Soil Biota and Global Change

Global change and root function

MEINE VAN NOORDWIJK,* PERTTI MARTIKAINEN,† PIERRE BOTTNER,‡
ELVIRA CUEVAS,§ CORNINE ROULAND¶ and SHIVCHARN S. DHILLION**
*ICRAF-S.E.Asia, P.O. Box 161, Bogor 16001, Indonesia, †National Public Health Institute, Lab of Environmental
Microbiology, P.O.Box 95, Fin-70801 Kuopio, Finland, ‡CNRS-UPR 8481 CEFE, BP 5051, F-34033 Montpellier Cedex 1,
France, §IVIC Centro de Ecologia, Apartado 21827, Caracas 1020-A, Venezuela, ¶Université Paris XII, Lab d'Ecophysiologie des
Invertebrés et de Zoologie, Av. du General de Gaulle, 94010 Creteil cedex, France, **Agricultural University of Norway,
Department of Biology, P.O.Box 5014, N-1432 Ås, Norway

Abstract

Global change includes land-use change, elevated CO_2 concentrations, increased temperature and increased rainfall variability. All four aspects by themselves and in combination will influence the role of roots in linking below- and above-ground ecosystem function via organic and inorganic resource flows. Root-mediated ecosystem functions which may be modified by global change include below-ground resource (water, nutrients) capture, creation and exploitation of spatial heterogeneity, buffering of temporal variations in above-ground factors, supply and storage of C and nutrients to the below-ground ecosystem, mobilization of nutrients and C from stored soil reserves, and gas exchange between soil and atmosphere including the emission from soil of greenhouse gases.

The theory of a functional equilibrium between root and shoot allocation is used to explore predicted responses to elevated CO_2 in relation to water or nutrient supply as limiting root function. The theory predicts no change in root:shoot allocation where water uptake is the limiting root function, but substantial shifts where nutrient uptake is (or becomes) the limiting function. Root turnover will not likely be influenced by elevated CO_2, but by changes in regularity of water supply. A number of possible mechanisms for root-mediated N mineralization is discussed in the light of climate change factors. Rhizovory (root consumption) may increase under global change as the balance between plant chemical defense and adapted root consuming organisms may be modified during biome shifts in response to climate change. Root-mediated gas exchange allows oxygen to penetrate into soils and methane (CH_4) to escape from wetland soils of tundra ecosystems as well as tropical rice production systems. The effect on net greenhouse gas emissions of biome shifts (fens replacing bogs) as well as of agricultural land management will depend partly on aerenchyma in roots.

Keywords: carbon balance, greenhouse gas emission, plant strategy, root turnover, shoot-root ratio

Received 26 June 1997; revised version received 28 August and accepted 5 October 1997

Roots and below-ground ecosystem functions

Plants spend a considerable part of the energy which they sequester in photosynthesis on the production and maintenance of roots, thus linking the above- and below-ground functioning of ecosystems (Curtis *et al.* 1996). Roots can be seen as heterotroph organisms living in the soil, but in direct symbiosis with autotroph above-ground

Correspondence: Meine van Noordwijk, fax + 62/ 251 625416, e-mail m.van-Noordwijk@cgnet.com

plants; they exchange carbohydrates for water and nutrients. Roots may 'subcontract' this energy-for-uptake deal to fungi or bacteria living in the rhizosphere or inside their cortical tissues (nodules, arbuscles of mycorrhizal fungi).

However, the integration of roots and shoots extends beyond this symbiotic exchange of above- and below-ground resources (Van Noordwijk *et al.* 1996). 'Root strategies' are as vital for whole plant survival as above-ground vegetative strategies, and their heritability seems
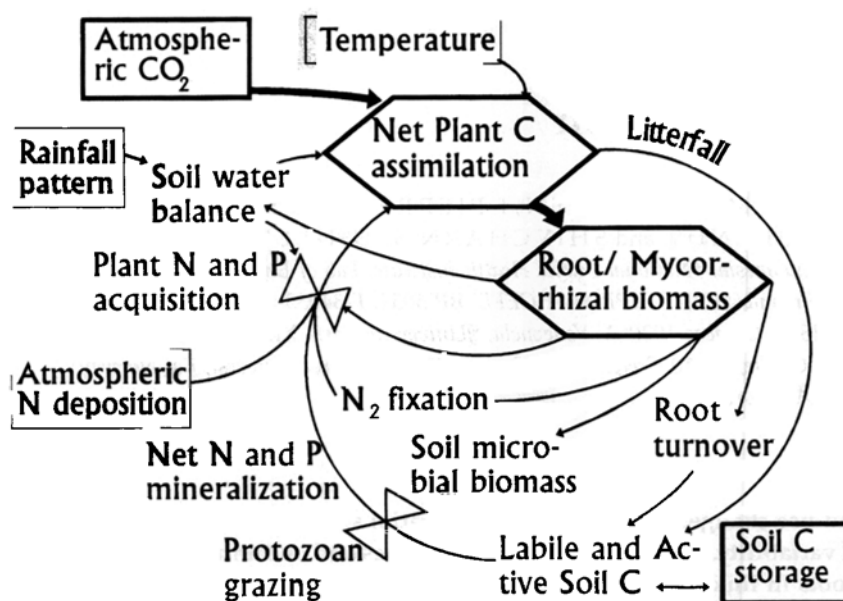
Fig. 1 Schematic feedback loops between above- and below-ground processes considered in this review; elevated atmospheric CO_2 will only lead to an increase in net plant C assimilation if it is matched by increased plant nutrient acquisition; increased C allocation to roots can affect nutrient acquisition via root growth, N_2 fixation, rhizosphere effects on mineralization and, at longer timescales, via increased turnover of root structural material.

to be no less. The considerable carbon costs involved in making and maintaining roots leads to trade-offs in root strategies (Buwalda 1993) and a close match of genotypes with the current biotic and abiotic environment. Changes in environmental conditions, e.g. increased availability of CO_2 as part of 'global change' may thus induce changes in root strategies. Patterns of above- and below ground resource availability determine the functionality (ultimate value) of the plant's strategy, as it emerges as a realization of genetically determined phenotypic plasticity and the actual environment during its development (proximate factors). Where much of current research is focused on an experimental approach to test the phenotypic response of current genotypes to the likely environment of the next century, we will try to assess the ultimate driving forces which determine the functionality of these strategies to explore possible directions of future change in plant strategies if, e.g. the ratio of CO_2 and water or nutrient availability is changing. This assessment is more speculative than a review of current physiological mechanisms, as none of the ongoing FACE (free air CO_2 enrichment) experiments has lasted long enough to include genotypic adaptation, but it may help to identify the new ecological opportunities created by global change, as well as the immediate problems caused.

Direct effects on soil of elevated atmospheric CO_2 concentrations are likely to be small because of the high CO_2 levels already present in most soils (Van·Veen et al. 1991; Young et al. 1998, this volume). Indirect effects via plants may induce several major feedbacks on plants (Fig. 1) and can thus be critical determinants of ecosystem response to climate change (e.g. Bazzaz 1990; Diaz et al. 1993; Zak et al. 1993; Rogers et al. 1994; Dhillion et al.

1996). In particular, an increasing number of studies point to below-ground systems as sinks in global C cycling (Van de Geijn & van Veen 1993; Norby 1994; O'Neill 1994).

In this review we will explore how components of global change such as changes in plant species composition (land-use change and climate-related biome shifts), as well as ecophysiology (elevated CO_2, temperature, water and N availability) may affect six root-mediated functions of the below-ground ecosystem (Table 1).

Elevated CO_2 impact on above and below-ground production

Overall an increase of the instantaneous rate of photosynthesis of 30–50% may be expected for a doubling of atmospheric CO_2 concentration (Poorter 1993; Luo & Mooney 1996; Amthor & Koch 1996), but various feedback mechanisms can reduce the increase to virtually zero when measured over longer time periods, depending on below-ground resource availability. Plants with an 'inherent' slow growth at current CO_2 levels may not be able to increase their growth rates and internal sinks for carbohydrates and will not respond as much as plants with a higher growth rate at current atmospheric conditions, even if water and nutrient supply are increased.

The response of the shoot:root ratios to elevated CO_2 depends largely on the water and nutrient supply in the experiment. A decrease in shoot:root ratio is often found in experiments on soils of limited nutrient (and/or water availability) and is nearly always caused by an absolute increase in root weight which exceeds the increase in shoot weight. In nutrient poor environments where shoot:root ratio is low at current CO_2 concentrations,

Table 1 Below-ground ecosystem functions considered in this review on global change effects

1   Below-ground resource capture (water, nutrients) for net primary production
2   Creating and exploiting spatial heterogeneity ('hot spots'); lateral resource capture by (tree) roots and effects on lateral flow of resources (water, nutrients, soil) in toposequences on slopes influence spatial landscape mosaics
3   Buffering and resilience in response to temporal pulses, by determining the effective water buffer via rooting depth, providing physical stability (trees)
4   Storage of carbon and nutrients; supplying energy to below-ground foodwebs
5   Mobilizing nutrients from 'stored' soil reserves via exudation of organic acids, enzymes and specific substances such as siderophores; supplying energy to and influence microorganisms able to fix atmospheric nitrogen and effecting N transformations such as nitrification
6   Gas exchange between soil and atmosphere via channels in live roots, by modifying soil macroporosity and soil aggregate structure

above-ground response may be near-zero. In situations where shoot:root ratio is already high initially, both shoot and root weight can increase under elevated CO_2 conditions. Many experiments in solution culture, where water and nutrient supply are maintained adequate to support the increased plant growth, found no change in shoot:root ratio (Stulen & Den Hertog 1993; Den Hertog et al. 1996). The more rapid growth of the plant at elevated CO_2 concentrations is to some extent a re-scaling of the time dimension; when parameters such as specific leaf area or specific root length are compared for plants of the same total biomass differences due to elevated CO_2 concentration are much smaller than when the comparison is made at a fixed point in time (Fonseca et al. 1996). Den Hertog et al. (1996) discuss this phenomenon as 'ontogenetic drift'.

Functional shoot:root equilibrium

Brouwer (1963) formulated the hypothesis that plants maintain a 'functional equilibrium' between shoot and root growth. The hypothesis emphasized the eco-physiological functionality of shifts in allocation of current growth resources over above- and below-ground parts during the development of an individual plant, depending on the relative supply of above (light, CO_2) and below-ground (water, nutrients) resources (Fig. 2). The hypothesis is supported broadly by agronomic experience (Van Noordwijk & De Willigen 1987) and allows a functional interpretation of plant strategies on shoot:root allocation across ecological zones (Chapin 1980; Sanford & Cuevas 1996). Shoot:root ratios in tropical forests range from 0.7:1 on poor spodosols, via 2:1 for tropical deciduous forest where seasonal water shortages occur, to 4:1 in montane and 8:1 in lowland humid forests (Fig. 2). On the wet side, the extremes are shoot:root ratios of 1:1 for mangroves with well-adapted below-ground systems to 100:1 in riparian forests without a substantial below-ground compartment.

The functional equilibrium theory also provides a first approximation to the 'local response' of root systems to situations with heterogeneous resource supply (Van Noordwijk et al. 1996).

A simple view of the physiological mechanism emphasizes the need of both above- and below-ground growing points for carbohydrates as well as nutrients and a favourable water potential, and stipulates that above-ground organs have primary access to the carbohydrates produced above-ground, while root tips have a competitive advantage for the resources acquired below-ground. Thus, where above-ground resources are limiting overall biomass production, above-ground growth will prevail, whereas root growth gains in importance whenever below-ground resources are limiting growth (Fig. 3). In the 'functional equilibrium' situation plant growth is limited to an equal degree by (internal) availability of the above- and below-ground resources, regardless of the external environment. The relative biomass allocation over shoot and root growth will thus reflect the relative abundance of above- and below-ground resources. Allocation over above- and below-ground biomass may change rapidly, reflecting changes in the environment or external disturbances of the shoot:root equilibrium, such as grazing of roots or shoots. When root growth stops temporarily after shoot damage, existing root tips may survive and resume growth subsequently. Under prolonged disturbance, existing roots die and new roots may have to start from the base of the stem.

The postulated feedback scheme is sufficient to generate many of the allocation patterns observed in actual plants (Brouwer & De Wit 1969; Reynolds & Thornley 1982; Spek & Van Oijen 1988). Further physiological research (Brouwer 1983; Lambers 1983) has led to the conclusion, however, that the mechanism of feedback is more complicated than initially formulated by Brouwer. The direct (proximate) mechanism of changes in shoot:root allocation is not as closely linked to the (ultimate) functionality. Plants may use a range of 'early warning' methods to adjust allocation over shoot and roots before the real resource deficiencies are felt. This allows for much more variation between species and genotypes in both the speed and the degree of return to
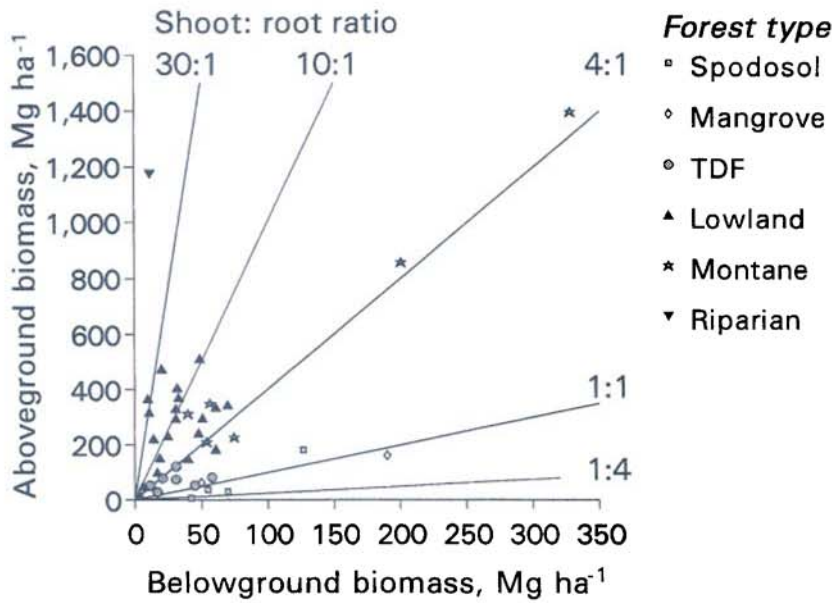
Shoot: root ratio

Fig. 2 Relation between above- and below-ground biomass in tropical forests on various types of soil, based on literature review by Sanford & Cuevas (1996). TDF = tropical dipterocarp forest
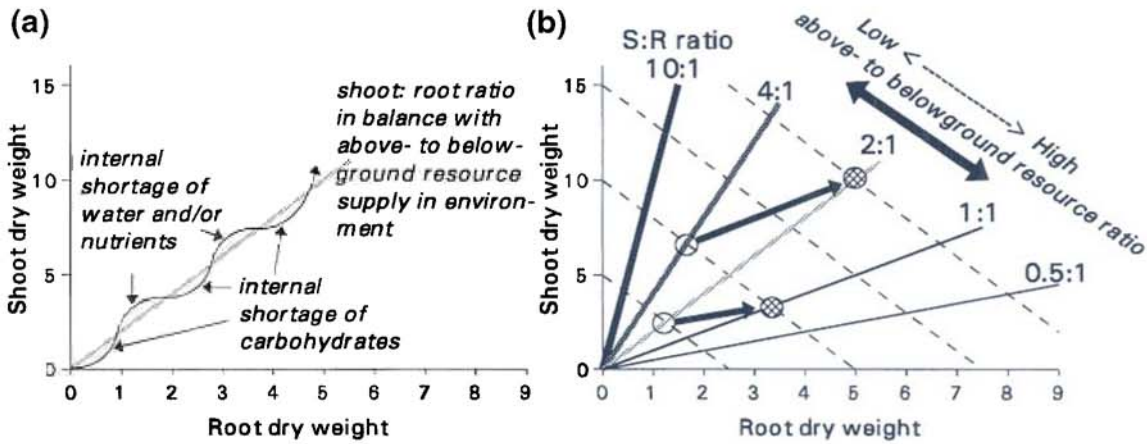

Fig. 3 (a) Relationship between shoot and root dry weight which may be expected if both above- and below-ground resource capture remain proportional to the size of the shoot and root, respectively. (b) The optimum shoot-to-root ratio will depend on the ratio of above- to below-ground resources. The interrupted lines represent equal total carbohydrate costs, assuming a doubled cost per unit root dry weight; the circles and arrows indicate likely responses to a doubling of total carbohydrate production rates in a nutrient-limited situation where the optimum S:R ratio will halve; the relative change in shoot weight will depend on the initial S:R ratio.

the original shoot-to-root ratio after disturbance. Kuiper *et al.* (1990) compared salt-tolerant and salt-sensitive barley cultivars. Survival of salt application by cultivars was strongly related to the capability to rapidly adapt their shoot-to-root ratio, a process that can be inhibited by added cytokinins. Such experiments suggest a complexity of mechanisms underlying the functional equilibrium response, making a direct incorporation into crop growth models difficult (Reynolds *et al.* 1996; Van Noordwijk & Van de Geijn 1996). Not only the average allocation of C over shoot and root, but also its responsiveness to external conditions is under strong genetic control. Where the response to the onset of dry conditions lies between a 'pessimistic' (reduce above-ground growth,

increase root growth) and an 'opportunistic/optimistic' approach (business as usual, hoping for the problem to disappear), the selection pressure will depend on the exact frequency of dry periods of critical duration for the 'optimists'. A fine-tuning of this response may thus be expected to be part of the evolutionary history of all plants. Experiments with present-day cultivars and tomorrow's atmosphere and climate may thus give a limited perspective on the real responses to be expected. A doubling of external CO_2 concentration will, however, only modify the external above- to below-ground resource ratio by a factor of 2, while all plants experience far wider changes in this ratio due to fluctuations in water availability.

A functional equilibrium model of optimum root strategies under global change

Assume a simple above-ground resource capture function:

$$\sigma = \int A \cdot S \, dt \qquad (1)$$

with σ = cumulative internal availability of carbohydrates (based on above-ground resources), A = daily rate of above-ground resource capture per unit shoot weight, S = shoot weight, and two below-ground resource capture functions:

$$\rho_w = \int B_w \cdot R \, dt \qquad (2)$$

$$\rho_n = \int B_n \cdot R \, dt \qquad (3)$$

with ρ_w and ρ_n = cumulative internal availability of water and nutrients, respectively, B_w and B_n = daily rate of water and nutrient uptake, respectively, per unit root weight, and R = root weight.

If WUE = water utilization efficiency = amount of carbohydrates which can be produced per unit water transpired, then:

$$WUE = \sigma/\rho_w = (\int A \, S \, dt)/(\int B_w \, R \, dt). \qquad (4)$$

If, in first approximation, A is independent of S and t and B_w independent of R and t, and S and R are symmetric, monotone functions of time, then

$$S/R = WUE \cdot B_w/A \qquad (5)$$

indicates the shoot-to-root ratio at which the internal resource availability of above- and below-ground resources is in balance if water supply is the external limiting resource below-ground.

Typical values for physiological water use efficiency (WUE) under the current climate are (3)-5-(7) g CH_2O per L H_2O (these values correspond with a net primary production of 20 g DW m^{-2} d^{-1} and a transpiration rate of 4 mm (= 1 m^{-2}) d^{-1}, as typically found in agricultural crops (De Wit 1958); plants with a C4 pathway in photosynthesis may have a WUE in the 5–7 range, and plants with a C3 physiology one in the 3–5 range.

Similarly, if NUE = nutrient utilization efficiency = ratio of carbohydrates vs. nutrients required for growth, then:

$$NUE = \sigma/\rho_n = (\int A \, S \, dt)/(\int B_n \, R \, dt), \qquad (6)$$

and hence, if B_n is independent of R and t:

$$S/R = NUE \cdot B_n/A \qquad (7)$$

indicates the shoot-to-root ratio at which the internal resource availability of above- and below-ground resources is in balance if nutrient supply is the external limiting resource below-ground. Internal nutrient/C ratios could provide a signal for regulation and coordination.

Overall, the shoot:root ratio which maximizes overall plant growth would be:

$$SRratio = \min(WUE \cdot B_w, NUE \cdot B_n)/A. \qquad (8)$$

For a SRratio above this value, there will be an internal excess of carbohydrates (or nutrient or water shortage) and additional root growth may be advantageous; for a SRratio below this value an opposite response may occur (Fig. 3a). At the optimum SRratio value neither above- nor below-ground resources are directly limiting. If the ratio in which external resources are available changes, an adjustment of the SRratio may be expected. The better the below-ground resource supply and thus the higher the B/A ratio, the higher the SRratio may be.

If A doubles in a doubled CO_2 environment, the response of the SRratio will depend on whether water or nutrients will be the limiting below-ground resource. If nutrients are the limiting resource below-ground, the optimum shoot:root ratio may be reduced by 50% as both B_n and NUE remain constant. If water is the limiting resource below-ground, however, the WUE may double as well in a doubled CO_2 environment as the rate of inward diffusion of CO_2 and outward diffusion of water vapour through the stomata doubles. No change in shoot:root ratio will be expected in this case. Intermediate responses may occur as well, as the below-ground limitation may shift from water to nutrients under a doubled CO_2 atmosphere and as the response of WUE may be less than proportional to the increase in A. Casella *et al.* (1996), for example, found an increase of WUE of about 25% for *Lolium perenne* in a doubled CO_2 environment (see also Swift *et al.* 1998 this volume). Schapendonk *et al.* (1997) found WUE of *Lolium perenne* swards to increase by a factor 1.5 in a doubled CO_2 environment, with increased net primary production but equal total water use, and substantially increased carbon allocation to roots.

Suppose that there is a different efficiency in using carbohydrate for making shoot and root dry weight, such that

$$S + \gamma R = S (1 + \gamma/SRratio) = constant, \qquad (9)$$

where γ = ratio of the amounts carbohydrate required to make one unit of root and of shoot dry weight.

The interrupted lines in Fig. 3b then indicate situations of equal carbohydrate use for growth (for $\gamma = 2$). The effect on shoot weight of a doubled overall growth rate in combination with a halving of the SRratio, depends on the initial SRratio:

$$S_2/S_1 = (SRratio_1 + \gamma)/(0.5 \, SRratio_1 + \gamma). \qquad (10)$$

If the initial SRratio is high (SRratio$_1$ >> γ), the S_2/S_1 ratio may nearly double; if the initial SRratio is low (SRratio$_1$ << γ), however, the S_2/S_1 ratio will approach unity.