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Do plants really need stomata?

F.I. Woodward[1]

Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

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Abstract

There are lower and higher plants, such as lichens, the gametophytes of bryophytes and some species of the isoetid life form which are astomatous. However, these species are small and often restricted to a narrow range of biotic and abiotic environments. The presence of stomata increases photosynthetic potential and the power to protect associated xylem developments from cavitation. Over the last 400 million years the CO_2 concentration of the atmosphere has changed considerably and plants have apparently responded, or evolved in parallel in terms of stomatal density, which has increased as atmospheric CO_2 concentration has decreased and in terms of the evolution of novel plant lineages. It is interesting to speculate that changes in plant stomatal density may have played a part in these evolutionary trends. However, there is no evidence that the supposed and differential controls by the convective boundary layer on dwarf and tall canopy transpiration has exerted any evolutionary effect, perhaps because convective boundary layers do not exert strongly differential effects on tall and dwarf canopies.

Key words: Boundary layer, nutrients, photosynthesis, stomata, transpiration.

Introduction

The earliest land plants of the Silurian and Devonian eras were astomatous with well-developed cuticles around their aerial organs (Edwards *et al.*, 1996), a feature which reduced water loss to the atmosphere but which will have reduced the diffusion rate of carbon dioxide to the underlying chlorenchymatous tissues. For the subsequent period of between 15–20 million years ago (*c.* 430–415 Ma, million years before present) stomatous species increased in sufficient frequency to be detectable in the fossil record (Niklas, 1992; Edwards *et al.*, 1996). Stomatal density appears to have increased monotonically to reach a peak in the Upper Carboniferous era of about 300 Ma (McElwain and Chaloner, 1995). Intriguingly, up to the Upper Carboniferous, as stomatal density and plant size increased the atmospheric concentration of carbon dioxide decreased (Berner, 1994), while that of oxygen increased (Berner and Canfield, 1989; Graham *et al.*, 1995). Terrestrial vegetation may well have played a role in these changes of atmospheric composition, through controls on the rates of carbonate formation and deposition (Berner, 1992) and also by the accumulation of un-decomposed plant litter (Berner and Canfield, 1989).

Edwards *et al.* (1996) discussed the physiological problems to be confronted by early, astomatous land plants. At a time of high atmospheric CO_2 concentrations (*c.* 0.35–0.4%, 10–12 times that of the present-day, Graham *et al.*, 1995) they suggest moderate but presumably adequate peak photosynthetic rates for small plants in the order of 6 μmol m^{-2} s^{-1}. In contrast, they suggest that the absence of stomata may have been a limitation to the supply of water and nutrients to different parts of these early but small land plants, because of a likely absence of a water potential gradient. The small amount of xylem likely to occur in these early plants is thought to be sufficient to supply the volume and rate of water for transpiration, even for early stomatous species (Raven, 1993). However, the rate of nutrient supply from the soil to the plant, which occurred in the transpirational flux, will have been very low and potentially limiting to plant growth (Edwards *et al.*, 1996). The development of rhizoids and roots, through evolution, will have increased plant exploration of the soil, reducing this problem. However, the very early presence of mycorrhizal associates (Smith and Read, 1996) will have greatly enhanced phosphorus and possibly nitrogen uptake, suggesting that the uptake of these nutrients may not have been a significant problem for early land plants.

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[1] Fax: +44 114 2760159. E-mail: F.I.Woodward@Sheffield.ac.uk

More recent concerns with astomatous plant species have centred on the occurrence and physiology of species of isoetids, which are astomatous (Keeley *et al.*, 1984). Significant ecological and physiological data have now accumulated to characterize these species which take up CO_2 from sediments rather than the atmosphere and which can illuminate some of the difficult questions which arise from the limited palaeobotanical evidence about the earliest land plants.

The paper addresses its title question in an essentially evolutionary manner. This will be initiated by considerations of the physiological behaviour of present-day astomatous species. The restricted distributions and ecological amplitudes of most, but not all, of these astomatous species indicate that the presence of stomata opens up a wider range of habitats for colonization. This increased ecological potential will be developed when discussing the fossil evidence for changes in stomatal occurrence and density through the Phanerozoic era or the last 450 Ma. Some of the problems encountered during the evolution of stomata are then discussed. The final issue addresses the importance of stomata for plants in canopies, in particular in light of the apparent limited stomatal control of transpiration in very short canopies (Jarvis and McNaughton, 1986).

Extant astomatous species

The gametophyte generation of mosses and liverworts does not possess true stomata, although air pores are present in liverwort gametophytes. In contrast, the sporophyte generations of the bryophytes generally possess stomata (Ziegler, 1987). Lichens, with a wider ecological amplitude than the bryophytes are completely astomatous. In the family Isoetaceae, and the genus *Isoetes* in particular, there is a number of species which are astomatous. Many species of *Isoetes* are aquatic and a much wider range of species, including flowering plant species, are astomatous when submerged, e.g. *Lobelia dortmanna* (Pedersen and Sand-Jensen, 1992) and species of *Ranunculus* (Bruni *et al.*, 1996). However, there are some species of *Isoetes* and *Stylites* which are terrestrial, occurring around the edges of oligotrophic bogs and which are astomatous (Keeley *et al.*, 1984, 1994). It has been argued that stomata are lost, i.e. either absent or non-functional, from species with plastic responses to submergence because gaseous exchange is no longer relevant through stomata, rather gaseous movement through aerenchyma is the norm (Sculthorpe, 1967; Raven, 1984). Stomata are also lost, or are non-functional, in at least some of the parasitic flowering plants, such as *Neottia nidus-avis* (Ziegler, 1987). In *Neottia* the guard cells are fused closed. In contrast, the stomata in aquatic species such as *Nymphaea alba*, *Nuphar lutea* and *Lemna minor* remain permanently open (Ziegler, 1987). In the case of *Lemna* the guard cells are dead, while the guard cells in *Nymphaea* and *Nuphar* appear to be cytologically intact, but the absence of a substomatal cavity prevents the closing operation of the guard cells (Ziegler, 1987).

There is, therefore, quite a diversity of species which are astomatous, or effectively so. It is clear that they fall into two evolutionary classes, those species which never possessed stomata, such as the gametophytes of bryophytes and lichens, and those species which were probably stomatous, but developed a wide range of different astomatous or effectively astomatous characteristics, such as the isoetid life forms and parasitic plants. How then do these properties limit the occurrence and behaviour of the species? In the case of moss gametophytes, the leaves are typically one-cell thick and so reasonable rates of CO_2 diffusion can occur into the leaves. However this life form is small, with the tallest moss, *Dawsonia superba* reaching a maximum height of about 50 cm (Parihar, 1965). The water transport mechanism in *Dawsonia* is by hydroids and leptoids (Parihar, 1965) which add little strengthening to the stem and Niklas (1992) suggests that 50 cm is close to the maximum height that a stem with an essentially parenchymatous-cell elastic modulus can attain.

Terrestrial isoetid plants are also very small, only reaching heights of perhaps 10 cm. Keeley *et al.* (1994) describe the occurrence of a number of species of *Isoetes* at high altitude (*c.* 3500 m) in the Andes. In all cases the plants occur in bogs around the edges of nutrient-poor lakes. The species of *Isoetes* are astomatous and their CO_2 for photosynthesis is nearly all derived from the sediments, entering the plants through their roots (Keeley *et al.*, 1994). The leaves (*Isoetes andicola*) have thick cuticles with low CO_2 conductances, at least three orders of magnitude less than open stomata (Kluge and Ting, 1978). The leaves, stems and roots possess very large air spaces or lacunae, which are more than sufficient to allow the movement of CO_2 to the photosynthetic cells of the leaf. In contrast, the vascular cylinder is very small.

Keeley *et al.* (1994) provide data on the growth of three different isoetid species and five non-isoetids occurring in the same environment. Growth of the eight species (Fig. 1) is very similar for all of the species, indicating no innate inferiority in the growth potential of the isoetids. An important feature for the isoetid species will be leaf temperature in this potentially very high irradiance environment. Measurements were made on the thermal environment of *I. andicola* on one day (Fig. 2, from Keeley *et al.*, 1994) and this shows that during moderate irradiance (up to 1200 μmol m^{-2} s^{-1}) leaf temperatures exceeded air temperature by about 10 °C. The potential for reaching lethal temperature thresholds may be high for brighter and warmer days, although at an altitude of 4180 m this may not be a major limitation.

Leaves of moss gametophytes are typically one cell

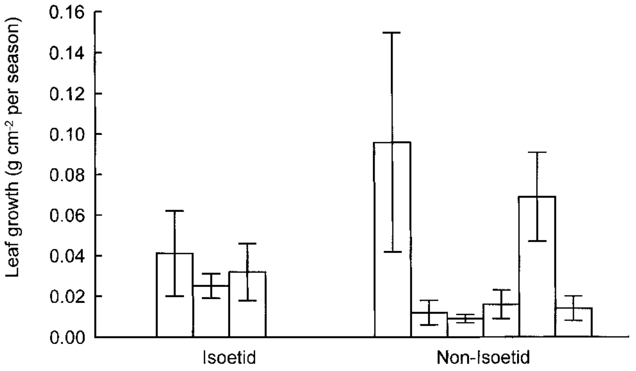

Fig. 1. Leaf growth in co-occurring isoetid and non-isoetid species, at high altitudes in the Andes (from Keeley *et al.*, 1994).

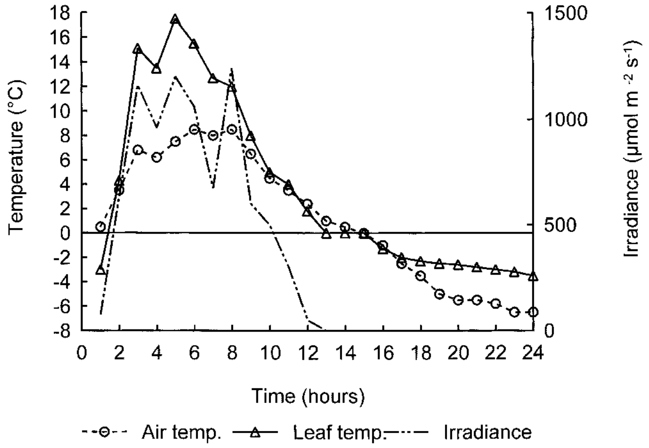

Fig. 2. Irradiance and leaf and air temperature of *Isoetes andicola* at 4180 m in the Andes (from Keeley *et al.*, 1994).

thick and with limited, if any intercellular air spaces. This lack of air space will severely limit CO_2 diffusion within the leaf (Raven, 1993) but, on the other hand this will match the limited rate of CO_2 diffusion across the leaf surface. Within a leaf with no intercellular spaces, CO_2 diffusion is expected to be at least 10 000 times slower than in air spaces and, therefore, there will be an important advantage in developing photosynthetic organs which have intercellular air spaces with a capacity for rapid CO_2 diffusion. Lichens have evolved such an approach for increasing the rate of CO_2 diffusion to the photosynthetic algal component of the lichen through, essentially, capillaries in the lichen thallus. Such an approach is not without its problems (Fig. 3, from Lange *et al.*, 1996) which is easily seen at current CO_2 concentrations when the photosynthetic rate is strongly variable with thallus water content. This is because the water content of the thallus has two effects. At water contents of less than 350% of dry weight photosynthesis is reduced, through a water supply limitation. At higher water contents than 400% the photosynthetic rate is reduced because the air capillaries in the thallus are increasingly filled with water, restricting the rate of CO_2 diffusion to the photosynthetic algae. This reduced rate of diffusion can be offset by increasing the ambient CO_2 concentration to levels characteristic of the early Phanerozoic. The benefits of increasing the rapidity of CO_2 diffusion in air to the site of photosynthesis is counteracted by a great sensitivity to water content, a feature which is only under the control of the atmospheric water vapour pressure deficit and the thickness of the boundary layer above the lichen. For plants with stomata, it is important therefore to ensure, when intercellular spaces are developed within the photosynthetic organ, that they prevent the ingress of water into the leaf (Ziegler, 1987), as such a response will greatly reduce the rate of photosynthesis.

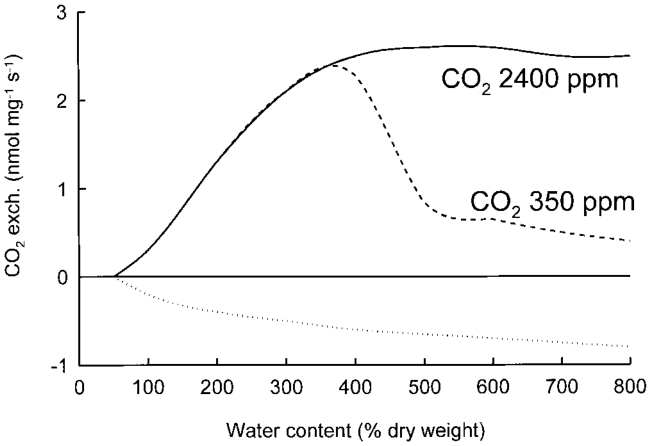

Fig. 3. The photosynthetic responses of the lichen *Peltigera neckeri* to thallus water content and atmospheric CO_2 concentration (from Lange *et al.*, 1996).

Evolutionary trends in stomatal density

Beerling and Woodward (1997) have collated fossil data of stomatal density which have been collected over the Phanerozoic (Fig. 4). Although this is obviously an imperfect sampling, it is quite clear that the ranges of observed stomatal densities at any particular time are also inversely correlated with the CO_2 concentration which has been estimated for the different times of the stomatal collections, using the model of Berner (1994). The figure makes a clear statement that stomatal density increases as atmospheric CO_2 concentrations decrease, in keeping with previous observations and experiments (Woodward, 1987; Woodward and Bazzaz, 1988; Beerling and Chaloner, 1993; Beerling and Woodward, 1996). The causes of the reductions in atmospheric CO_2 are not clear but they may have been due, at least in part, to an increasing capacity of vegetation and soils to sequester carbon (Berner, 1992).

The earliest land plants and stomata evolved during periods of high atmospheric CO_2 concentrations (Fig. 5).

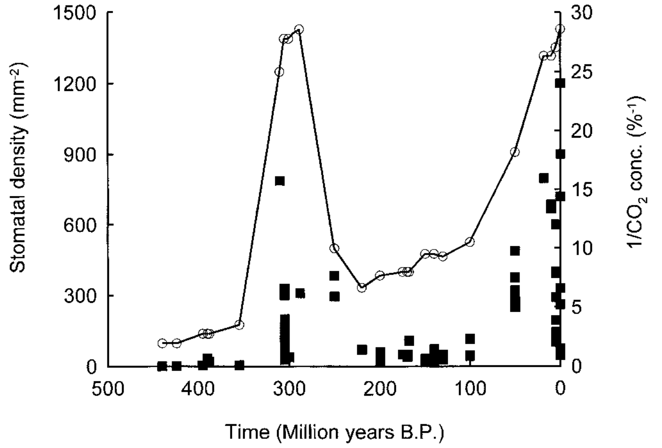

Fig. 4. Fossil records of stomatal density (from Beerling and Woodward, 1997), (■), and estimated inverse CO_2 concentrations, (○), at the times of the fossil records (from Berner, 1994), plotted on an inverse scale of concentration.

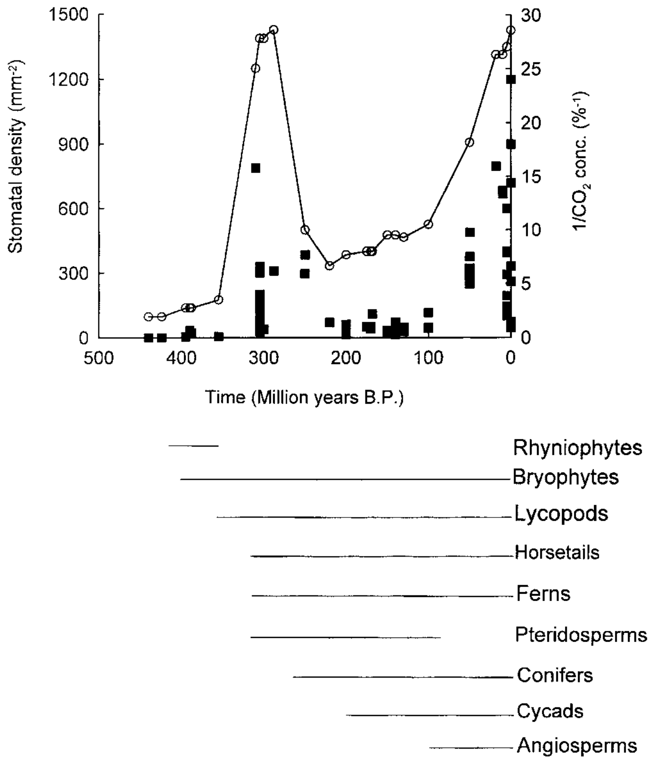

Fig. 5. As Fig. 4 with estimated time spans of occurrences of different fossil groups (from Niklas, 1992; Edwards *et al.*, 1996).

However, subsequent periods of low atmospheric CO_2 concentrations may have been a sufficient selective force to drive evolutionary change and so it is of interest (Fig. 5) that the evolutionary emergence of the horsetails, ferns, pteridosperms, conifers, and angiosperms occurred at times when stomatal densities were generally high. Such a general feature is also in accord with Raven's hypothesis (1993) that in early evolution, stomata preceded the occurrence of a xylem system, a precedence which he considers necessary because stomata, with the ability to close when necessary, need to be present in order to prevent, or control, the occurrence of xylem cavitation (Tyree and Sperry, 1989). Therefore, extending this theory a little further suggests that the presence of stomata, and high stomatal densities in particular, may actually favour or enhance the rate of evolutionary development of plant groups. Such a response may perhaps occur by protecting the increasing length of the xylem pathway found in taller and more competitive genotypes. Partial opening or closing of stomata also provide a fine control on the rate of water loss and plant water use efficiency in general, also offering, therefore, a mechanism for increasing survival and competitive ability.

The benefits of increasing plant height are not only relevant to increasing competitive ability but also in increasing the potential environmental range in which species can occur. This is shown (Fig. 6) for a simulated canopy of short (2 cm) plants, differing in stomatal conductance. The lowest stomatal conductance (5 mmol m^{-2} s^{-1}) corresponds with the cuticular conductance of an astomatous species, with the higher stomatal conductances being determined by increasing stomatal densities (from 10–65 mm^{-2}) in this simulation, using the model described in Beerling and Woodward (1997). In the simulation, which also incorporates the Penman–Monteith model of canopy transpiration (Monteith, 1965), the minimum boundary layer conduct-

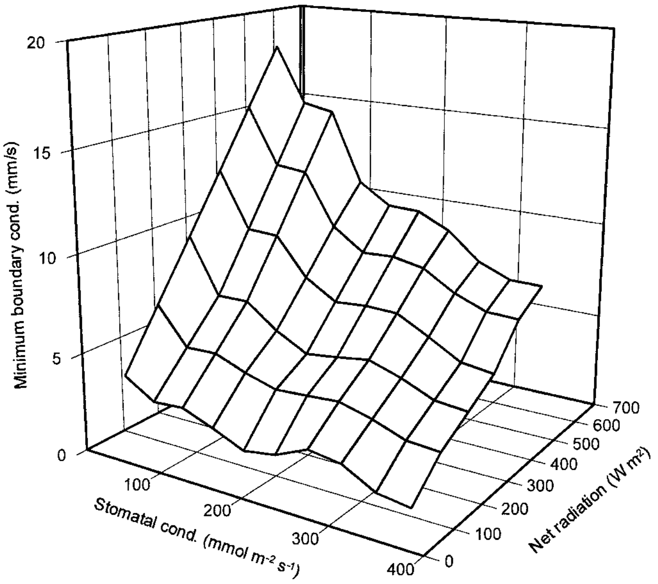

Fig. 6. Minimum boundary layer conductances required, for canopies of 2 cm tall plants, to avoid lethal temperature thresholds of 45 °C, at a range of net radiant balances and for canopy stomatal conductances ranging from 5 mmol m^{-2} s^{-1} (astomatous) to 355 mmol m^{-2} s^{-1} (stomatal density 65 mm^{-2}). The model is described in Jones (1992). The imposed environmental conditions are a canopy leaf area index of unity, a plant stem density of 10^4 m^{-2}, an air temperature of 20 °C and a relative humidity of 66%.

ance is predicted for a canopy surface temperature of 45 °C, taken to be a lethal temperature. When the net radiant balance of the canopy is 100 W m^{-2} and with only cuticular transpiration, then the minimum boundary layer conductance of *c.* 5 mm s^{-1} is typical of very short vegetation, in the order of a few centimetres in height (Jones, 1992). This would be typical of a dwarf vegetation of early Silurian plants. However, if the net radiant balance increases, as in full sunlight, then the boundary layer conductance must increase in order to allow a concomitant increase in sensible heat loss, in order to avoid lethal temperatures. The increase in conductance would occur with either taller canopies, or in windy environments. However, the occupation of high irradiance habitats could only be realized, in plants only possessing cuticular transpiration, by either of these responses. The presence of stomata markedly increases energy dissipation by latent heat transfer, increasing the thermal tolerance of high irradiance sites.

The problem when stomata are open is achieving the balance between necessary water loss, and therefore avoiding desiccation which was not considered in the previous section and water gain into the plant. Assuming an even distribution of 2 cm tall plants, with stems of 0.2 cm in diameter and a plant stem density of 10^4 m^{-2} then the stems will be a reservoir of water containing the equivalent of 0.63 mm of precipitation. The transpiration rate for the canopy can then be used to determine the maximum period of transpiration supply by the stems, assuming a continuous no-replenishment loss (Fig. 7). For astomatous plants the supply is around 40 h at a net radiant balance of 100 W m^{-2}. Any presence of open stomata decreases the supply potential to a few hours, indicating a strong selection pressure for any system of water capture and xylem-like conductivity.

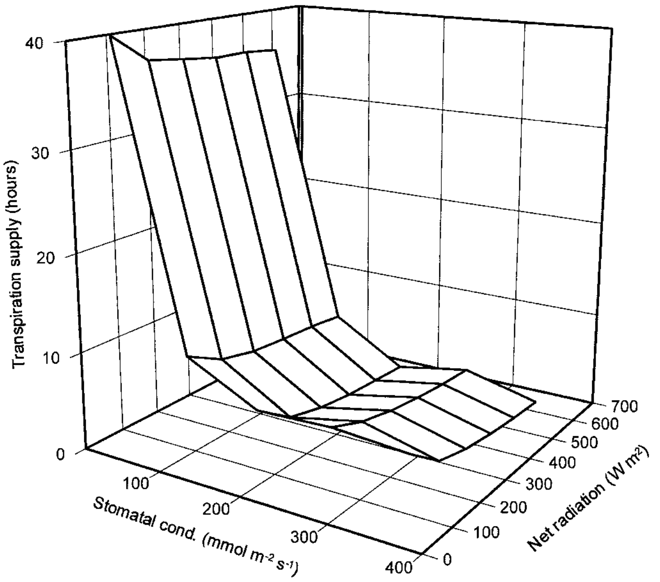

Fig. 7. The period of water loss which can be supplied by the plant canopy described in Fig. 6 (at the minimum boundary layer conductance) without any replenishment.

The high CO$_2$ concentrations of the early Silurian and Devonian atmospheres will have diminished, to some extent, the diffusional limitations to the rates of photosynthesis of the early land plants. However, the presence of stomata will have greatly increased photosynthetic potential (Fig. 8) and, with an increase in stomatal density, an increase in the rate of Rubisco carboxylation. The increasing rates of carboxylation will also have led to an increase in the plant requirements for nitrogen (Field, 1983), to support the increased Rubisco requirements.

Edwards *et al.* (1996) suggest that the presence of stomata improves the availability of nutrients to the plant by increasing the rate of transpiration throughput of major nutrients, a characteristic which may have been more limiting to the plant than the supply of water, even in a very rudimentary xylem. However, recent work by Pedersen and Sand-Jensen (1997), on *Mentha aquatica*, has clearly demonstrated for this flowering plant that transpiration is not necessary for supplying nitrogen to the leaves. Nitrogen concentrations in emergent and submerged plants were not significantly different (Fig. 9), with non-transpirational mass flow of water being sufficient, at least for this species, to supply the necessary nitrogen. Observations on the astomatous *Isoetes andicola* (Keeley *et al.*, 1994) also indicate no limitation of nitrogen supply to green leaves.

Canopy-scale considerations

Leaf and plant-level considerations of stomatal activity indicate that stomatal density and opening both exert considerable controls on the rate of transpiration (Beerling and Woodward, 1997). At the canopy level

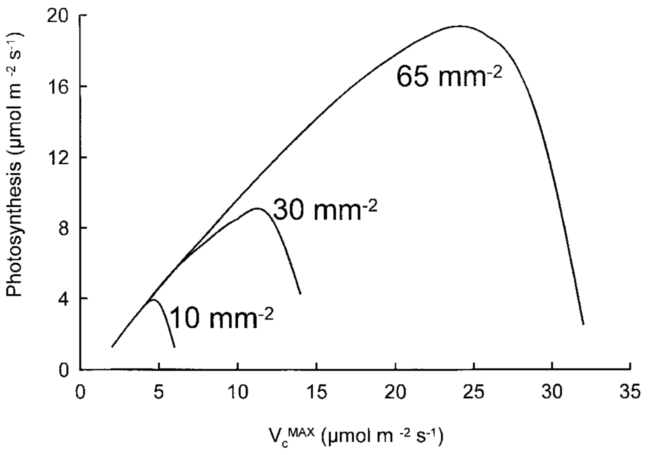

Fig. 8. Maximal photosynthetic rates and optimal rates of carboxylation calculated for leaves differing in stomatal density, at a CO$_2$ concentration of 2000 ppm, using the photosynthesis model of Woodward *et al.* (1995).

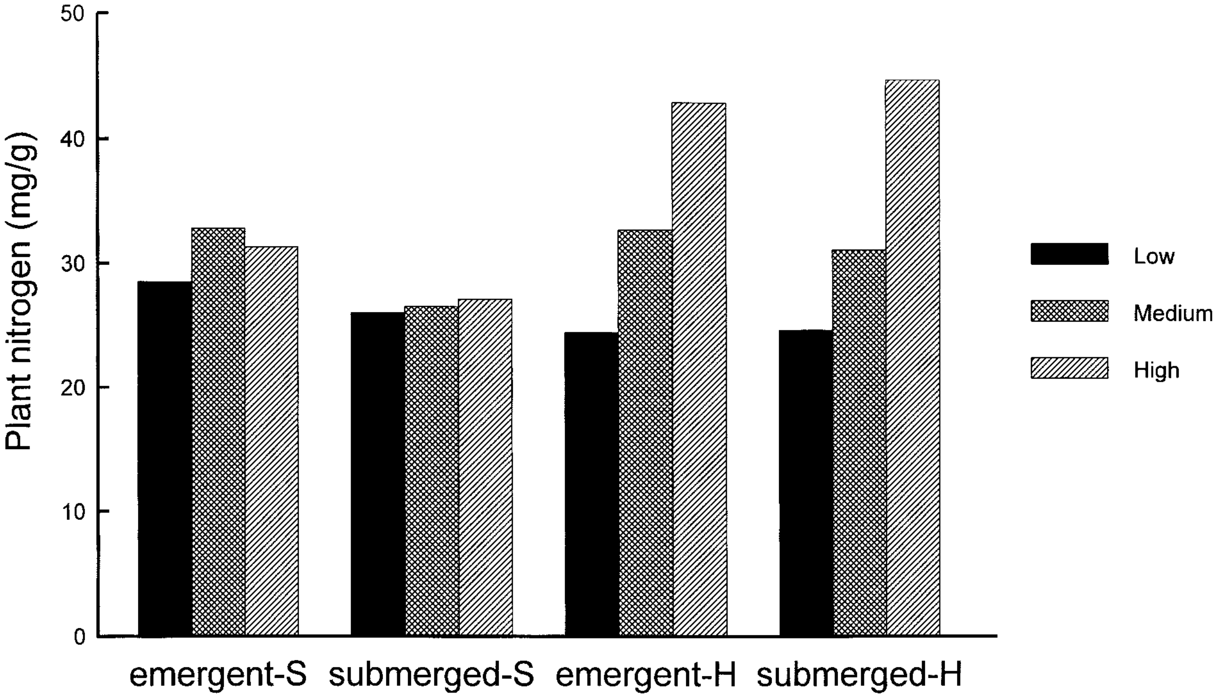

Fig. 9. Plant nitrogen concentrations of *Mentha aquatica*, grown either submerged under water, or emergent and with low, medium and high levels of nutrients supplied from a sedimentary source (S) or by hydroponics (H), (from Pedersen and Sand-Jensen, 1997).

stomata may not be the major controllers, because the low boundary layer conductance from the canopy to the convective boundary layer assumes significance, particularly for dwarf vegetation (McNaughton and Jarvis, 1983; Jarvis and McNaughton, 1986). Indeed, Jones (1992) presents a caricature of the system in which plants are transpiring in a glasshouse, the glass of the glasshouse representing the upper boundary of the convective boundary layer. Within the glasshouse in daylight both the plant canopy and the air temperature will rise. The vapour pressure deficit of the air will increase, but the canopy surface temperature will also increase so that the canopy to air gradient for transpiration will remain close to constant. Therefore, in such a situation, the net radiant balance and not the vapour pressure deficit of the air will control the rate of transpiration.

A graphical description of the aerodynamic coupling effects is provided (Fig. 10) for a dwarf canopy and a total boundary layer conductance, including that into the convective boundary layer, of 3 mm s^{-1}. The very dwarf canopy is contrasted with that of a very tall canopy, with a greater boundary layer conductance (320 mm s^{-1}) and a smaller transpirational control by the convective boundary layer. For the dwarf canopy, stomatal control of transpiration is only noticeable at very low conductances, while stomatal control of transpiration is dominant for the tall canopy. In evolutionary terms, and for the dwarf canopy, apart from stomatal-dependent transpiration at canopy stomatal conductances up to *c.* 3 mm s^{-1} there seems no benefit of higher stomatal conductances. When RuBP-supply limited, photosynthesis will be little affected by high conductances (Farquhar *et al.*, 1980) and transpirational cooling is primarily dependent on the net radiant balance. For dwarf canopies it should therefore be predicted that the constituent species will maintain low stomatal densities and conductances, maximizing the control on water loss (Fig. 7). In contrast, tall canopies with a need to transport water over long xylem pathways, with the capacity to develop high leaf area indices and perhaps the need to depend on the transpirational stream for distributing nutrients should develop higher stomatal densities and conductances, at least when not droughted.

Data for the stomatal densities (Woodward and Kelly, 1995) and maximal leaf stomatal conductances (Körner, 1994) of arboreal and herbaceous species (Fig. 11) indicate no differences between the two life forms. One explanation for the lack of any difference may relate to the need for transpirational cooling of the dwarf canopy. Model predictions of canopy surface temperature (Fig. 12 using the model of Jones, 1992) indicate that the dwarf canopy temperature may reach close to lethal levels under a high net radiant balance. However, even in this situation canopy stomatal conductances of about 5 mm s^{-1} (*c.* 200 mmol m^{-2} s^{-1}) would provide adequate cooling of the canopy. In general, maximal canopy conductances of dwarf canopies may be greater than double this threshold.

The high temperatures predicted for the dwarf canopy might be tolerated by plants with low stomatal conduct-

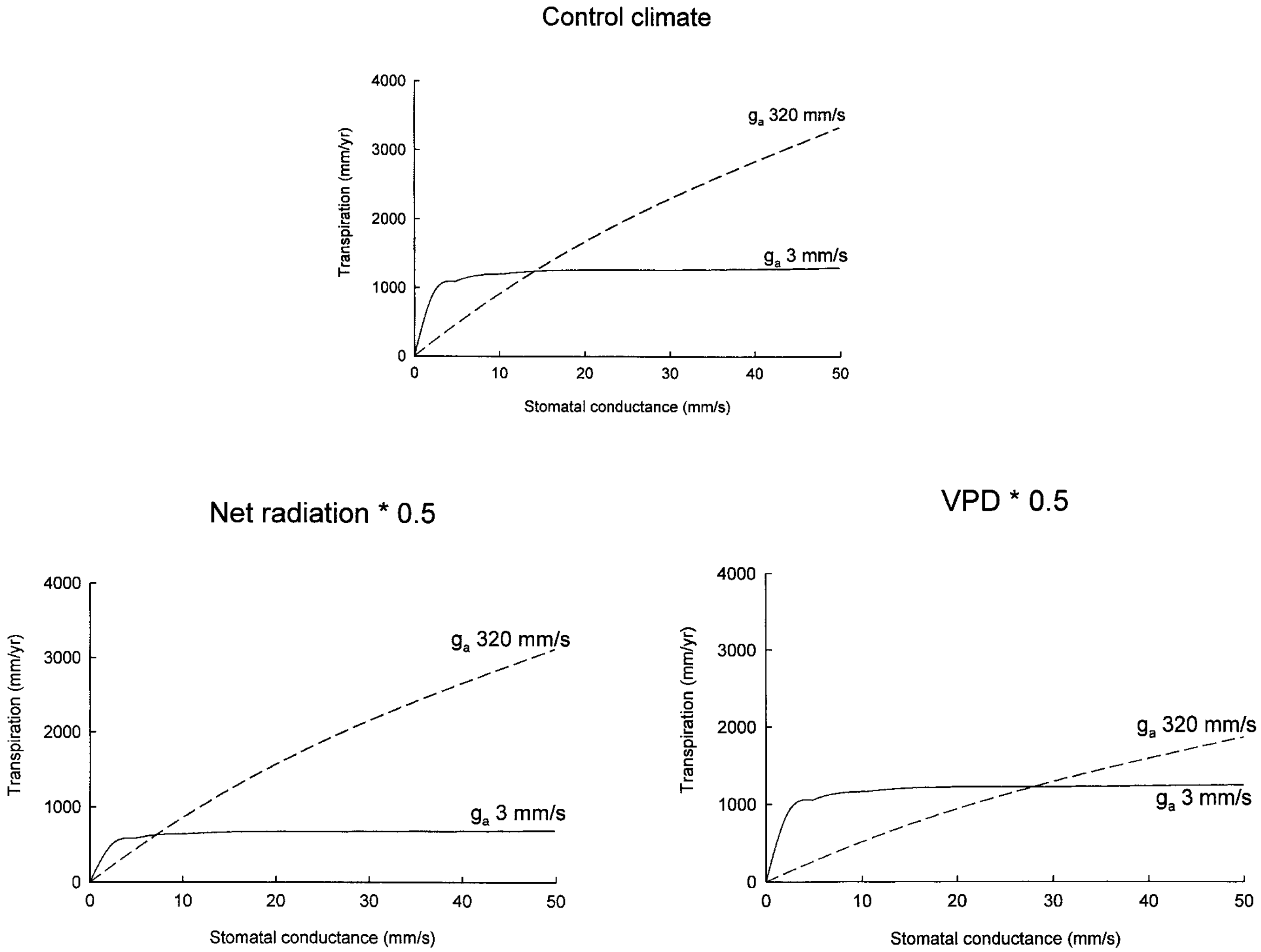

Fig. 10. Predictions of the annual total of transpiration from a dwarf canopy (boundary layer conductance, g_a of 3 mm s^{-1}) and a tall canopy (g_a of 320 mm s^{-1}), for a range of canopy stomatal conductances, using the Penman–Monteith model of transpiration (Monteith, 1965) and for the climate of Taranto, Italy (control climate) and with a 50% reduction in the net radiant load (net radiation × 0.5) or a 50% reduction in the water vapour pressure deficit of the air (*VPD* × 0.5). The predicted annual totals of transpiration were determined by integrating daily predictions, based on daily weather values generated from monthly mean meteorological station data (Woodward *et al.*, 1995).

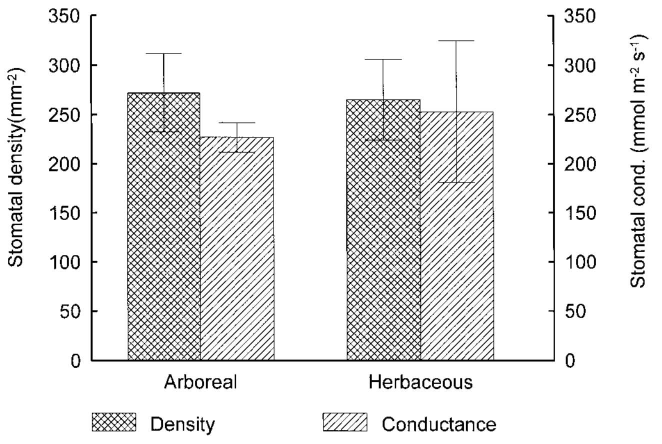

Fig. 11. Stomatal densities and maximal conductances of arboreal and herbaceous species (Körner, 1994; Woodward and Kelly, 1995). Error bars are standard error of the mean.

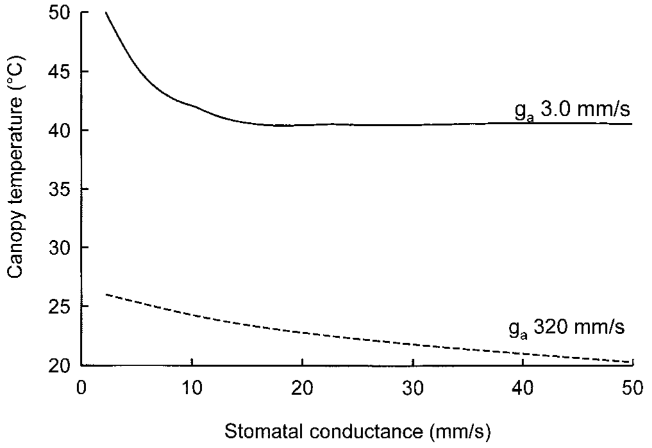

Fig. 12. Canopy surface temperature responses to canopy stomatal conductance, at an air temperature of 20 °C, net radiant flux 200 W m^{-2} and a water vapour pressure deficit 800 Pa.

ances, if they developed the high temperature-tolerance characteristic of succulent species, which also possess low stomatal conductances (Nobel, 1988). There is no evidence (Woodward and Kelly, 1997) of such a response.

Plant stomatal responses, therefore, appear not to have evolved in response to the low control capacity on transpiration of dwarf canopies in the convective boundary layer. Recently Dickinson *et al.* (1997) have suggested that the convective boundary layer (CBL) exerts less of a control on canopy transpiration than described for the glasshouse case above. They envisage the CBL not as equivalent to a glasshouse with a solid upper boundary, but as a well-mixed layer of humid air into which (usually) dry air is entrained from above the boundary layer, maintaining close-to-constant specific humidities during diurnal cycles (Fig. 13). Therefore the CBL is buffered to a nearly constant diurnal specific humidity (Fig. 13), a feature which will greatly enhance the effectivity of the stomata in controlling transpiration, even for dwarf canopies. Data from the FIFE campaign (Betts, 1992) support the observation of an almost invariant specific humidity during the day, in contrast to an expected rise and fall in humidity (Fig. 13) if there was no entrainment drying of the CBL and the CBL was more like a closed glasshouse.

The height of the CBL increases during the day and this influences canopy transpiration by influencing the rate at which the equilibrium saturation deficit of the CBL, D_{eq}, is reached and described as (from McNaughton, 1989):

$$D_{\mathrm{eq}} = \frac{\epsilon(R_{\mathrm{n}} - G)}{\rho\lambda g_{\mathrm{s}}(1+\epsilon)} \tag{1}$$

and:

$$\tau = h\left\{\frac{1}{g_{\mathrm{a}}} + \frac{1}{(1+\epsilon)g_{\mathrm{s}}}\right\} \tag{2}$$

where ϵ is the ratio of the slope of the saturation water vapour pressure with temperature divided by the psychrometric constant, $R_{\mathrm{n}} - G$ is the net radiant flux absorbed by the canopy, ρ is the density of air, λ the latent heat of vaporization of water and g_{s} the canopy stomatal conductance. The time constant, τ, of the rate at which the CBL saturation deficit reaches the equilibrium value (equation 2) is primarily determined by the height of the CBL, h, and the canopy boundary layer and stomatal conductances, g_{a} and g_{s} (equation 2). Therefore the rate at which the equilibrium saturation deficit of the CBL is reached will increase with canopy conductance, and the time constant will increase with the height of the CBL. With entrainment of air into the CBL the actual canopy transpiration rate, E, is then defined as follows (McNaughton, 1989):

$$E = \left\{\frac{\epsilon}{1+\epsilon}\,\frac{R_{\mathrm{n}} - G}{\lambda}\right\} + \left\{\frac{\rho g_{\mathrm{a}}(D_{\mathrm{m}} - D_{\mathrm{eq}})}{1+\epsilon+g_{\mathrm{a}}/g_{\mathrm{s}}}\right\} \tag{3}$$

where D_{m} is the saturation deficit of the CBL, at any particular time. The left term is the equilibrium rate of transpiration in which the vegetation exerts no control by varying stomatal conductance (Fig. 10). The right term allows for entrainment of (usually) dry air into the CBL. The equilibrium rate of transpiration only then occurs when the saturation deficit of the CBL, D_{m}, equals the equilibrium saturation deficit of the CBL. This equality will be reached slowly for dwarf canopies with low stomatal conductances and so the right hand term of equation 2 will be generally operative, indicating the importance of stomatal conductance in controlling transpiration, even for the case which had earlier been expected to operate at the equilibrium rate (Fig. 10). Short well-watered canopies can frequently reach transpiration rates greater than the equilibrium rate (McNaughton, 1989). It is clear, therefore, that under many situations even dwarf canopies will exert a stomatal control of transpiration, supporting the observation that stomata of dwarf and tall canopies are rather similar in terms of densities and maximal conductances (Fig. 11) and therefore requirements for canopy controls of water loss.

Conclusion

Many plant species are astomatous and their continued existence indicates that, for these species, stomata are not necessary prerequisites for survival. However, all astomatous species are small, probably less than 20–50 cm in height, and they occur in a limited set of environments, such as for most bryophytes and plants of the isoetid life form. Lichens are found in a wide range of environments, some of which are very extreme, as in the Antarctic, in warm deserts, or on bare rock. They are constrained to be small in height and this smallness in height can probably only be circumvented by the joint possession, by plants, of stomata and a xylem water pathway. Being tall confers a competitive advantage, particularly in terms of the capture of light and the evolution of increasing height can be envisaged to be driven by strong competition. Stomata allow transpiration to occur and a pull of water and nutrients to result and also allow an increased photosynthetic capacity, albeit with a greater requirement for nutrients. However, for small plants at least, there is no evidence to support the notion that a low rate of transpiration will limit the rate of accumulation of nutrients in the growing plant.

Ideas which suggest that the convective boundary layer (CBL) exerts a cap over vegetation such that the net radiant balance controls transpiration, with little effective

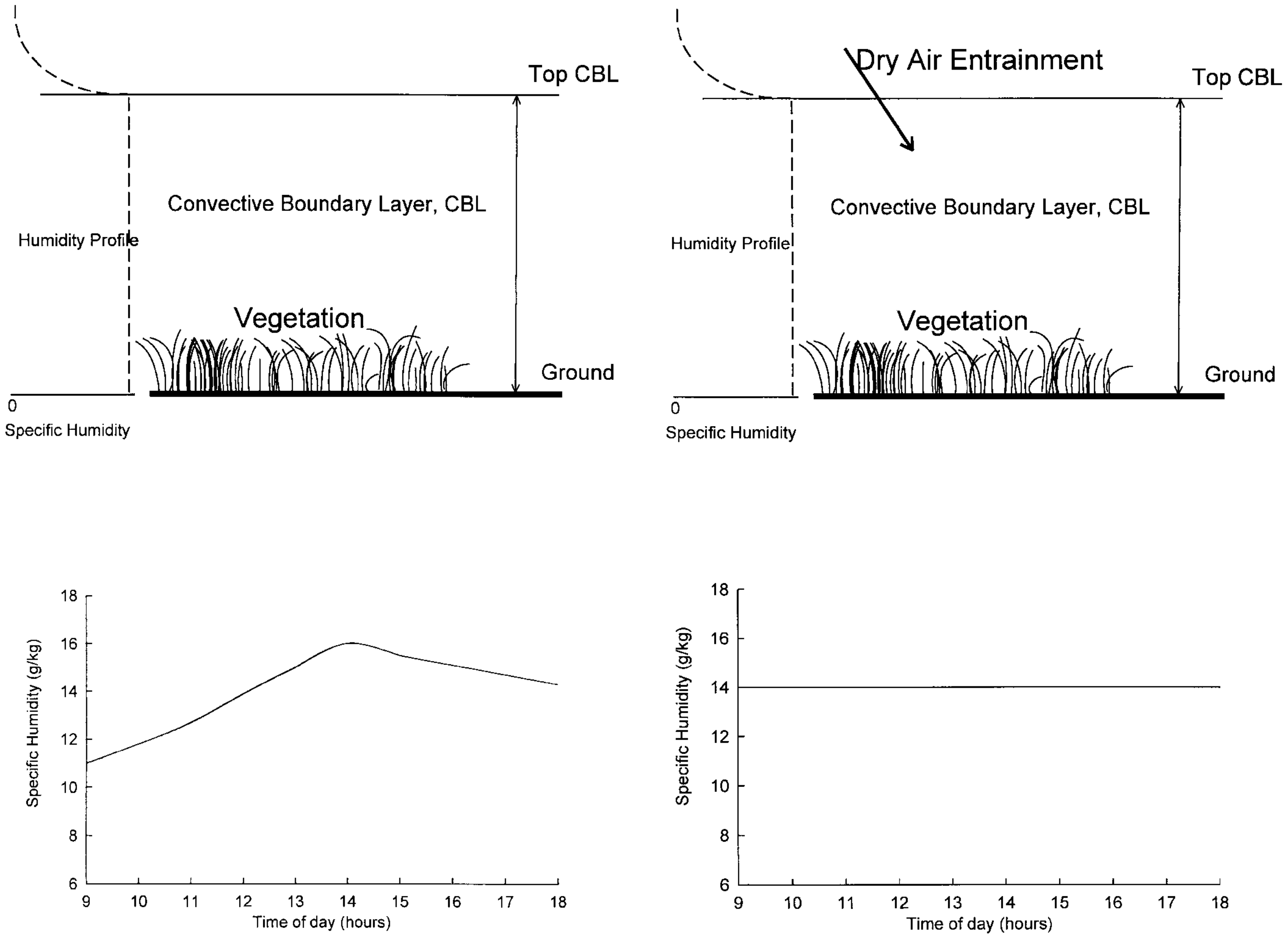

Fig. 13. Two views of the convective boundary layer (CBL), based on Dickinson *et al.* (1997). The left model (top figure indicates maximum height of CBL) includes no dry air entrainment from above the CBL and it is suggested that the specific humidity should follow the diurnal trend shown beneath, due to combined effects of the canopy conductances to water vapour (boundary layer and stomatal) and the growth and decay in height of the CBL, which is primarily sensitive to the canopy boundary layer conductance. With dry air entrainment (the right model) the specific humidity remains close to constant on a diurnal basis, as measured by Betts (1992).

control by stomata, might lead to the evolution of dwarf life forms with low stomatal densities and conductances. There is no evidence of such a response and further analysis of the CBL suggests it is far from an impervious cover over vegetation and more a zone which operates to maintain a constant humidity over all types of vegetation, returning an important emphasis on the stomatal control of transpiration, for both dwarf and tall vegetation.

In general, therefore, there appears to be no canopy and regional level control on the evolution of stomatal characteristics. However, fossil evidence does suggest that periods of globally-low atmospheric CO_2 concentrations are positively correlated with periods of high stomatal density and increased probability of rapid plant evolution.

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References

Beerling DJ, Chaloner WG. 1993. Evolutionary responses of stomatal density to global CO_2 change. *Biological Journal of the Linnean Society* **48,** 343–53.

Beerling DJ, Woodward FI. 1996. Palaeo-ecophysiological perspectives on plant responses to global change. *Trends in Ecology and Evolution* **11,** 20–3.

Beerling DJ, Woodward FI. 1997. Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record. *Botanical Journal of the Linnean Society* **124,** 137–53.

Berner RA. 1992. Weathering, plants and the long-term carbon cycle. *Geochimica Cosmochimica Acta* **56,** 3225–31.

Berner RA. 1994. 3GEOCARB II a revised model of atmospheric CO_2 over Phanerozoic time. *American Journal of Science* **294,** 59–91.

Berner RA, Canfield DE. 1989. A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science* **289,** 333–61.

Betts AK. 1992. Budget analyses of FIFE atmospheric boundary layer budget methods. *Journal of Geophysical Research* **97,** 18523–31.

Bruni NC, Young JP, Dengler NG. 1996. Leaf developmental plasticity of *Ranunculus flabellaris* in response to terrestrial and submerged environments. *Canadian Journal of Botany* **74,** 823–37.

Dickinson RE, Hahmann AN, Shao Q. 1997. Commentary on Mecca sensitivity studies. Chapter 10. In: Howe W, Henderson-Sellers A, eds. *Assessing climate change: the story of the model evaluation consortium for climate assessment*. Basel, Switzerland: Gordon & Breach Science Publishers.

Edwards D, Abbott GD, Raven, JA. 1996. Cuticles of early land plants: a palaeoecophysiological evaluation. In: Kersteins G, ed. *Plant cuticles: an integrated functional approach*. Oxford: Bios, 1–31.

Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149,** 79–90.

Field C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56,** 341–7.

Graham JB, Dudley R, Aguilar NM, Gans C. 1995. Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature* **375,** 117–20.

Jarvis PG, McNaughton KG. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research* **15,** 1–49.

Jones HG. 1992. *Plants and microclimate: a quantitative approach to environmental plant physiology*, 2nd edn. Cambridge University Press.

Keeley JE, Osmond CB, Raven JA. 1984. *Stylites*, a vascular land plant without stomata absorbs CO_2 via its roots. *Nature* **310,** 694–5.

Keeley JE, DeMason DA, Gonzalez R, Markham KR. 1994. Sediment-based carbon nutrition in tropical alpine *Isoetes*. In: Rundel PW, Smith AP, Meinzer FC, eds. *Tropical alpine environments: plant form and function*. Cambridge University Press, 167–94.

Kluge M, Ting IP. 1978. *Crassulacean acid metabolism*. New York, Springer-Verlag.

Körner C. 1994. Leaf diffusive conductances in the major vegetation types of the world. In: Schulze ED, Caldwell MM, eds. *Ecophysiology of photosynthesis*. Berlin: Springer-Verlag, 463–90.

Lange OL, Green TGA, Reichenberger H, Meyer A. 1996. Photosynthetic depression at high thallus water contents in lichens: concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera* species. *Botanica Acta* **109,** 43–50.

McElwain JC, Chaloner WG. 1995. Stomatal density and index of fossil plants track atmospheric carbon dioxide in the Palaeozoic. *Annals of Botany* **76,** 389–95.

McNaughton KG. 1989. Regional interactions between canopies and the atmosphere. In: Russell G, Marshall B, Jarvis PG, eds. *Plant canopies: their growth, form and function*. Society for Experimental Biology, Seminar Series 31. Cambridge University Press, 63–81.

McNaughton KG, Jarvis PG. 1983. Predicting effects of vegetation changes on transpiration and evaporation. In: Kozlowski TT, ed. *Water deficits and plant growth*, Vol. VII, New York, Academic Press, 1–47.

Monteith JL. 1965. Evaporation and environment. *Symposia of the Society for Experimental Biology* **19,** 205–34.

Niklas KJ. 1992. *Plant biomechanics: an engineering approach to plant form and function*. University of Chicago Press.

Nobel PS. 1988. *Environmental biology of agaves and cacti*. Cambridge University Press.

Parihar NS. 1965. *An introduction to the embryophya*, Vol. 1. *Bryophyta*. Allahabad, Indian Universities Press.

Pedersen O, Sand-Jensen K. 1992. Adaptations of submerged *Lobelia dortmanna* to aerial life form: morphology, carbon sources and oxygen dynamics. *Oikos* **65,** 89–96.

Pedersen O, Sand-Jensen K. 1997. Transpiration does not control growth and nutrient supply in the amphibious plant *Mentha aquatica*. *Plant, Cell and Environment* **20,** 117–23.

Raven JA. 1984. *Energetics and transport in aquatic plants*. New York: AR Liss.

Raven JA. 1993. The evolution of vascular plants in relation to quantitative functioning of dead water-conducting cells and stomata. *Biological Reviews* **68,** 337–63.

Sculthorpe CD. 1967. *The biology of aquatic vascular plants*. London: Edward Arnold.

Smith SE, Read DJ. 1996. *Mycorrhizal symbiosis*, 2nd edn. London: Academic Press.

Tyree MT, Sperry JS. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* **40,** 19–38.

Woodward FI. 1987. Stomatal numbers are sensitive to CO_2 increases from pre-industrial levels. *Nature* **327,** 617–18.

Woodward FI, Bazzaz FA. 1988. The response of stomatal density to CO_2 partial pressure. *Journal of Experimental Botany* **39,** 1771–81.

Woodward, FI, Kelly CK. 1995. The influence of CO_2 concentration on stomatal density. *New Phytologist* **131,** 311–27.

Woodward FI, Kelly CK. 1997. Environmental and physiological constraints in defining plant functional types. In: Smith TM., Shugart HH, Woodward FI, eds. *Plant functional types*. Cambridge University Press (in press).

Woodward FI, Smith TM, Emanuel WR. 1995. A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles* **9,** 471–90.

Ziegler H. 1987. The evolution of stomata. In: Zeiger E, Farquhar GD, Cowan IR, eds. *Stomatal function*. Stanford University Press, 29–57.