopy structure. In Section II, we summarize the main constraints involved. In Sections III and IV, we discuss the effects of water regime and C_a on net primary and ecosystem production as mediated through these different components.

II. The Constraints

The conservation of an internal aqueous medium requires that the plant water losses not exceed the amount of water available over a given time period. For a plant, the water available includes water stored in soil, plant reservoirs, and the net input by precipitation. In the vast majority of ecosystems, plants rely solely on rainfall input during the growing season, although this is not always the case—for example, plants can extract water from deep subsoil reserves or riparian ecosystems. The atmospheric variables that govern water transfer through plants can change rapidly during a day; in contrast, soil water availability typically varies on a time scale of days to weeks. Terrestrial plants must therefore control their water loss, which faces both short-term fluctuations of climatic demand and long-term fluctuations in water availability (Cowan, 1982).

The sensitivity of evapotranspiration (E) at the leaf, plant, and canopy lev-

els has been analyzed by Jarvis and MacNaughton (1986), who introduced the useful notion of coupling. They demonstrated that ecosystem E is affected to different degrees by stomatal conductance and leaf area according to the canopy aerodynamic roughness. Water regime should thus differentially constrain the leaf area and stomatal conductance of terrestrial plants, depending on canopy structure. Indeed, it has long been recognized that water regime affects (1) the canopy leaf area, (2) stomatal behavior, and (3) canopy structure. These effects of water regime are described below.

A. Impact of Water and Nitrogen Availability on Leaf Area

1. Water The restriction of leaf size and number by water limitation is documented for a wide range of crop, grass, and tree species. Many experimental studies have reported detailed information on the processes involved in the control of leaf and stem growth by the water regime. Processes vary according to the plant growth type and life form. Storage factors of carbohydrates required for leaf growth—either in seeds or in perennial vegetative plant parts—(Andriani *et al.*, 1991), leaf number (Cavelier *et al.*, 1992), leaf expansion (Zahner, 1968; Van Volkenburgh and Boyer, 1985; Metcalfe *et al.*, 1990; Zhang and Davies, 1990; Belaygue *et al.*, 1996) and leaf life-span (Pook, 1985; Andriani *et al.*, 1991) are all sensitive to water stress. Leaf cell division and elongation rates are affected by water stress (Durand *et al.*, 1995; Lecoecur *et al.*, 1995). This sensitivity explains both the direct effects (e.g., leaf shedding; Tyree *et al.*, 1993) and indirect effects (e.g., initiation of cell number and leaf primordia of future foliage) of drought on the leaf area of individual plants and canopies (Lecoecur *et al.*, 1995). The combination of these control mechanisms with different response times allows plant communities to integrate the effects of the water regime on short and long time scales. Indeed, even if long time series of simultaneous measurements of leaf area index and water balance are scarce, there is some empirical evidence showing the indirect effects of water stress on leaf area, primary production, and plant growth in natural ecosystems (Webb *et al.*, 1983). One example is given in Fig. 7-2.

Canopy evaporation depends on leaf area index, L , through both the net energy absorbed by the canopy, and the canopy conductance, g_c . At the individual plant scale, decreased leaf area reduces transpiration and conserves water, whatever the canopy structure and roughness. At the canopy scale, the response of ecosystem E to leaf area is not linear but reaches a plateau at high leaf area, due to mutual shading between leaves, compensatory effects of soil evaporation, and related effects on radiation absorption and turbulence. Kelliher *et al.* (1995), analyzing the relationship between L and g_c , demonstrated that the response of the maximal canopy conductance to L may show a plateau above a threshold value close to $L = 4$, depending on the net radiation available, vapor pressure deficit, and aerodynamic con-

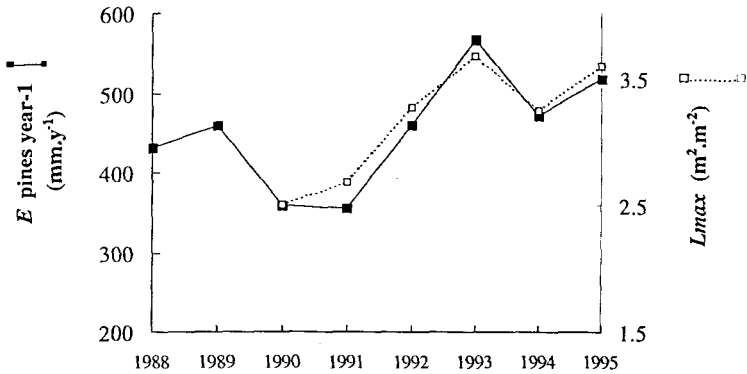


Figure 7-2 Time course of annual maximum of needle area (L) and previous year's evapotranspiration (E) in a 25-year-old maritime pine forest (EUROFLUX Site FR2, "Bray site," Southwest France). The L values were measured by optical methods (Demon system; CSIRO) (P. Berbigier, unpublished results). Estimates of E were based on the Penman-Monteith equation and the stand water balance model, published in Loustau *et al.* (1997).

ductance. Any further increase in L affects only slightly the maximal canopy conductance. Similarly, in an analysis of the sensitivity of the annual water balance of a three-layer forest canopy, Loustau *et al.* (1997a) showed that a change in tree leaf area affected the tree layer transpiration but has a smaller effect on E , because the reduction in pine transpiration is offset by increased soil and understorey evapotranspiration. The dependence of transpiration on leaf area index is thus more sensitive at low values of L . Accordingly, the dependence of L on site water balance is strongest in dry environments, characterized by unpredictable rainfall, very low values of L , and strong seasonality in leaf area and plant life (Nicholson *et al.*, 1990). This is illustrated by Fig. 7-3, which shows variations in L along a water availability gradient from deserts, savannas, and grasslands to sclerophyllous forests and rainforests: with increasing water supply, the canopy structure changes from sparse canopies with seasonal vegetation (ephemerals) such as desert, to canopies in patches, e.g., tiger bush, continuous low vegetation (savannas, grasslands), to continuous, tall, multilayered canopies. The relationship between site water balance and leaf area index has also been established for other vegetation types, such as temperate forests (Grier and Running, 1977; Gholz, 1982; Gholz *et al.*, 1990) or mediterranean ecosystems (Poole and Miller, 1981; Rambal and Leterme, 1987).

2. Nitrogen Availability Photon harvesting, photochemical conversion, and biochemical photosynthetic energy fixation require that leaves contain a certain amount of nitrogen and nutrients incorporated in structural compounds, enzymes, and other metabolic components. The N concentration

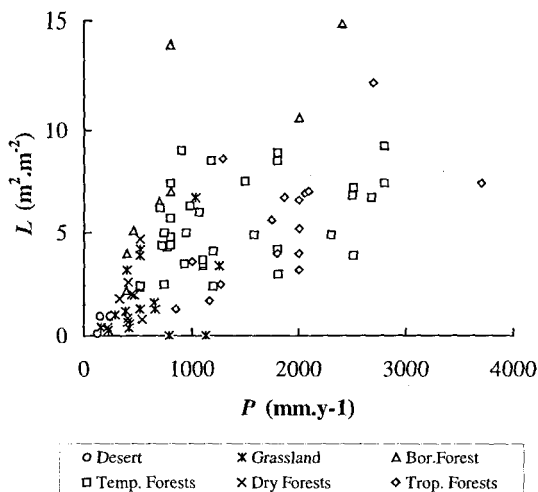


Figure 7-3 Relationship between the annual maximum leaf area index (L) and annual precipitation (P) for terrestrial ecosystems (same data as Fig. 7-1).

in plants is highest in leaves, particularly young leaves, reflecting the nitrogen cost of photosynthesis. This includes nitrogen required for light harvesting and for CO_2 fixation, e.g., for the CO_2 carboxylation enzyme, ribulose biphosphate carboxylase/oxygenase (rubisco), which constitutes 5–30% of leaf nitrogen (Field, 1991), the proportion generally increasing as nitrogen concentration increases (Evans, 1989). The proportions and activity of nitrogenous compounds in leaves change according to the balance of available resources (Chapin *et al.*, 1987): when carbon acquisition is enhanced (by increasing photosynthesis in elevated Ca , for example), rubisco content and activity decrease, freeing N for other functions (Woodrow, 1994). Similarly, the CO_2 concentrating mechanism in C_4 plants allows a greater photosynthetic capacity per unit N compared to C_3 plants—concentrating intracellular $[\text{CO}_2]$ in C_4 plants makes C less limiting, and thus N can be allocated to other functions (Sage and Percy, 1987). Similarly, nitrogen in chlorophyll constitutes 15–20% of total leaf nitrogen when plants are grown under high light; this proportion varies inversely with irradiance and can increase to 60% when plants are grown in the shade (Evans, 1989). Plants adapted to shade conditions show greater N investment in light harvesting (Bjorkman, 1981), whereas high-light adapted plants invest relatively more in rubisco (CO_2 fixation) (Seemann *et al.*, 1987).

In response to increasing N supply, production of leaf area increases more than photosynthetic rate per unit leaf (Sage and Percy, 1987). For example,

the response of coniferous forests to increased nutrient availability was a large increase in leaf area and stem growth with only a small increase in the photosynthetic capacity (Brix, 1981; Linder and Rook, 1984). Similarly, decreasing N supply decreases the rate of leaf expansion more than the rate of photosynthesis per unit leaf area (Evans, 1983; Pettersson and McDonald, 1992). Plant growth rate is therefore not strongly correlated with photosynthetic capacity, but is strongly correlated with the rate of leaf expansion (Potter and Jones, 1977).

Relatively high N partitioning to new leaves should tend to maximize growth, because of the compounding effect on growth of producing new photosynthetic tissue. However, producing new leaves creates additional demand for nitrogen (and other belowground resources). Thus, when nutrients become limiting to growth, plants increase partitioning of resources to roots (Davidson, 1969; Reynolds and D'Antonio, 1996). In response to nitrogen stress, N can be remobilized from shoots and distributed to roots to enhance acquisition of the more limiting resource (Vessey and Layzell, 1987). For carbon allocation, as well, decreasing N availability reduces the rate of leaf expansion, reducing foliar sink strength, and shifting carbon allocation from developing leaves to roots. Conversely, increasing nitrogen availability enhances shoot growth relatively more than root growth. As shown by Vessey and Layzell (1987), coordination of root and shoot growth in response to increasing N supply involves translocation of N between shoots and roots. When leaf N concentration is high, foliar nitrogen is transported as amino acids to roots. The nitrogen the roots do not use is returned to shoots to support growth of new leaves.

The morphology of leaves and roots also changes in response to variation in nitrogen supply. Specific leaf area increases with increasing N supply, and fine root production decreases (e.g., Boot and Mensink, 1990; Linder and Rook, 1984; Fitter and Hay, 1981; Hunt *et al.*, 1985; Fitter, 1985), reflecting a shift in partitioning toward carbon acquisition when nitrogen is abundant. According to several plant growth models, the shift in biomass partitioning in response to increased or decreased nitrogen supply maximizes growth rate (Mooney *et al.*, 1988; Hirose, 1987; Kachi and Rorison, 1989). With increasing nitrogen supply and plant internal nitrogen concentration, leaf weight ratio, specific leaf area, and net assimilation rate all increase, resulting in higher relative growth rate (Hirose, 1988). In fact, plant internal nitrogen concentration alone is a powerful predictor of plant growth rate and primary production (Agren, 1985; Agren and Ingestad, 1987). Nitrogen limitation of net primary production has been demonstrated in many temperate ecosystems by N addition experiments and is inferred in many cases based on carbon:nutrient ratios (Vitousek and Howarth, 1991), because limited nitrogen supply reduces foliar nitrogen concentration relative to other nutrients (Ingestad, 1979; Birk and Vitousek, 1986).

B. The Role of Stomatal Control

The vulnerability of water transport tissues to cavitation implies that vascular plants must control their internal water tensions and transpiration over short time scales (Tyree and Sperry, 1988). They modulate loss of water through stomatal control (Woodward, 1998). The water transfer system of most plants operates under tension, i.e., at negative water potentials (Sperry *et al.*, 1996), and plants must keep their water potential above the point of catastrophic runaway embolism, which varies from above -1.0 MPa for riparian species (Tyree *et al.*, 1994) and some rainforest tree species (Machado and Tyree, 1995) to -10 MPa in less vulnerable species, e.g., *Juniperus* sp. (Sperry and Tyree, 1990). Depending on the value of the soil-to-leaf hydraulic conductance and soil water potential in the rooting zone, vulnerability to cavitation sets an upper limit on water flow through the plant. This constraint must therefore be exerted on stomatal conductance (Tyree and Sperry, 1988; Jones and Sutherland, 1991; Cochard *et al.*, 1996). From this point of view, it is worth noting that the main external variables constraining stomatal function—water availability at the soil–root interface, and leaf-to-air vapor pressure deficit—also determine the water potential difference between the end points of the soil-to-leaf pathway.

In aerodynamically rough canopies, stomatal closure is a very efficient mechanism for adjusting both individual plant transpiration and stand E (Choudhury and Monteith, 1986; Kelliher *et al.*, 1993). This has been shown, e.g., in sclerophyllous Mediterranean vegetation (Tenhunen *et al.*, 1990) or coniferous canopies (Granier and Loustau, 1994; Loustau *et al.*, 1996). In such canopies, atmospheric vapor pressure deficit, D , at the leaf surface is only weakly dependent on plant transpiration, so that plant transpiration and ecosystem E depend strongly on canopy conductance, i.e., on leaf conductance and leaf area. Additionally, the increase in sensible heat flux caused by stomatal closure leads to a vertical expansion of the convective boundary layer (Jacobs and De Bruin, 1992). Incorporation of drier air from above the convective boundary layer dilutes the vapor emitted by the canopy within a larger volume of air, which leads to a positive feedback on D . Indeed, there is increasing evidence showing that stomatal function effectively allows woody plants to operate above their cavitation threshold (Alder *et al.*, 1996), as illustrated in Fig. 7-4 (Cochard *et al.*, 1996).

In a smooth canopy, whole-ecosystem E is less sensitive to leaf area or stomatal conductance because stomatal variation has a negative feedback effect on D at the canopy surface, canceling the impact on E . The transpiration of an individual plant is more sensitive to its leaf area than to its stomatal conductance, because plant transpiration is dominated by the equilibrium term, i.e., the amount of absorbed energy. Additionally, small leaf size confers a high boundary layer conductance, favoring heat dissipation, which is advantageous in dry environments. In aerodynamically smooth canopies,

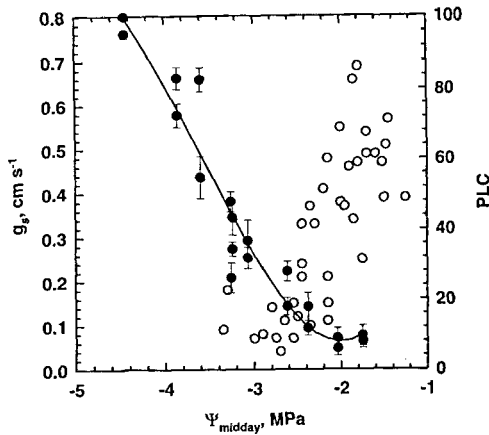


Figure 7-4 Percent loss in conductivity due to xylem embolism (●) and midday stomatal conductance (○) vs. leaf water potential at midday (Ψ_{midday}) in *Quercus petraea*. Vertical error bars represent one standard deviation. Embolism significantly increased in petioles and twigs, $\Psi_{\text{midday}} < -2.7$ Mpa, at which point stomatal conductance (g_s) was reduced to about 10% of its maximal value. From Cochard *et al.* (1996), with permission.

the sensible heat flux and, in turn, the height of the convective boundary layer are less sensitive to stomatal conductance. Therefore, plant transpiration is rather regulated by control of the net absorption of radiation by leaves, through such processes as leaf growth, leaf rolling, leaf shedding, and leaf orientation (Dingkuhn *et al.*, 1989). Avoidance of critically low water potentials may also be less important for systems (e.g., grass species) in which the nocturnal repair of embolized vessels may be more common due to positive root pressures (Tyree *et al.*, 1986).

The hydraulic constraint may also restrict species expansion, precluding the survival of a given species in environments that are too dry (or cold), environments according to their hydraulic vulnerability and stomatal function characteristics. Convincing examples may be found in Sperry and Tyree (1990) and Tyree and Cochard (1996), who compared the hydraulic vulnerability of coniferous and *Quercus* species, respectively, and concluded that the differential vulnerabilities to embolism contribute to their geographical distribution.

C. Impact of Water Availability on Canopy Structure

The constraints on L and g_c by the water regime, with related effects on assimilation rate, are, together with temperature, major factors determining the distribution of plant life form over the land surface (Raunkiaer, 1934; Schulze, 1982; Woodward, 1987). This influence has been widely recognized

and we shall not add further comments on this point. Although water stress has been shown to affect plant architecture through qualitative processes involved in morphogenetic development, here we will focus on two water-related processes involved in the control of plant height—plant carbon balance and hydraulic architecture.

It is relatively straightforward to understand the potential impacts of the water and nutrient availability on plant height and canopy structure from an analysis of the carbon balance of a single plant, using the pipe model formalism (Makela, 1986; Valentine, 1990). The net production of a leaf over an annual cycle must account for the cost of maintenance and renewal of the tissues that support the water transfer system to the leaf, i.e., sapwood, cambium, and root (Fig. 7-4). As canopy height increases, so does the length of the pathway between roots and leaves and the size of the sapwood connecting them. Water and nutrients affect the amount and distribution of assimilates, and in turn plant and canopy height through different components of the plant carbon balance.

First, as detailed in Section III,B, the time integral of leaf net assimilation rate, and, in turn, the amount of carbohydrates available for stem maintenance, depend on the water regime and nutrient availability. Furthermore, this effect interacts with increasing plant height as a consequence of increased gravitational force and decreased stem conductance (Mencuccini and Grace, 1996). Both of these factors increase the water stress in leaves and impair their photosynthetic production.

Second, the root:shoot ratio is increased under drought conditions because carbon allocation shifts in favor of roots under water- or nutrient-limiting conditions. This is well exemplified by the data obtained by Schulze *et al.* (1996) along an aridity gradient in Patagonia. Consequently, humid and fertile environments, where leaf assimilation is not restricted by drought, allow growth of larger plants and taller canopies, with proportionally less belowground biomass. In these conditions, height growth provides a competitive advantage for light capture. Nutrient-poor or dry environments limit the development of the plant aerial structure and produce larger root systems. The competition for light will not play a major role in canopy structure.

Finally, Mencuccini and Grace (1996) reported convincing evidence that the age-related decrease of soil-to-leaf hydraulic conductance could explain the maximal height reached by a Scots pine stand at Thetford Forest (South England), through a decrease in apical growth rate linked to lack of turgor (Tyree and Ewers, 1991). This may also place a ceiling on the maximal height sustainable in a given environment. Similarly, Margolis *et al.* (1995) derived an expression relating the maximal height as a function of internal hydraulic conductance, leaf surface/sapwood ratio, and variables determining the transpiration of canopy (Whitehead *et al.*, 1984). From this re-

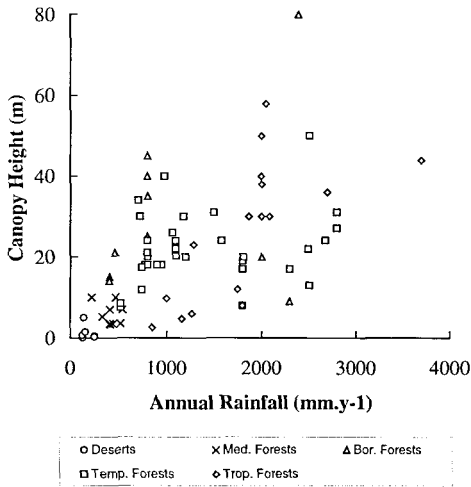


Figure 7-5 Relationship between canopy height and annual rainfall for a range of terrestrial ecosystems. (same data as Fig. 7-1).

lation, Beerling *et al.* (1996) explained some of the effects of drought on the height growth of *Fagus sylvatica* in England.

The relative extent to which carbon balance, hydraulic architecture, and availability of nutrients limit plant height is under debate (Ryan and Waring, 1992; Ryan *et al.*, 1994). The major difficulty when attempting to provide a quantitative estimate of the upper limit in canopy height is the assessment of the carbon balance of the whole plant and canopies over long periods. Some components, e.g., root turnover and respiration costs, are notoriously difficult to estimate and can account for 10–60% of the carbon assimilated. The maintenance and renewal costs of stem transfer tissue expressed per meter length may account for typically 0.5–1.5% of total net assimilation as calculated from Ryan (1990), Ryan *et al.* (1994), or Bosc (1999). This order of magnitude is quite compatible with the hypothesis of control of canopy height by carbon balance: the maximum height sustainable by a canopy would then be around 80 m and a more reasonable estimate will be around 60 m for the most humid part of the world where the tallest forests occur (Fig. 7-5).

III. Effects of Water Regime on Net Primary Production

Leaf area index, stomatal function, and canopy structure differentially affect NPP and NEP of terrestrial ecosystems. Carbon assimilation by terres-

trial plants can be regarded as the result of three interrelated processes: light interception and energy conversion by photochemical reactions, diffusion of CO_2 to chloroplastic carboxylation sites, and carbon fixation by carboxylation of ribulose-1,5-bisphosphate (RuBP) (C_3) or phosphoenol pyruvate (PEP) (C_4). Leaf area primarily affects light interception, whereas canopy structure and stomatal function influence the diffusion of CO_2 into leaves. Photochemical energy conversion and carbon metabolism are controlled by the amount and efficiency of enzymes per unit leaf area, which appear to be controlled by nutrient availability. This will be analyzed in the next section.

A. Impact of Leaf Area on NPP

The primary impact of leaf area on net production derives from the interception of photosynthetically active radiation by the canopy. The impact of leaf area on light interception and ecosystem production has been widely documented (Monteith, 1977; Gosse *et al.*, 1986; Cannell *et al.*, 1987), and there is strong empirical evidence that differences in leaf area between ecosystems explain most of the geographical variations in primary production. For instance, Webb *et al.* (1983) demonstrated that a unique linear relationship between maximal annual foliar standing crop and NPP can well describe the variations observed over a range of ecosystems, from desert to coniferous forests, in North America. This relationship has also been established within particular biomes, e.g., coniferous forest (Runyon *et al.*, 1994; McMurtrie *et al.*, 1994), eucalypt forests (Landsberg and Hingston, 1996), and along aridity transects, e.g., *Acacia koa* in Hawai (Harrington *et al.*, 1995). Water regime contributes also to explaining local and temporal variations in NPP through variations in L . This is clearly shown by irrigation experiments, e.g., in annual crops such as sunflower and soybean (Cox and Jolliff, 1986; Huck *et al.*, 1986) or lucerne (Durand *et al.*, 1989) or for some forest stands (Linder *et al.*, 1987). Figure 7-6 illustrates the relationship between annual net primary production and leaf area index for a range of ecosystems.

B. Stomatal Control and Related Effects

1. Leaf Level

a. Effects of D Stomatal closure under increasing atmospheric deficit is commonly observed in arid (Schulze *et al.*, 1974; Roessler and Monson, 1985), mediterranean (Eckardt *et al.*, 1975; Tenhunen *et al.*, 1984), temperate (Beadle *et al.*, 1985), and even tropical (Smith, 1989; Roy and Salager, 1992; Koch *et al.*, 1994; Zotz and Winter, 1996) environments. In the early 1980s, the observed decrease in carbon assimilation accompanying a mid-day increase in D and temperature was attributed to both stomatal and non-stomatal effects (Tenhunen *et al.*, 1984). However, these conclusions have been questioned in the light of observations of drought-induced patchy

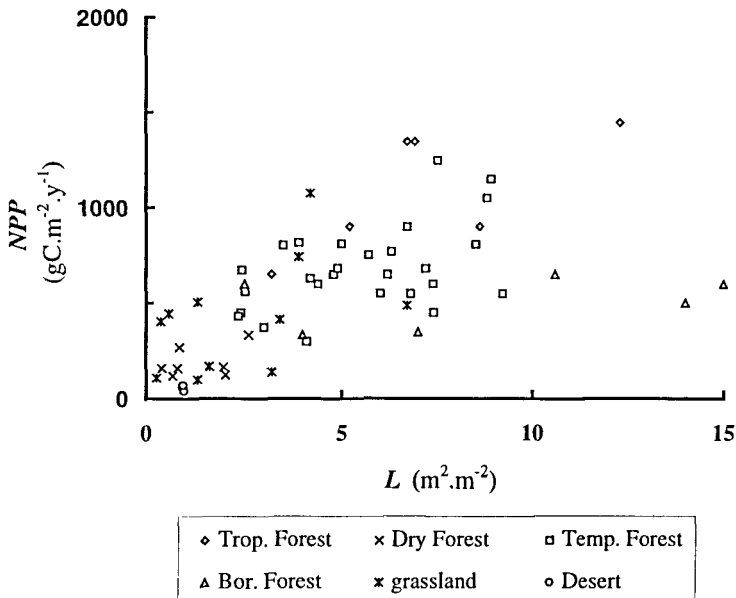


Figure 7-6 Relationship between annual net primary production and leaf area index for the data referenced in Fig. 7-1.

stomatal closure, the consequences of which for the internal CO_2 concentration C_i computations were made explicit by Terashima *et al.* (1988). The effect of stomatal response to D on assimilation rate appears to be primarily a drop in C_i , as can be readily understood from current leaf photosynthesis models (e.g., Farquhar *et al.*, 1980). In particular, it is worth noting that the light limited- and light-saturated photosynthetic rates are not equally affected by internal CO_2 concentrations. Stomatal closure affects the light-saturated rate more than the apparent quantum efficiency of carbon assimilation, and therefore decreases the light threshold intensity for saturating photosynthesis.

There is now little evidence that atmospheric drought may produce a substantial change in C assimilation through enzymatic activities. When patchiness effects were taken into account, a decrease in enzymatic activities in the short-term response of leaf assimilation to atmospheric D or mild water stress could not be demonstrated (Sharkey and Seemann, 1989), leading authors to postulate that the effect of D on carbon assimilation could be considered as a purely stomatal limitation (Comstock and Ehleringer, 1993; Dai *et al.*, 1992). The linear decrease of C_i induced by D found in a wide range of plants by Zhang and Nobel (1996) is consistent with this hypothesis.

b. Soil Water Deficit Stomatal closure and the related drop in C_i is the first mechanism that affects carbon assimilation during a period of soil water shortage. However, nonstomatal effects, i.e., a reduction in enzyme activity, are also commonly involved during soil water deficits. Adjustment of photosynthetic enzymatic capacity has a longer time constant, typically hours to days, and requires a longer application time of the primary signal. There is an abundant literature showing a down-regulation of enzymatic activities when photosynthesis is decreased by CO_2 availability, e.g., under drought-induced stomatal closure, in both C_3 (Jones, 1973; Martin and Ruiz-Torres, 1992; Wise *et al.*, 1990; Sharkey and Seeman, 1989; Kaiser, 1987) and C_4 (Du *et al.*, 1996) plants.

Following the work of Kaiser (1987), Cornic *et al.* (1989), and Quick *et al.* (1992), who suppressed artificially the diffusional limitations induced by water stress using CO_2 concentrations as high as 15%, it is now commonly accepted that leaf water stress or dehydration has no effect per se on the photon-harvesting systems and thylakoid enzymes controlling the light reaction processes of photosynthesis, at least in the range encountered under natural conditions (Chaves, 1991; Dreyer *et al.*, 1992; Epron and Dreyer, 1992). However, under high radiation load, stomatal closure can raise leaf temperature to supraoptimal levels. Under such conditions, the capacity of leaves to recycle the excess reducing power through processes such as heat dissipation, the Mehler reaction (e.g., Biehler and Fock, 1996), and photorespiration (Heber *et al.*, 1996) may be overridden. This leads to irreversible damages to the photosynthetic apparatus. In the field, reversible photoinhibition, leading to a decrease in light-saturated rate of photosynthesis, has been shown to occur typically during the afternoon, for grapevine (Correia *et al.*, 1990) and *Quercus cerris* (Valentini *et al.*, 1995), and is attributed to indirect effects induced by high light and temperature on photosystem II (PSII).

A consequence of the stomatal effects on carbon assimilation and transpiration lies in the characteristics of discrimination between stable carbon isotopes by C_3 plants. Farquhar *et al.* (1989) demonstrated that the discrimination rate is proportional to the ratio A/g_s , or intrinsic water use efficiency, and decreases with stomatal closure. This finding opened interesting possibilities for the use of carbon isotope analysis of plants (more particularly, annual rings of trees) to assess fluctuations in water use efficiency and net primary production caused by drought (Dupouey *et al.*, 1993; Livingston and Spittlehouse, 1996; Bert *et al.*, 1997; Walcroft *et al.*, 1997; Nguyen-Queyrens, 1998; Duquesnay *et al.*, 1998).

2. Ecosystem Level

a. Impacts of D A significant decrease in the radiation use efficiency (RUE) concurrent with high vapor pressure deficit values has been observed in a wide variety of terrestrial ecosystems, e.g., tall canopies such as coniferous forests (Fan *et al.*, 1995; Baldocchi and Vogel, 1996; Lamaud *et*

al., 1997), tropical forests (Grace *et al.*, 1995), and broadleaved temperate forests (Hollinger *et al.*, 1994). Only a few exceptions report the absence of any contribution of *D* to variations in net carbon exchanges over a deciduous forest (Verma *et al.*, 1986). Runyon *et al.* (1994) estimated that *D* reduced the NPP of coniferous ecosystems in the Oregon transect by 10–20%, and a stronger effect of *D* can be presumed in more arid environments. A decrease in the net carbon exchange by increased *D* was also observed for medium-size canopies, such as *Andropogon* tallgrass prairie (Verma *et al.*, 1989, 1992), and even for shorter-statured grasslands (Kim and Verma, 1990; Pettigrew *et al.*, 1990) and crops (Stockle *et al.*, 1990). A positive interaction of the effect of *D* with soil drought is commonly observed (e.g., Verma *et al.*, 1992). The effects of *D* on stomatal conductance and net assimilation can certainly account for a part of the midday (or afternoon) depression in RUE reported in most studies of CO₂ exchanges above rough canopies, either in water-limited or well-watered conditions (e.g., Valentini *et al.*, 1996; Lamaud *et al.*, 1997). However, high *D* occurs simultaneously with high temperature and radiation, which raise leaf and biomass temperatures and increase their respiration rates. Additionally, photosynthesis may also decrease when temperature exceeds an optimal value. These effects are confounded in the above-mentioned decrease of NEP, and cannot be discriminated easily.

Unfortunately, the variety of sites and climate conditions precludes a comprehensive comparison of the impact of *D* on RUE between canopies of different roughness. The impact of *D* on canopy net exchanges may explain some differences in the behavior of different ecosystems, because grassland plant species would be expected to be less sensitive to *D* than tree species (Jarvis, 1985). Because large values of *D* occur mostly under saturating light conditions, the difference RUE of forest and crops might be explained in part by the difference in response of their canopy conductances to atmospheric *D* (Ruimy *et al.*, 1995). The observation that the assimilation rate of uncoupled canopies, e.g., grasslands, does not saturate with increasing photosynthetically active radiation (PAR), as coupled canopies do (Ruimy *et al.*, 1995), suggests that the light saturation point of net assimilation could be reduced more by *D* in rough canopies.

b. Impact of Soil Water Deficit Effects of soil drought on RUE have also been reported for a wide range of ecosystems. A drought-induced decrease in RUE has been demonstrated in most forests, e.g., a canopy of *Pinus pinaster* (Fig. 7-7), *Fagus sylvatica* (Valentini *et al.*, 1996), or mixed deciduous forest (Greco and Baldocchi, 1996). However, this drought impact can be tenuous for temperate forests growing under high rainfall, as in the case of the deciduous forest studied by Goulden *et al.* (1996).

Only the NPP of lowland boreal or flooded forests, where the water table remains close to the soil surface during the growing season, escapes such soil water limitations (Black *et al.*, 1996; Baldocchi *et al.*, 1997). There is some current uncertainty concerning the extent of the effects of soil moisture

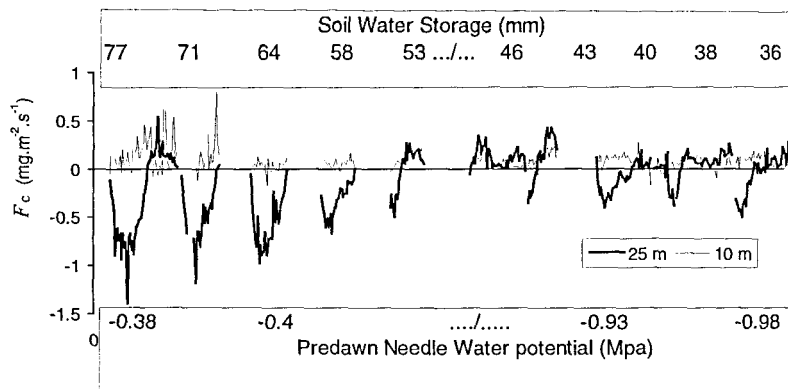


Figure 7-7 Time course of CO_2 fluxes beneath ($z = 10$ m) and above ($z = 25$ m) a maritime pine canopy, for selected days covering a range of soil moisture deficits in summer, 1995. Soil water content, predawn needle water potential, and daily sum of downward PAR are given for each day. Flux data are from Lamaud *et al.* (1997).

deficit on net exchange between tropical rainforest and atmosphere (see Chapter 17, this volume), but there is no doubt that soil water can also play a role in these systems, at least where there is a significant dry season (Monteny, 1989). The RUE of grass and savannas is also affected by soil moisture deficit. Estimates of NPP from biomass changes (Knapp *et al.*, 1993; Petersson and Hansson, 1990; Long *et al.*, 1989, 1996) and from continuous measurements of net ecosystem exchanges (Kim and Verma, 1990; Verma *et al.*, 1989, 1992; Redmann, 1978) show a clear decline linked to soil water deficit. Such effects have also been widely documented for agricultural crops, for which some continuous measurements of ecosystem exchanges have been made using crop chambers (Jones *et al.*, 1986), Bowen ratio- CO_2 combined measurements (Baldocchi *et al.*, 1981a, 1983, 1985), or eddy covariance techniques (Baldocchi, 1994). Nevertheless, it should be noted that the growth habits of some adapted species exhibit a high tolerance to water stress and are affected weakly by soil moisture deficit, e.g., alfalfa (Baldocchi *et al.*, 1981b).

C. Impact of Canopy Roughness

An important characteristic of the control of transpiration and assimilation by L or g_c is that the efficiency of control by L (or g_c) varies according to the degree of coupling of the canopy to the atmosphere (Jarvis and MacNaughton, 1986). As pointed out by Jarvis (1985), the effects of a fractional change in canopy conductance on net assimilation are expected to be stronger in tall canopies than in short canopies, because the drop in C_i caused by stomatal closure is partially offset by an increase in C_a in the latter. Figure 7-8 shows the theoretical relationship between g_c and the light-

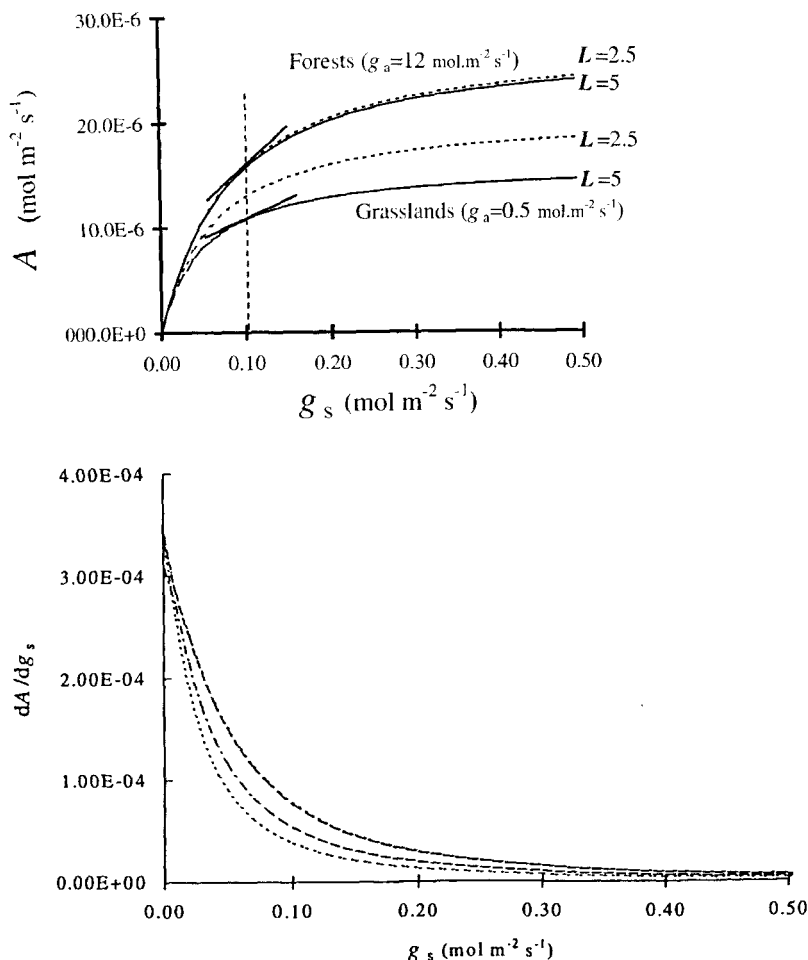


Figure 7-8 Impact of a change in g_s on the light-saturated carbon assimilation of theoretical "big C_3 leaf" canopies differing in leaf area index and aerodynamic conductance, at 25°C and $[\text{CO}_2] = 350 \mu\text{mol mol}^{-1}$ (upper graph). The tangents drawn at $g_s = 100 \text{ mmol m}^{-2} \text{s}^{-1}$ give the absolute sensitivities of the forest and grassland to g_s . The lower graph gives the sensitivity of carbon assimilation to g_s . Assimilation was calculated using the model of Farquhar *et al.* (1980). Parameters values are maximal carboxylation rate, $V_{c \text{ max}} = 100 \mu\text{mol m}^{-2} \text{s}^{-1}$; day-light respiration $R_d = 1 \mu\text{mol m}^{-2} \text{s}^{-1}$; CO_2 light-insensitive compensation point, $\Gamma^* = 31 \mu\text{mol mol}^{-1}$; Michaelis-Menten constant for carboxylation, $K_c = 0.46 \text{ mmol mol}^{-1}$; and oxygenation $K_o = 0.33 \text{ mol mol}^{-1}$.

saturated rate of photosynthesis for short and tall canopies. Both canopies are modeled as a big C_3 leaf. Photosynthesis is calculated from Farquhar *et al.* (1980), internal mesophyll resistance is neglected, and other parameters are given in the legend of the figure. The figure shows clearly that the sensitivity of net assimilation to stomatal conductance is higher for forest canopies than for short, smooth canopies: when C_i drops below $100 \mu\text{mol mol}^{-1}$ a fractional reduction in stomatal conductance reduces A almost twice as much for a forest than for a short grass. Unfortunately, available data describing the effects of soil water deficit or D on stomatal conductance and carbon assimilation in natural canopies remain scarce, making it difficult to compare the behavior of aerodynamic contrasting canopies. Indeed, there is some experimental evidence showing that the midday CO_2 mixing ratio within a sunlit canopy does not deviate from the reference value by more than $20 \mu\text{mol mol}^{-1}$ in tall canopies (Buchmann *et al.*, 1996), but can decrease by $100 \mu\text{mol mol}^{-1}$ in short canopies. Turbulent mixing has been shown to have a positive effect on net assimilation at high irradiance in short C_3 canopies such as rice (Yabuki *et al.*, 1978) or alfalfa (Baldocchi, 1981b), but does not appear to affect the carbon exchange of tall canopies to the same extent. In tall canopies, Buchmann *et al.* (1996) showed that the CO_2 profile between the soil and the top of the canopy was more depleted in a broadleaved, smooth canopy than in a conifer canopy. In addition, Baldocchi and Vogel (1996) observed that D had more severe effects on net assimilation for a boreal coniferous canopy than for a broadleaved, smoother, temperate forest.

IV. Effects of CO_2 on NPP and NEP

The effects of rising C_a on net primary production and net ecosystem production depend on the physiological responses of plants to elevated C_a , how these responses interact with environmental stresses, and feedbacks and constraints that modulate their translation to the ecosystem level. Experimental CO_2 doubling stimulates photosynthesis at the leaf level, and in most cases at the canopy level as well, in both managed and unmanaged ecosystems. Elevated C_a often reduces stomatal conductance and transpiration, and the stimulation of photosynthesis by elevated C_a is generally larger when plants are under water-stressed conditions. In some cases, photosynthetic and growth responses to elevated C_a are smaller in plants under nutrient stress, but they are rarely eliminated and in many cases do not seem to depend on nutrient stress at all. Furthermore, elevated C_a reduces the requirement for rubisco, contributing to the reduction in foliar nitrogen concentrations in elevated C_a , and this plasticity in plant C:N allows a positive response to elevated C_a in nitrogen-limited systems. In field experiments in

herbaceous systems, where enough data are available to construct partial carbon budgets, the enhancements of above- and belowground biomass by elevated C_a are usually smaller than measured increases in CO₂ uptake at the leaf and canopy levels. This discrepancy suggests that much of the extra carbon in elevated C_a is distributed belowground, making it difficult to confirm directly increases in carbon mass in response to elevated C_a . Determining the trajectory of increased NEP beyond the time scales of C_a -enrichment experiments requires considering the distribution of carbon to pools of differing turnover times, and also biogeochemical and atmospheric feedbacks that operate on temporal and spatial scales beyond those of manipulative experiments.

A. CO₂ Stimulation of Photosynthesis: Interactions with Nitrogen

The evidence that elevated C_a stimulates photosynthesis is overwhelming. In experiments conducted in pots with large rooting volumes or with high nitrogen supply, growth in elevated C_a increased photosynthesis 57–58% compared to the rate for plants grown in normal ambient C_a (Table 7-1). While restricted rooting volume and low nitrogen supply reduced the C_a enhancement to 28 and 23%, respectively (Table 7-1), neither eliminated the

Table 7-1 Stimulation of Photosynthesis
by Elevated C_a ^a

Attribute (A)	R	Species (n)
A at growth C_a		
Large rv	1.58 ^b	45 (60)
Small rv	1.28 ^c	28 (103)
High N supply	1.57 ^b	8 (10)
Low N supply	1.23 ^b	8 (10)
Protein	0.86 ^b	11 (15)
[Rubisco]	0.85 ^b	11 (8)
Leaf [N]		
High N	0.85 ^b	8 (10)
Low N	0.81 ^b	22 (39)

^aDetermined as the ratio (R) of the value of the attribute for plants grown in elevated C_a compared to normal ambient C_a in various species and experiments (n), and for plants grown in containers with large (>10 liters) or small (<10 liters) rooting volumes (rv) and under high or low N supply. Also shown are the effects of elevated C_a on protein, rubisco, and leaf N concentrations. After Drake *et al.* (1997).

^bMeans statistically different from 1.0 ($p < 0.01$) by Student's *t*-test.

^cMeans statistically different from 1.0 ($p < 0.01$) by Mann-Whitney rank sum test for data normality test.

stimulation of photosynthesis by elevated C_a . Acclimation of photosynthesis to elevated C_a clearly reduces photosynthetic capacity (Sage, 1994; Gunderson and Wullschlegel, 1994), but rarely enough to compensate completely for the stimulation of the rate by high C_a .

The primary carboxylase of C_3 photosynthesis, rubisco, is the most abundant protein in the biosphere and constitutes as much as 30% of total leaf N mass. In current ambient C_a , light-saturated rates of photosynthesis require large quantities of rubisco (Masle *et al.*, 1993), but elevated C_a reduces this requirement markedly. For example, *Nicotiana tabacum* transformed with antisense RbcS to produce 13–18% less rubisco photosynthesized and grew more slowly than the wild type when both were grown in ambient C_a , but there was no difference in C gain or growth when both were grown at 80 Pa C_a (Masle *et al.*, 1993), showing the decreased requirement for rubisco at elevated C_a . Similarly, calculations suggest that in doubled C_a , 35% of rubisco could be lost before it would colimit photosynthesis (Long and Drake, 1991). Because of the strong temperature dependence of CO_2 stimulation of photosynthesis, the amount of rubisco required in elevated C_a will decline further with increasing temperature. For example, at 25°C, elevated C_a reduces by 41% the amount of rubisco necessary to maintain a given photosynthetic rate, while at 35°C, elevated C_a reduces this requirement by 58% (Woodrow, 1994). This reduced requirement for rubisco in elevated C_a partly causes the commonly observed reduction in leaf N concentration in elevated C_a (Table 7-1) (Conroy, 1992; Curtis *et al.*, 1992; Hocking and Meyer, 1991; Norby *et al.*, 1986; Wong, 1979).

B. Stimulation of Photosynthesis by Elevated C_a : Interactions with Water

The effect of elevated C_a on photosynthesis and plant growth interacts with water stress (Chaves and Pereira, 1992; Grant *et al.*, 1995). Elevated C_a not only enhances CO_2 availability at the leaf surface, but also reduces stomatal conductance in various species. For 23 species and 29 observations, the average reduction of g_s was 23%, leading to an average reduction in leaf transpiration of 27% (Table 7-2) (see also Field *et al.*, 1995). Responses in trees are highly variable (Curtis, 1996), and in some species there is no response to elevated C_a . Differences among species are at least partly related to growth form, as the stomatal response of coniferous trees to elevated C_a tends to be smaller than the response of herbs, and deciduous trees tend to be intermediate (Saxe *et al.*, 1998). It is also possible that the failure of some species to respond directly to elevated C_a is due to acclimation of stomata to high humidity. For example, stomata of *Xanthium strumarium* grown in a greenhouse in high humidity failed to respond to elevated C_a until given a cycle of chilling stress (Drake and Raschke, 1974).

Elevated C_a increases water use efficiency (WUE), the ratio of net photo-

Table 7-2 Effects of Growth in Elevated C_a^a

Attribute	<i>R</i>	Species (<i>n</i>)
<i>g</i> _s	0.80 ^{a,b}	28 (41)
<i>E</i>	0.72 ^b	35 (81)
<i>C</i> _i / <i>C</i> _a	0.99	26 (33)
<i>L</i>	1.03	8 (12)

^aEffects are on acclimation of stomatal conductance (*g*_s), transpiration (*E*), the ratio of intercellular to ambient CO₂ concentration (*C*_i/*C*_a), and leaf area index (*L*; field-grown species only), using a number of species and studies (*n*). *R* is the mean of *n* observations in various species of the ratio of the attribute in plants grown in elevated C_a compared to that for plants grown in current ambient C_a. After (Drake *et al.*, 1997a).

^bMeans statistically different from 1.0 (*p* < 0.01) by Student's *t*-test.

^cMeans statistically different from 1.0 (*p* < 0.01) by Mann-Whitney rank sum test for data that failed normality test.

synthesis to transpiration, either by reducing *g*_s, increasing *A*, or both. In a study of oats, mustard, and two cultivars of wheat, WUE increased 40–100% as the ambient C_a was increased from about 15 to 35 Pa (Polley *et al.*, 1993). In a free-air CO₂ enrichment (FACE) study in wheat, C_a elevated to 55 Pa increased WUE by 76 and 86% in cotton crops, averaged over two full growing seasons (Pinter *et al.*, 1996). Elevated C_a also increased WUE in both C₃ and C₄ wetland species (Arp, 1991) and in annual grasses (Jackson *et al.*, 1994; Hungate *et al.*, 1997a). Water use efficiency determined from gas exchange measurements is increased by elevated C_a in almost every species studied in chambers or greenhouse experiments, and this result has been confirmed in the longer term by growth analysis and carbon isotope discrimination (Jackson *et al.*, 1994; Guehl *et al.*, 1994; Picon *et al.*, 1996).

Elevated C_a can also mitigate plant water stress by improving osmoregulation capacity (Vivian *et al.*, 1996), activating the deoxydative metabolic pathway (Schwanz *et al.*, 1996), and, in some but not all cases, increasing root to shoot ratio (Rogers *et al.*, 1994; but see Norby, 1994). Through these mechanisms, elevated C_a partially alleviates the effects of drought on net assimilation and plant growth (Jackson *et al.*, 1994; Idso and Idso, 1995; Owensby *et al.*, 1997). For example, the increase in carbon assimilation by C_a doubling is 2- to 10-fold higher under drought than under well-watered conditions (Idso and Idso, 1995; Guehl *et al.*, 1994; Clifford *et al.*, 1993). So far, there is no indication of an effect of elevated C_a on hydraulic characteristics of plants—e.g., in *Quercus suber*, *Pinus pinaster*, or *Quercus pubescens*

(H. Cochard, personal communication)—and thus no evidence of associated changes in primary production, although relatively few studies have addressed this issue.

C. Respiration

1. Mechanism of the Direct Response to Elevated C_a Within minutes of a doubling of C_a , respiration often declines by about 20% (reviewed in Drake *et al.*, 1997a). This has been observed in many different tissues—leaves, roots, stems, and even soil bacteria—suggesting that the basic mechanism involves a fundamental aspect of respiration. Elevated C_a reduces the *in vitro* activity of both cytochrome *c* oxidase (Cyto_x) and succinate dehydrogenase, key enzymes of the mitochondrial electron transport system, by about 20% (Gonzalez-Meler *et al.*, 1996; Palet *et al.*, 1991; Reuveni and Gale, 1985), but has no effect on the activity of the alternative pathway (Gonzalez-Meler *et al.*, 1996). Under experimental conditions in which Cyto_x controlled the overall rate of respiration in isolated mitochondria, O_2 uptake was inhibited by about 15% (Gonzalez-Meler *et al.*, 1996). Another proposed mechanism for the apparent inhibition of respiration is that elevated C_a stimulates dark CO_2 fixation (Amthor, 1997). However, measurements of the respiratory quotient (consumption of O_2 /emission of CO_2) show that this is unlikely, because reduced CO_2 evolution is balanced by an equal reduction of O_2 uptake in elevated C_a (Reuveni *et al.*, 1993).

The possibility that CO_2 inhibition of these enzymes mediates the direct effect of C_a on respiration in plants is supported by measurements on different types of plant organelles and tissues. Doubled C_a reduced O_2 uptake by soybean mitochondria and by extracts from excised shoots of the sedge *Scirpus olneyi* (Gonzalez-Meler *et al.*, 1996). Experiments in which CO_2 efflux was used to measure dark respiration showed that doubling C_a reduced respiration in excised shoots removed from the field to the lab and from intact stands in which respiration was determined in the field on the C_3 sedge, *S. olneyi* (Drake, 1992). The importance of this effect for carbon metabolism of plants and ecosystems is that it apparently occurs at a very fundamental level of organization—the mitochondrial electron transport system. Thus, all respiring tissues are subject to this effect.

2. Acclimation of Respiration to Elevated C_a Elevated C_a could also affect respiration by altering tissue composition. As tissues age, the rate of dark respiration of foliage declines. This occurs as tissue N and protein concentrations decline, indicating a decreased demand for energy to sustain growth and/or maintenance. Thus, the reduction in protein and N concentration of plants grown in elevated C_a (Table 7-1) suggests that rising C_a could reduce growth and maintenance respiration associated with protein turnover (Amthor, 1997; Curtis, 1996; Wullschlegel *et al.*, 1992). We re-

viewed data on measurements of respiration on leaves of 17 species grown in current ambient and elevated C_a. Acclimation of dark respiration was determined by comparison of the rate of CO₂ efflux or O₂ consumption measured on samples of tissue grown in current ambient or elevated C_a at a common background C_a. In our survey of the literature we found no overall difference between the specific rates of respiration of shoots and leaves grown in elevated or ambient C_a. However, some C₃ species—*S. olneyi*, *Lindera benzoin*, and *Triticum aestivum*—do show acclimation to high C_a, apparently by reducing the activity of enzymatic complexes of the mitochondrial electron transport chain (Cytochrome and Complex III), resulting in diminished capacity of tissue respiration (Aranda *et al.*, 1995; Azcon-Bieto *et al.*, 1994). Reduction of the activity of these enzymes was not found in the C₄ species, *Spartina patens*.

D. Canopy CO₂ Uptake, Ecosystem Carbon Mass, and Net Ecosystem Production

Based on results from a number of elevated C_a experiments in a variety of ecosystems, there is broad agreement that the stimulation of leaf-level photosynthesis by elevated C_a (Drake *et al.*, 1996, 1997) (Table 7-1) is reflected in increased CO₂ uptake at the canopy level (Drake and Leadley, 1991). For example, even with acclimation of photosynthesis to elevated C_a, in the sedge, *S. olneyi*, elevated C_a stimulated ecosystem carbon uptake in the salt marsh community where *S. olneyi* is dominant (Drake *et al.*, 1996). Increased canopy CO₂ uptake in response to elevated C_a has been observed in field experiments in a number of herbaceous systems, including arctic tundra (Oechel *et al.*, 1994), alpine grassland (Diemer, 1994), annual Mediterranean grassland (Field *et al.*, 1997), tallgrass prairie (Ham *et al.*, 1995), and calcareous grassland (Stocker *et al.*, 1997). In two of these cases, the stimulation of canopy CO₂ uptake was short-lived, disappearing after 3 years in the alpine grassland (Körner *et al.*, 1997) and after 2 years in arctic tundra (Oechel *et al.*, 1994). Photosynthesis in the dominant species in the tundra system rapidly adjusted to elevated C_a in controlled environment studies (Oberbauer *et al.*, 1986; Cook *et al.*, 1998). Low temperatures in tundra and alpine grasslands may reduce the response to elevated C_a (Long and Drake, 1991). Similarly, high temperatures tend to amplify the stimulation of photosynthesis by elevated C_a at both the leaf level (in *Pinus taeda*) (Lewis *et al.*, 1996) and at the canopy level (in cotton and wheat) (Pinter *et al.*, 1996). In summary, in the majority of field experiments conducted to date in both crops and native species, elevated C_a increased canopy CO₂ uptake, and the stimulation was sustained over the duration of the experiment.

Net ecosystem production integrates annual carbon inputs through photosynthesis and annual carbon losses through respiration for a given land area over time (e.g., g C m⁻² yr⁻¹), so canopy gas exchange measurements,

such as those cited above, can be used to estimate NEP and its response to elevated C_a . Usually, however, annual NEP and instantaneous canopy gas exchange differ in time scale. Chamber-based gas exchange measurements are rarely continuous for an entire annual period, because maintaining the measurement system is too costly or could introduce artifacts that alter the fluxes being measured (e.g., altered microenvironment, excluded rainfall), and also because gas exchange rates during certain periods of the year are deemed negligible. Thus, a potential source of error in determinations of NEP from gas exchange measurements is the extrapolation to the nonmeasured periods, including the assumption that net fluxes during certain periods (e.g., winter) are zero. The effects of elevated C_a on NEP can also be determined by comparing carbon stocks in the C_a treatments after a given period of time (Hungate *et al.*, 1997b). This approach, although somewhat simpler in methodology, requires that experiments are of sufficient duration that biologically important differences in NEP yield statistically detectable differences in ecosystem carbon mass (Hungate *et al.*, 1996). Usually, this means ignoring large, relatively inert, ecosystem carbon pools in order to reduce the noise (e.g., excluding soil, or soil below the top 15 cm), which can also yield erroneous estimates of NEP.

There have now been a number of elevated C_a experiments conducted under field conditions in native ecosystems), but there are only a few in which estimates of the effect of elevated C_a on NEP have been reported from canopy gas exchange measurements, inventories of ecosystem carbon stocks, or, most instructive, from both approaches (Table 7-3). These experiments support the general conclusion that elevated C_a increases NEP (with the exception of the arctic tundra study). In cases where enough information is available, the effects of elevated C_a on NEP determined by gas exchange are larger than those determined by carbon inventories, dramatically so in the salt marsh study, but also the case in the alpine grassland.

The stimulation of carbon uptake at the canopy level is only partly accounted for by increases in measured ecosystem carbon pools (Drake *et al.*, 1996; Diemer, 1997; Körner *et al.*, 1997; Canadell *et al.*, 1996), suggesting that much of the extra carbon taken up in elevated C_a is distributed to large carbon pools, where changes are difficult to detect, which, in the case of the herbaceous ecosystems listed in Table 7-3, is most likely the soil carbon pool (Kuikmann *et al.*, 1991; Canadell *et al.*, 1996; Gorissen, 1996; Hungate *et al.*, 1997b). Determining the fate of this carbon is critical for extrapolating to long-term carbon storage in such systems, and presents a challenge to researchers in this area. First, it must be demonstrated unequivocally that carbon is accumulating in soil in these experiments, either by measuring a change in soil carbon mass, or by ruling out other fates of the extra carbon, including leaching or horizontal transfer of labile carbon, or return of carbon to the atmosphere as CO_2 during periods when net CO_2 exchange is

Table 7-3 Estimates of Net Ecosystem Productivity from Elevated C_a Field Experiments^a

Ecosystem	Plant + litter (g C m ⁻²)		Soil (g C m ⁻²)		ΔNEP_{stocks} (g C m ⁻² yr ⁻¹) ^b	CO ₂ exchange (g C m ⁻² yr ⁻¹)		$\Delta NEP_{gas\ exchange}$ (g C m ⁻² yr ⁻¹) ^c
	A	E	A	E		A	E	
Salt marsh ^d	3910	3910	1400	1470	10	1450	2170	720
Alpine grassland ^e	548	595	NR	NR	16	191	233	42
Serpentine grassland ^f	186	246	1994	2086	38	NR	NR	—
Sandstone grassland ^f	418	565	2385	2383	36	NR	NR	—
Tallgrass prairie ^g	850	1223	6290	6365	72	NR	NR	—
Arctic tundra ^h	NR	NR	NR	NR	—	-60	-60	0

^a ΔNEP is estimated, first, from reports of ecosystem carbon stocks (shown as plant + litter, and soil), expressed as the difference in carbon stocks between elevated (E) and ambient (A) C_a treatments divided by the duration of the experiment at the time the measurements of carbon stocks were made (ΔNEP_{stocks}). NR, not reported. NEP is also estimated from reports of canopy CO₂ exchange, extrapolated to an annual flux, and the difference between elevated and ambient C_a treatments for one annual period is shown ($\Delta NEP_{gas\ exchange}$).

^bCalculated as the difference in total carbon stocks between elevated and ambient C_a treatments divided by the duration of the experiment.

^cCalculated as the difference in integrated canopy gas exchange between elevated and ambient C_a treatments.

^dAll data for 1994 season, from Drake *et al.* (1996), after 8 years of experimental treatment.

^eKörner *et al.* (1997). Canopy gas exchange calculated from the reported 22% stimulation of seasonal C uptake and reported absolute difference of 42 g C m⁻² yr⁻¹ between the ambient and elevated C_a treatments.

^fPlant and litter C mass from Hungate *et al.* (1997b); 1994 sample, after 3 years of experimental treatment; soil C mass from Hungate *et al.* (1996); 1995 sample, after 4 years of experimental treatment.

^gPlant C only. Data from website <http://spuds.agron.ksu.edu/>, assuming plant mass is 50% C; aboveground biomass from 1996; belowground estimated by summing root ingrowth from 1990 to 1995. Soil data from Rice *et al.* (1994) for the third year of treatment.

^hOechel *et al.* (1994); calculated for a 60-day growing season using 1985 data.

not being measured. Second, soil carbon comprises several carbon pools of varying turnover times, and plant carbon allocation partly determines carbon distribution among these pools (Parton *et al.*, 1987). Because the potential for carbon storage in a given soil pool depends on its turnover time, shifts in plant carbon allocation in elevated C_a (e.g., increased allocation to fine roots and root exudates) will affect long-term carbon storage. Thus, quantitative predictions of long-term increases in NEP require understanding how elevated C_a affects the distribution of the carbon to pools of varying carbon storage potential.

In field experiments, the quantitative evidence that elevated C_a enhances carbon distribution to soil is indirect, resting on observations that the carbon increments from increased canopy photosynthesis are larger than observed increases in plant biomass. Although some pot studies using soils with low background amounts of carbon (Lutze, 1996) or carbon isotope labels (Ineson *et al.*, 1996; Gorrisen, 1996) provide direct evidence for carbon accumulation in soil, others show that much of the extra carbon distributed belowground in elevated C_a is preferentially allocated to relatively labile pools, limiting carbon accretion in recalcitrant pools with high storage potential (Tate *et al.*, 1995; Hungate *et al.*, 1997a,b). In these cases, elevated C_a may cause a larger increase in carbon turnover than in soil carbon mass (Newton *et al.*, 1995; Tate and Ross, 1997).

V. Interactions between CO_2 and Nutrients

Interactions between rising C_a and nutrients can occur in two ways: (1) the response of plants to elevated C_a can depend on nutrient availability and (2) the responses of plants to elevated C_a can alter nutrient availability, changes that can further modify both NPP and NEP. The effects of elevated C_a are rarely eliminated by nitrogen stress, at least partly because the decreased demand for rubisco in elevated C_a (as discussed above) allows a positive response even without an expansion of plant nitrogen mass. For example, in a 4-year study of a native Australian grass, elevated C_a reduced tissue nitrogen concentration irrespective of the availability of N in the soil, and this was accompanied by accumulation of carbon in the microcosm, although the lower N availability levels reduced the relative effects of C_a on carbon accumulation (Lutze, 1996). Whether growth responses to elevated C_a are relatively smaller under conditions of nutrient limitation remains ambiguous. In some cases, responses to elevated C_a are markedly smaller when nitrogen supply is restricted (Curtis *et al.*, 1994, 1995; McGuire *et al.*, 1995; Saxe *et al.*, 1998; (Table 7-1), whereas other experiments show no evidence for a short-term nitrogen constraint (reviewed in Lloyd and Farquhar, 1996; Idso and Idso, 1995). In native ecosystems, whereas nitrogen addition augments re-

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sponsiveness to elevated C_a in tallgrass prairie (Owensby *et al.*, 1993), small responses in alpine grasslands are apparently unrelated to nitrogen availability (Körner *et al.*, 1997). The relatively large C_a stimulation of net ecosystem carbon uptake in a C_3 saltmarsh (Drake *et al.*, 1996) is widely attributed to its "nutrient-rich" status, but this explanation seems unlikely given that net primary production in these coastal salt marshes is limited by nitrogen, as demonstrated by marked increases in aboveground production in response to experimental nitrogen addition (Valiela and Teal, 1974; Jefferies, 1977; Jefferies and Perkins, 1977; Kiehl *et al.*, 1997). Decreased growth responses to elevated C_a under restricted phosphorus supply have also been observed in some cases (Cure *et al.*, 1988; Goudriaan and DeRuiter, 1983; Conroy *et al.*, 1988, 1990), and not in others (Conroy, 1992; Israel *et al.*, 1990). More striking than the presence or absence of a putative nutrient constraint on production responses to elevated C_a is the wide variation in responses among different experiments, matched by the variety of conclusions drawn in reviews of the topic (e.g., Idso and Idso, 1994; McGuire *et al.*, 1995; King *et al.*, 1997; Curtis and Wang, 1998). As suggested by Johnson *et al.* (1998), limitation by any growth factor is more likely to be a continuum than a dichotomy of the presence or absence of limitation. When the data are reexamined with a quantitative assessment of the degree of nutrient limitation, a weak dependence of the response to elevated C_a on the degree of nutrient limitation emerges, with smaller responses under more nutrient-limiting conditions (Poorter and Garnier, 1996).

Nutrient constraints on the productivity responses to elevated CO_2 fall into two classes: (1) whether the relative growth response to elevated C_a depends on nutrient availability (which, as described in the preceding paragraph, is controversial), and (2) whether, over longer time scales (10–100 yr), sequestering nutrients in biomass and soils that occurs in concert with greater carbon storage in elevated C_a will diminish the potential for further increases in productivity. Greater carbon uptake in elevated C_a will result in nutrient sequestration that reduces nutrient availability to plants, unless, as C_a continues to rise, N inputs increase, N losses decrease, or distribution of N to ecosystem pools with high C:N ratios increases (Field 1999), particularly, from soils to wood. Widening C:N ratios of plant tissues allow some increased productivity in response to rising C_a , but this is limited by plant stoichiometry. To date, field experiments have not lasted long enough to test whether elevated C_a causes redistribution of nitrogen between ecosystem pools of varying C:N ratios, but there have been a few tests of the effects of elevated C_a on nitrogen inputs and losses.

Plants with direct access to atmospheric nitrogen through nitrogen fixation generally show a relatively larger growth response to elevated C_a compared to nonfixing species, in both the laboratory (Poorter, 1993) and in the field (Sousanna and Hartwig, 1996). Nitrogen fixation is energetically

expensive, but it is usually not directly regulated by the availability of photosynthate (Hartwig *et al.*, 1990, 1994; Hunt and Layzell, 1993; Weisbach *et al.*, 1996). Rather, increased growth of N fixers in elevated C_a might be viewed as a realisation of the CO_2 limitation of photosynthesis matched by a ready supply of fixed nitrogen. Nitrogen fixation is a very small part of the annual nitrogen cycle in most ecosystems, but it is nevertheless the major mechanism for the entry of nitrogen. Summed over many years, a sustained increase in nitrogen fixation in high C_a could increase ecosystem N mass enough to partially counteract reduced N availability through sequestration in biomass and soils (Gifford *et al.*, 1996). However, this will be less important in cases where low phosphorus availability restricts the growth of nitrogen-fixing plants (Vitousek and Howarth, 1991). For example, elevated C_a strongly increased growth and aboveground N mass of a legume in a scruboak ecosystem in which soil phosphorus availability was high, but in a calcareous grassland, elevated C_a increased the growth of legumes only with additional phosphorus supply, and had no effect on legume growth under field conditions where phosphorus availability was low (Niklaus *et al.*, 1998).

Changes in the processes that control nitrogen losses from ecosystems will amplify or counteract increased inputs of nitrogen through fixation. Studies to date are inconclusive. Elevated C_a can increase nitrogen losses by increasing carbon supply to rhizosphere denitrifiers (Smart *et al.*, 1997) and by increasing soil moisture and N/N_2O efflux (Arnone and Bohlen, 1998). By contrast, elevated C_a can decrease N losses by increasing N immobilization by microbes and thereby reducing NO efflux (Hungate *et al.*, 1997a). Small changes in N inputs, losses, or distribution will substantially modify the productivity responses to elevated C_a , underscoring the importance of further experimental and modeling studies of these potential changes.

VI. Interactions between Water Regime and CO_2 Concentrations

C_a affects the two main canopy characteristics determining ecosystem water balance, L and g_s , but with opposite impacts on water balance: the increase in L enhances plant transpiration and ecosystem E , but the reduction in g_s decreases transpiration, depending of canopy roughness. The water balance constraint may allow effects on L to take place in water-limited ecosystems, provided its impact on the water balance is low. No savings in water can be expected in canopies where elevated C_a stimulates increase in L relatively more than it decreases g_s .

In smooth canopies, low atmospheric coupling explains the lack of sensitivity of E to surface conductance (Hileman *et al.*, 1994; Kimball *et al.*, 1995; Bunce *et al.*, 1997). However, an improvement in soil water status due to a

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decrease in E under doubled C_a has been observed in rice crops (Baker *et al.*, 1997), Mediterranean grasslands (Field *et al.*, 1995), and a C_4 -tallgrass prairie, which suggests that reduction in g_s (e.g., Owensby *et al.*, 1997) can overcome the impact of increased L on E . However, our survey shows that L did not increase in any of the long-term field studies of the effects of elevated C_a on crops or native species (Table 7-1). This survey included studies of wheat (*Triticum aestivum*) and cotton in Arizona, where FACE was used to expose the plants to 55 Pa, as well as open-top chamber studies of native species. Elevated C_a (>68 Pa) reduced E compared with normal ambient in the Maryland wetland (Arp, 1991), Kansas prairie (Ham *et al.*, 1995), and California grassland ecosystems (Field *et al.*, 1995). In the wetland ecosystem, E was evaluated for a C_3 -dominated and a C_4 -dominated plant community. In these two communities, instantaneous values of E averaged 5.5–6.5 and 7.5–8.7 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ for the C_3 and C_4 communities, respectively, at present ambient C_a , but at elevated C_a (68 Pa), evapotranspiration (ET) was reduced 17–22% in the C_3 and 28–29% in the C_4 community, indicating the relatively greater effect of elevated C_a on g_s in the C_4 species. In the prairie ecosystem, cumulative ET over a 34-day period in mid-summer was 180 kg m^{-2} at present ambient C_a whereas it was 20% less at elevated C_a . In several grassland ecosystems, elevated C_a reduced E to the extent that soil water availability increased (Fredeen *et al.*, 1995; Rice *et al.*, 1994).

In aerodynamically rough canopies, the effect of L on E is potentially large, but the extent to which it could be compensated by effects on g_s will vary among species (Eamus and Jarvis, 1989; Saxe *et al.*, 1998). Also, in contrast to most grass and crop species, the sensitivity of g_s to D or soil drought seems unaffected in species such as sunflower (Bunce, 1993) or *Pinus pinaster* (Picon *et al.*, 1996). The E from forest canopies composed of species unresponsive to C_a would therefore be potentially affected only through changes in leaf area or when root growth enhancement gives access to new sources of soil water. In humid and fertile environments, where a change in L has little effect on ecosystem water balance, the associated impact on radiation interception will be low. In forest exposed to water limitations, the water regime will limit any impact of C_a on L , unless root growth enhancement will allow plants to access new sources of water. However, primary production may be increased through the enhancement of CO_2 availability, as far as plant growth can use the additional assimilated carbon in stem or root growth, depending on other limiting conditions. For species responsive to C_a , such as numerous *Quercus* species, reduction in g_s may allow L to increase with little effect on transpiration. Then C_a can have a larger potential impact on primary production and growth. But still, this improvement will only take place providing that the other possible climatic and trophic limitations of primary production can be overcome.

The reduction in E possibly caused by increased C_a would also alter canopy energy balance and shift some energy loss from transpiration to convective heat loss. This effect has important consequences for climate. Incorporating a model of stomatal response to elevated C_a into a coupled simple biosphere-atmosphere global circulation model (SiB2-GCM) showed that decreased g_s and latent heat transfer will cause a warming of the order of 1–2°C over the continents (Sellers *et al.*, 1996) in addition to warming from the CO₂ greenhouse effect. Implicit in this development is that any loss of photosynthetic capacity, through acclimation, would lead to further decreased g_s .

VII. Interactions between CO₂, Water, and Nitrogen

In arid and semiarid grasslands, increased water availability in elevated C_a can extend the length of the growing season (Fredeen *et al.*, 1995) and increase nitrogen availability (Hungate *et al.*, 1997b), both potentially amplifying the effect of elevated C_a on NPP (Hungate *et al.*, 1997b). However, increased soil moisture in elevated C_a will also stimulate decomposition and thus CO₂ release from soils (Rice *et al.*, 1994). Because appreciable carbon storage in grasslands is largely restricted to soils, the balance of the effects of increased soil water content in elevated C_a is to reduce the effects of elevated C_a on NEP. In forests, greater nutrient mineralization associated with wetter soils could support greater tree growth and thus carbon accumulation in wood, which has a higher C:N ratio than soils (e.g., Shaver *et al.*, 1992). However, as mentioned earlier, elevated C_a tends to cause smaller reductions in g_s in woody species compared to herbs, so this interaction between C_a , water, and nitrogen may be less important in forest ecosystems.

Acknowledgments

DL acknowledges gratefully J. Grace, P. G. Jarvis, and E. Dreyer for their comments and suggestions, and E. Lamaud, P. Berbigier, and H. Cochard, for providing the data used in this analysis.

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