



Fig. 4 (a) Amount of available water which remains nonaccessible at the rate required for transpiration as a function of root length density, showing a diminishing return to further investment in root growth; the exact shape of the relation depends on soil physical properties (and the uptake model used). Where the slope of the line equals the marginal root efficiency, the carbohydrate costs for constructing a unit root length can just be recovered by the photosynthesis possible on the basis of additional water uptake. A reduction in half of the amount of water needed per unit photosynthesis will halve the marginal root efficiency and allow for a (slight) increase in root length density. (b) Potential uptake rate and demand (arbitrary scale) for a poorly mobile resource such as P; the intersections of the demand and supply lines indicate the desirable L_{rv} values for three resource supply situations. Doubling of the demand will require at least a doubling of L_{rv} .

This derivation assumes that NUE is independent of the shoot:root ratio and thus presents only a first approximation, as more nitrogen is needed for green leaves than for stem or root tissue. Deviations from this simple model may also be expected as soon as the resource capture functions become nonlinear, e.g. in closed crop canopies or where interroot competition reduces uptake per unit root weight.

Non-linear resource capture functions

For more realistic nonlinear resource capture functions (Fig. 4) we can attempt to predict the absolute (rather than relative) root length density which may be attained in a 'doubled growth' environment. Where water is a limiting resource, a doubled WUE will double the marginal root efficiency and thus allow a (slight) increase in the maximum attainable root length density in each layer to more fully exploit the available water resources in the soil (Fig. 4a). Where the supply of poorly mobile nutrients such as P determines the constraints on root length density, a doubling of demand will lead to a need for at least doubling root length density (Fig. 4b).

We can define a minimum 'marginal' uptake efficiency which will just allow for the carbohydrate (CH₂O) costs of growth, maintenance and uptake respiration of an additional root to be offset by additional water uptake allowing transpiration and photosynthesis. Total carbon costs (including 'growth respiration') for making new root tissue is typically: 2 g CH₂O per g root DW; the carbon conversion efficiency (CUE) is thus 0.5 (Lambers

1987). This means that, apart from CH₂O costs for maintenance respiration, an additional g of root tissue has to yield at least 0.7 L of water during its life time ($\int B_{w,t} dt$) for plants with a WUE of 3 g CH₂O L⁻¹. For a specific root length (SRL) of 200 m g⁻¹, this means an additional uptake per unit root length ($\int B_{l,t} dt$) of 3.5 mL m⁻¹, as

$$\int B_{l,t} dt = 1 / (\text{WUE} \cdot \text{CUE} \cdot \text{SRL}). \quad (11)$$

At a root length density L_{rv} of 1 cm cm⁻³, this means an additional uptake of 0.035 mL of water per cm³ of soil during the lifetime of the additional root. The possible uptake of an additional length of roots in a volume of soil depends on the soil physical properties as well as the physiological entry resistance of the root (De Willigen & Van Noordwijk 1991), but it is unlikely that increases of root length density above 2–3 cm cm⁻³ can be justified on the basis of water uptake for a plant with the parameter values assumed to be 'typical' in the above calculation, during a single soil drying period. In climates where the soil is likely to be replenished during the life of a plant root, higher root length densities may be justified, as long as the maintenance costs for the roots are recovered.

Shoot:root changes in elevated CO₂ experiments

The difference in shoot:root response between water- and nutrient-limited situations which the above model predicts can be linked directly to the experimental evidence only in experiments where both water supply and nutrients (at least N) are varied in factorial designs with elevated CO₂. In such an experiment, Soussana *et al.*

(1996) found a 45–52% increase in root dry weight of a perennial ryegrass sward at doubled CO₂, with an increase in above-ground biomass of 14–19%; effects of elevated CO₂ were much higher in summer than in spring and autumn. Unless additional N fertilizer was used, the grass became clearly N limited at elevated CO₂. Total water use was little affected by elevated CO₂, so that WUE could increase. A temperature increase of 3 °C, however, significantly increased water use.

Enhanced root biomass is often reported in plants grown under elevated CO₂, for example increases of up to 65% in *Bouteloua gracilis* (Morgan *et al.* 1994), 143% in *Glycine max* (Rogers *et al.* 1992b), 31% in *Bromus madritensis* (Dhillion *et al.* 1996) and 50% in a grass/clover mixture (Ross *et al.* 1995). Fewer studies report increases in root length. An increase of 88% in root length in *B. madritensis* (Dhillion *et al.* 1996) and similarly Rogers *et al.* (1992b) reported a 110% increase in the root length of *G. max*. In a study of cotton seedlings total root length and mass density increased as well as the number, length and mass of lateral roots (Rogers *et al.* 1992a). Körner & Arnone (1992) showed substantial increases in fine root length in artificial tropical communities under elevated CO₂.

Symbiotic organisms, rhizobia and mycorrhizas, may also be influenced by increased carbohydrate supply under elevated CO₂ (Norby 1987; Thomas *et al.* 1991; O'Neill 1994; Rogers *et al.* 1994). A substantial amount of literature has been amassed showing that mycorrhizas respond in varied ways under enhanced CO₂ conditions, in turn affecting plant growth, nutrient uptake, altering quality and quantity of soil C, and causing shifts in C sources (O'Neill *et al.* 1987; Lewis *et al.* 1994; Rygielwicz & Andersen 1994; Morgan *et al.* 1994). The responses observed for arbuscular mycorrhizas (AM) are highly varied, for example under elevated CO₂ AM infection increased in *Bouteloua gracilis* and remained unchanged in *Pascopyrum smithii* (O'Neill *et al.* 1987; Lewis *et al.* 1994; Morgan *et al.* 1994).

Large increases in root biomass have also been found for (young) trees: 100% in *Pinus ponderosa* (Johnson *et al.* 1994), 60% in *Fagus sylvatica* (Mousseau *et al.* 1996). Fine as well as woody roots more than doubled in *Quercus alba* but in *Liriodendron tulipifera* only fine root biomass increased significantly (Norby *et al.* 1996). In *Castanea sativa* grown in pots doubling atmospheric CO₂ did not have a significant effect on root biomass, but it stimulated 'rhizodeposition' of C (Rouhier *et al.* 1994, 1996); Mousseau *et al.* (1996) found, however, a significant increase in root biomass for *Castanea sativa* trees planted out in infertile soils.

At scales above the individual plant, consequences of elevated atmospheric CO₂ are less clear, as, e.g. the competitive balance between C3 and C4 plants may be modified in grasslands (Campbell *et al.* 1997).

Root turnover

Maintenance respiration of roots is of the order of 0.03 g g⁻¹ d⁻¹. To justify maintaining a fine root, an additional daily water uptake of 0.0003 mL H₂O per cm⁻³ of soil is needed (for the parameter values used above). Another approach is to compare how long costs of maintenance respiration can be endured, before it is better for the C economy of the plant to let roots die and make new roots when favourable conditions return. For a growth respiration of 2 g CH₂O per g root DW and maintenance respiration of 0.03 g g⁻¹ d⁻¹, 60 days of root maintenance under unfavourable conditions costs as much as one cycle of root death plus re-growth, provided that subsequent root functioning is equivalent. Veen (1980) concluded that 40% of total respiration in growing maize root systems was due to root growth, 40% to maintenance respiration and 20% to uptake respiration. If maintenance respiration over the lifespan of a root indeed equals the respiration costs of its initial construction, an average lifespan of 60 days is indicated (2/0.03). Costs for respiration during stress periods may be more difficult to bear than costs for re-investment when favourable conditions return, but plants will have to balance this against the possible competitive edge of other plants with surviving roots which may benefit faster from a rewetting of the soil. This calculation of optimum root turnover does not involve physiological water use efficiency, so an increase in atmospheric CO₂ concentration is not likely to increase optimum root turnover rates. Higher turnover rates may, however, become desirable for the plant if rainfall variability increases and thus the likely time span between drying and re-wetting.

In summary, optimum root length density is likely to increase under elevated atmospheric CO₂ concentrations, but root turnover and average life span of fine roots may remain the same. Changes in plant strategies on root turnover may be expected, however, if the likely period of water stress in between rainfall events increases.

Rhizovory under global change

The major part of the soil fauna is able to consume dead roots, but only a few groups feed on live roots. This rhizovory is observed mainly in nematodes, termites and some arthropod larvae, such as Coleoptera or Diptera. Yet, rhizovory and plant-parasitic nematodes may play a far greater role in determining succession of vegetation and distribution of plant species than often considered (Van der Putten *et al.* 1993). Rhizovory on crops can be of major agronomic significance (Brown & Gange 1991). Plant roots are an attractive food and thus need effective defense mechanisms, based on their structure or chemical content. Root structures such as an exodermis can be

effective against bacterial and fungal intruders, but not against larger rhizovores. Within the rhizovores, obligate and facultative root feeders can be distinguished. For the facultative root-feeders, such as termites, the attack on roots depends on the availability and attractiveness of other food sources, such as surface litter and dead wood. For the obligate root feeders, such as plant-parasitic nematodes and the larvae of beetles and crane flies (tipuloids), chemical defence may be the major factor in regulating rhizovory. Roots, especially of trees and perennial herbs, tend to have high concentrations of secondary metabolites and are important sources of medicine, insecticides and fish poison. Lavelle *et al.* (1989) tested roots as feed for earthworms and found them to be unsuitable. Although little studied, a coevolution of plant chemical defense and rhizovore adaptations may exist below-ground, as it does above-ground (Janzen 1970; Coley & Kursar 1996). The dominant type of secondary metabolites depends on relative resource availability: on soils with low nutrient supply polyphenolic secondary compounds dominate, on soils richer in nitrogen alkaloids and other toxins are more prominent (Waterman & Mole 1989).

The probable coevolution of plant defence and herbivore/rhizovore adaptations raises important questions on the impacts of global change:

- in the domestication of crops an implicit selection against antinutritional factors and for higher harvest indices normally reduces the effectiveness of chemical defense; hybrid date palms of poorer quality were reported to be more resistant to termites than high-yielding varieties; screening of 500 groundnut cultivars indicated a wide range (from 0 to 44%) of resistance to termites (Logan *et al.* 1990);
- agricultural use of crops and trees outside their original habitats exposes them to other types of rhizovores (Pimentel 1986); termite attack is one of the major reasons why trees fail when tried in new locations; in Africa, sorghum and millet which are indigenous, have more effective resistance to termites than the more recently introduced maize (Cowie & Wood 1989);
- climate change and biome shifts can have different effects on the rhizovores and plants. Biome shifts may introduce plant species into soils with rhizovores against which they have no defense, or it may extend the reach of rhizovores into ecosystems with ill-adapted plants. There is some evidence that termites are expanding to the North in Europe (they have crossed the Loire river in France which was considered to be their boundary), possibly linked to milder winters. Termites occur in cities like Paris, beyond their original domain, and are critical to tree survival. The incidence of plant parasitic nematodes may increase with rising soil temperature (Jones

1975). Increased rainfall variability may increase termite damage, as Cowie & Wood (1989) found more termite damage to a range of food crops in rain fed than in irrigated crops. Research on sugar cane in Central African Republic (Mora *et al.* 1996) and in Chad (Rouland *et al.* 1993) indicated that sugarcane under water stress was attacked more than healthy and vigorous plants.

Nutrient mobilization under global change

When carbohydrates become more freely available in the plant, the strategic options for spending them on nutrient acquisition increase. Such options include rhizosphere-induced N mineralization, mycorrhiza formation for obtaining nutrients of low mobility such as P, excretion of organic acids to mobilize P and N₂ fixation (Fig. 1). Increased investment of carbohydrates in root structures may lead to increased uptake efficiency for nutrients from the soil — provided that there are accessible pools. For mineral nitrogen, either in nitrate or ammonium form, fairly low root length densities are sufficient to gain access to almost the complete stock. Exploring larger horizontal zones may help the individual plant, but not overall productivity of the system. Exploring greater depth may be relevant for access to stored reserves or current subsurface flows from other landscape units, but in many systems the opportunities are limited.

Another 'frontier' may be organically stored nitrogen. There has been a considerable debate on the possible mechanisms for roots to influence the rate of N mineralization in the soil. Before we review this discussion, it is good to realize that although root-induced N-mineralization will be important for the individual plant which can thus obtain a competitive edge, the long-term effects of any such mechanism on ecosystem productivity may be small, once a new equilibrium of supply by litterfall and decomposition will be reached. Litter quality and subsequent decomposition depends not only on nutrient contents in the live tissues, but also on the degree of remobilization of nutrients before litterfall (Arp *et al.* 1997). Prediction of the detailed time course of N mineralization remains one of the most critical aspects of current models of the N balance in the soil-plant system (De Willigen 1991), but at the timescale of a crop season it can be estimated from the history of organic inputs.

Exudation or leakage

Exudation of soluble carbohydrates, including sugars, is, contrary to what the term suggests, probably due to leakage, while roots have an active uptake mechanism to retrieve sugars from their rhizosphere (Jones & Darrah 1996). This combination of leakage and pump can make net exudation a function of internal sugar concentration

in the root both by increased leakage and by reduced effectiveness of the pump. Increased sugar availability in the root cells, during a period of water or nutrient stress, can thus induce increased rhizosphere activity as well as mycorrhizal development. If this rhizosphere activity helps to alleviate the nutrient shortage of the plant, it may form a negative feedback loop on the nutrient deficiency, similar to the overall shoot:root equilibrium.

Microbial biomass C has often been shown to increase in relation to enhanced root growth observed under elevated CO₂ (Whipps 1985; Sadowsky & Schortemeyer 1997; Paterson *et al.* 1997). The increase has been attributed largely to the increase in root substrate deposition in the soil (e.g. Diaz *et al.* 1993; O'Neill 1994; Norby 1994). Microbial biomass C increased by 42% in soil associated with plants under elevated CO₂. In an acidic grassland herbaceous community an increase of up to 80% in microbial biomass carbon occurred under elevated CO₂ (Diaz *et al.* 1993). However, contrary results have also been reported. For example in tallgrass prairie only a small increase of 4% occurred in the first year and no increase in the second year in the upper 5 cm soil layer (Rice *et al.* 1994). The increase in hyphal lengths, examined in only one study, which predominantly comprise saprophytic fungi, is significant for decomposition and turnover of organic matter in the soils (Dhillion *et al.* 1996). It also implies that substrates are being made available for the growth of these fungi.

Effects of CO₂ on root-induced N and P mineralization

Large amounts of N are immobilized in stable organic structures. Its mobilization requires enzyme diversity and metabolic microbial activities able to disrupt the stable structures.

Decomposition and biochemical mineralization are the dominating processes for P release from organic matter. Roots, mycorrhizal fungi and microorganisms can selectively release P from organic matter through the production of ester-hydrolysing phosphatases. Activity of this enzyme increased by 53%, although not significantly ($P = 0.07$) under elevated CO₂ (Dhillion *et al.* 1996). Most of microbial variables measured show significant and substantial increases under elevated CO₂ conditions. In addition related to the increases in root mass and length there are increases in variables relating to microbial activity in soil. An increase in microbial biomass does not necessarily mean higher activity. However, enhanced enzymatic activities and bacterial physiological abilities clearly indicate increased activity in the soil (Dhillion *et al.* 1996; Roy *et al.* 1996). Not only was activity associated with the bacterial communities changed but also that of the saprophytic fungal community which was represented by the changes in hyphal lengths. All of the

increases observed in the microbial community suggest that more substrates, and potentially different types, may be made available by plants and altered by the microbial community.

Van Veen *et al.* (1991) found that the rhizosphere activity was stimulated by a double CO₂ atmospheric concentration and this was accompanied by increased mineralization of soil carbon. Stimulation of SOM mineralization and of microbial biomass turnover was also illustrated by long-term ¹⁴C labelling experiments comparing bare and cultivated soils by Bottner *et al.* (1988) and Sallih & Bottner (1988).

Curtis *et al.* (1996) and Zak *et al.* (1993) reviewed the evidence for the postulated feedback loop from increased availability of carbohydrates in the plant, via an increased turnover of microbial biomass in the rhizosphere to increased N mineralization and N acquisition by the plant. In their experiments with *Populus grandidentata* over 142 days substantial increases in root biomass (+60% under a doubled CO₂ environment) were accompanied by smaller increments in labile soil C in rhizosphere and bulk soil (15–18%) and microbial C (43–46%). N mineralization rate of the bulk soil increased dramatically from a low initial value (+540%), but plant N acquisition only increased by 15%. As the relative increments in labile C and microbial biomass were smaller than those in the root biomass, there is no indication that roots became more effective **per unit biomass** in inducing N mineralization in the soil.

Griffiths & Robinson (1992) showed that the observed stimulatory effect of plants on the net mineralization of soil organic nitrogen cannot be adequately explained by the C in exudates as an energy source for microbial activity. The presence of roots, however, might improve the availability of other energy sources. An exudate front diffusing ahead of relatively slow growing roots (Darrah 1991) may induce a microbial and soil structural response in the soil before the root tip has arrived. The soil sheaths associated with young maize roots (McCully 1987) and the micromorphological evidence of reorientation of clay particles in the rhizosphere (Jaillard 1987) indicate a destabilization of the initial soil structure and disturbance of 'physically protected' soil organic matter, followed by a re-stabilization of soil particles (Van Noordwijk *et al.* 1993). Root-induced N mineralization could be based on such principle, but little hard data are available and little ideas exist how this effect depends on the quality and quantity of root exudates of different plant species.

Root-mediated gas exchange

Vascular plants and their roots have important effects on gas exchange in wetlands. Air channels in the cortex have obvious benefits for the plant root under periods of