Table 2 Examples of effects of 'global change' on below-ground ecosystem functions mediated by roots

Below-ground ecosystem functions of roots	Land use change	Increased temperature	Increased rainfall variability	Increased CO_2
Below-ground resource capture for NPP	lower plant diversity can reduce efficiency	increased demand for water	more frequent drought-induced nutrient deficiency	overall increase in NPP = > increased nutrient demand at equal water demand via higher WUE
Creating and exploiting spatial heterogeneity	scale changes from trees to annuals; simplification (segregation of functions) in complex agro-ecosystems			–
Buffering against 'pulses'	–		variability of soil water content will increase by higher demand and less regular supply	
Storage of C and nutrients	forest to nonforest conversion reduces below-ground C storage	decomposition and mineralization increase	–	more carbohydrate available for below-ground processes leading to larger C storage
Mobilization of nutrients	replacing 'specialists' by more 'generalist' species			more carbohydrates available for rhizosphere activities
Facilitating gas exchange	creating and managing rice paddies, vegetation change in boreal bogs and fens			

oxygen stress; yet, they are formed as part of normal root development only in wetland species (mostly monocotyledons), and are secondary adaptations during waterlogging in other species. A drawback of such air spaces may be a reduction in the ability of the root to overcome mechanical impedance in compacted soils, but also that they provide easy access to intruders (Van Noordwijk *et al.* 1993). A suberized exodermis may act as a seal around the aerenchyma and allow oxygen to penetrate deeper into the root and only leak out around the unsuberized root tip. Normally, barriers for air transport exist on the transition of main axes and branch roots. Air channels (aerenchyma) in the root cortex will not only supply O_2 to the root tissue, but will also leak out to the rhizosphere. Such O_2 leakage may be functional for the plant as it can help in detoxifying Fe^{3+} forms and inducing nitrification (Engelaar *et al.* 1995). Gases such as CH_4 and N_2O produced on the edge of the rhizosphere and in bulk soil, under (partial) anaerobic conditions can reach the atmosphere via these channels. An important difference exists between the two trace gasses CH_4 and N_2O in this respect. The likelihood of CH_4 oxidation in aerobic surface layers causes a large difference in net emissions if the CH_4 can bypass these zones via the chimneys provided by roots by diffusion in air (Watson *et al.* 1997). Oxidation of CH_4 to CO_2 in the rhizosphere is usually only partial. For N_2O no comparable effect exists and effects of roots on net emissions appear to be small.

The two ecosystems where this root-mediated gas exchange have received most attention are rice fields and peatlands in the boreal zone. While net CH_4 emissions from rice fields can be reduced by adjusted water management (Nugroho *et al.* 1996) and possible selection of rice genotypes, the responses of natural vegetation in the boreal zone are less under human control and yet effects on root-mediated CH_4 emission may be substantial from a global climate change perspective (Torn & Chapin 1993; Schimel 1995).

Watanabe *et al.* (1995) found two-fold differences in methane emission between rice cultivars; these differences were not correlated with the amount of roots of the cultivar, but apparently to differences in functioning of the air channels and / or effects on rhizosphere organisms. Gas exchange via root aerenchyma not only depends on the air-filled root porosity and the size of the air channels, but also on their wall properties (De Willigen & Van Noordwijk 1989). In plants such as rice an effective 'coating' (suberized cell layers in the exodermis) prevents gas exchange with the rhizosphere for most of the distance between atmosphere and root tips. Only where new branch roots break through the root cortex can leaks occur, as can be visualized by redox indicator dyes (Van Noordwijk *et al.* 1993; Van Noordwijk & Brouwer 1993). Details of the root architecture are thus important for this gas exchange function and in crops such differences can be exploited.

In the boreal zone the fens dominated by monocotyledons such as sedges have the highest CH_4 emissions. *Sphagnum*-dominated bogs on nutrient-poor sites release little CH_4, and thus the transitions between bog and fen vegetation have consequences for net greenhouse gas emissions (Nykänen *et al.* 1995; Bubier 1995). When peatlands are drained for agriculture (Armentano & Menge 1986), the practices of drainage, liming, fertilization and ploughing all contribute to an increase in peat decomposition and rapid loss of C (Nykänen *et al.* 1995). Organic matter inputs from the crop can never compensate for such losses.

Drainage of natural peatlands will reduce the root-mediated CH_4 emissions, but it can induce substantial increases in emissions of N_2O and NO (Lång *et al.* 1995; Regina *et al.* 1996). Emissions are higher on fen sites than on bogs, and corresponds to differences in nitrification rates and C:N ratio of the peat (Martikainen *et al.* 1993; Regina *et al.* 1996).

Discussion—research priorities

Examples of global change effects on root mediated ecosystem functions discussed here are summarized in Table 2. Contradictory effects may be noted between changes in temperature and atmospheric CO_2 concentrations on likely changes in below-ground C storage. Although it is clear that there are several possible feedback loops leading to increased nutrient acquisition under elevated CO_2 conditions (Fig. 1), few studies have been successful in separating the direct effects of more roots from possible changes in 'rhizosphere effect per unit root'. The current concept of the mechanism of root-induced N mineralization is still open to debate and has been challenged quantitatively.

In this review we make a plea for combining direct physiological studies, with the exploration of 'strategic' opportunities for genetic adjustment. If more carbohydrates become available, how should the plant use these? Root functions such as nutrient acquisition, chemical defense against rhizovores and increased buffering against 'pulses' in water supply are all likely to gain in importance under a global change scenario.

Priority areas for future research are:

- measurement of root turnover under field conditions across current (and future) ecosystems;
- inventory of rhizovory and chemical defense in roots across current ecosystems, in view of likely changes in soil fauna during 'biome shifts';
- clarification of the interactions between roots, rhizosphere and soil structure in their effects on C and nutrient storage and mobilization;
- limits to the ecophysiological tolerance mechanisms on trees and other plants with long life cycles, where genotypic adaptation may be too slow to deal with global change;
- effects of discoupling ecosystems during biome shifts on specialized root–rhizosphere interactions, both favourable ones (mycorrhiza, nodulation) and detrimental (rhizovory).

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References

Amthor JS, Koch GW (1996) Biota growth factor β: stimulation of terrestrial ecosystem net primary production by elevated atmospheric CO_2. In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney H), pp. 399–414. Academic Press, San Diego, CA.

Armentano TV, Menge ES (1986) Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. *Journal of Ecology*, **74**, 755–774.

Arp WJ, Kuikman PJ, Gorissen A (1997) Climate change: the potential to affect ecosystem functions through changes in amount and quality of litter. In: *Driven by Nature: Plant Litter Quality and Decomposition* (eds Cadisch G, Giller KE), pp. 187–200. CAB International, Wallingford.

Bazzaz FA (1990) The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecological Systematics*, **21**, 167–196.

Bottner P, Sallih Z, Billès G (1988) Root activity and carbon metabolism in soils. *Biology and Fertility of Soils*, **7**, 71–78.

Brouwer R (1963) Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek IBS*, **1953**, 31–39.

Brouwer R (1983) Functional equilibrium: sense or non-sense? *Netherlands Journal of Agriculture Science*, **31**, 335–348.

Brouwer R, De Wit CT (1969) A simulation model of plant growth with special attention to root growth and its consequences. In: *Root Growth* (ed. Whittington WJ), pp. 224–244. Butterworths, London.

Brown VK, Gange AC (1991) Effects of root herbivory on vegetation dynamics. *In:* Plant Root Growth: an Ecological Perspective (ed. Atkinson D), pp. 453–470. Blackwell Scientific Publications, Oxford.

Bubier JL (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *Journal of Ecology*, **83**, 403–420.

Buwalda JG (1993) The carbon costs of root systems of perennial fruit crops. *Environmental and Experimental Botany*, **33**, 131–140.

Campbell BD, Stafford Smith DM, McKeon GM (1997) Elevated CO_2 and water supply interactions in grasslands: a pastures and rangelands management perspective. *Global Change Biology*, **3**, 177–187.

Casella E, Soussana JF, Loiseau P (1996) Long-term effects of CO_2 enrichment and temperature increase on a temperate grass sward. I. Productivity and water use. *Plant and Soil*, **182**, 83–99.

Chapin FS III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.

Coley PD, Kursar TA (1996) Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological trade-offs. In: *Tropical Forest Plant Ecophysiology* (eds Mulkey SS, Chazdon RL, Smith AP), pp. 305–336. Chapman and Hall, New York.

Cowie RH, Wood TG (1989) Damage to crops, forestry and rangeland by fungus-growing termites (Termitidae: Macrotermitinae) in Ethiopia. *Sociobiology*, **15**, 139–153.

Curtis PS, Zak DR, Pregitzer KS, Lussenhop J, Teeri JA (1996) Linking above- and belowground responses to rising CO_2 in northern deciduous forest species. In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney H), pp. 41–52. Academic Press, San Diego, CA.

Darrah PR (1991) Models of the rhizosphere. II. A quasi three-dimensional simulation of the microbial population dynamics around a growing root releasing soluble exudates. *Plant and Soil*, **138**, 147–158.

De Willigen P (1991) Nitrogen turnover in the soil-crop system; a comparison of fourteen simulation models. *Fertilizer Research*, **27**, 141–149.

De Willigen P, Van Noordwijk M (1989) Model calculations on the relative importance of internal diffusion for aeration of roots of non-wetland plants. *Plant and Soil*, **113**, 111–119.

De Willigen P, Van Noordwijk M (1991) Modelling nutrient uptake: from single roots to complete root systems. In: *Simulation and Systems Analysis for Rice Production (SARP)* (eds Penning de Vries FWT, van Laar HH, Kropff MJ), Simulation Monographs, pp. 277–295. PUDOC, Wageningen.

De Wit CT (1958) Transpiration and crop yields. *Verslagen van landbouwkundige onderzoekingen*, **64**, 88 pp 6.

Den Hertog J, Stulen I, Fonseca F, Delea P (1996) Modulation of carbon and nitrogen allocation in *Urtica dioica* and *Plantago major* by elevated CO_2: impact of accumulation of nonstructural carbohydrates and ontogenentic drift. *Physiologia Plantarum*, **98**, 77–88.

Dhillion SS, Roy J, Abrams M (1996) Assessing the impact of elevated CO_2 on soil microbial activity in a Mediterranean model ecosystem. *Plant and Soil*, **187**, 333–342.

Diaz S, Grime JP, Harris J, McPherson E (1993) Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. *Nature*, **364**, 616–617.

Engelaar WMHG, Symens JC, Laanbroek HJ, Blom CWPM (1995) Preservation of nitrifying capacity and nitrate availability in waterlogged soil by radial oxygen loss from roots of wetland plants. *Biology and Fertility of Soils*, **20**, 243–248.

Fonseca F, Den Hertog J, Stulen I (1996) The response of *Plantago major* ssp. *pleiosperma* to elevated CO_2 is modulated by the formation of secondary shoots. *New Phytology*, **133**, 627–635.

Griffiths B, Robinson D (1992) Root-induced nitrogen mineralisation: a nitrogen balance model. *Plant and Soil*, **139**, 253–263.

Jaillard B (1987) Techniques for studying the ionic environment at the soil/root interface. 20th International Colloquium on Potash, Institute of Baden bei Wien, pp. 247–261.

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.

Johnson D, Geisinger D, Walker R, Newman J, Vose J, Elliot K, Ball T (1994) Soil pCO_2, soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine. *Plant and Soil*, **165**, 129–138.

Jones FGW (1975) The soil as an environment for plant parasitic nematodes. *Annals of Applied Biology*, **79**, 113–139.

Jones DL, Darrah PR (1996) Re-sorption of organic compounds by roots of *Zea mays* L. & its consequences in the rhizosphere. III. Characteristics of sugar influx and efflux. *Plant and Soil*, **178**, 37–48.

Körner Ch, Arnone IIIJA (1992) Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science*, **257**, 1672–1675.

Kuiper D, Schuit J, Kuiper PJC (1990) Actual cytokinin concentration in plant tissue as an indicator for salt resistance in cereals. *Plant and Soil*, **123**, 243–250.

Lambers H (1983) 'The functional equilibrium', nibbling on the edges of a paradigm. *Netherlands Journal of Agricultural Science*, **31**, 305–311.

Lambers H (1987) Growth, respiration exudation and symbiotic associations: the future of carbohydrates translocated to the roots. In: *Root Development and Function* (eds Gregory PJ, Lake JV, Rose DA), pp. 125–145. Cambridge University Press, Cambridge.

Lång K, Silvola J, Ruuskanen J, Martikainen PJ (1995) Emission of nitric oxide from boreal peat soils. *Journal of Biogeography*, **22**, 1157–1:162.

Lavelle P, Schaffer R, Zaini Z (1989) Soil ingestion and growth in *Millsonia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested. *Pedobiologia*, **33**, 379–388.

Lewis JD, Thomas RB, Strain BR (1994) Effect of elevated CO_2 on mycorrhizal colonization of loblolly pine (*Pinus taeda* L.) seedlings. *Plant and Soil*, **165**, 81–88.

Logan JW, Cowrie RH, Wood TG (1990) Termite control in agriculture and forestry by non-chemical methods: a review. *Bulletin of Entomological Research*, **80**, 309–330.

Luo Y, Mooney HA (1996) Stimulation of global photosynthetic carbon influx by an increase in atmospheric carbon dioxide concentration. In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney H), pp. 381–397. Academic Press, San Diego, CA.

Martikainen PJ, Nykänen H, Crill P, Silvola J (1993) Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. *Nature*, **366**, 51–53.

McCully ME (1987) Selected aspects of the structure and development of field-grown roots with special reference to maize. In: *Root Development and Function* (eds Gregory PJ, Lake JV, Rose DA), pp. 53–70. Cambridge University Press, Cambridge.

Mora P, Rouland C, Renoux J (1996) Foraging, nesting and damage caused by *Microtermes subhyalinus* (Isoptera: Termitidae) in a sugarcane plantation in the Central African republic. *Bulletin of Entomological Research*, **86**, 387–395.

Morgan JA, Knight WG, Dudley LM, Hunt HW (1994) Enhanced root system C-sink activity, water relations and aspects of nutrient acquisition in mycotrophic *Bouteloua gracilis* subjected to CO_2 enrichment. *Plant and Soil*, **165**, 139–146.

Mousseau M, Dufrêne El Kohen A, Epron D, Godard D, Liozon R, Pontailler JY, Saugier B (1996) Growth strategy and tree response to elevated CO_2: a comparison of beech (Fagus sylvatica) and sweet chestnut (*Catanea sativa* Mill.). In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney H), pp. 71–86. Academic Press, San Diego, CA.

Norby RJ (1987) Nodulation and nitrogenase activity in nitrogen-fixing plants stimulated by CO_2 enrichment of the environment. *Plant Physiology*, **71**, 77–82.

Norby RJ (1994) Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. *Plant and Soil*, **165**, 9–30.

Norby RJ, Wullschleger SD, Gunderson CA (1996) Tree responses to elevated CO_2 and implications for forests. In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney H), pp. 1–21. Academic Press, San Diego, CA.

Nugroho SG, Lumbanraja J, Suprapto H, Sunyoto Ardjasa WS, Haraguchi H, Kimura M (1996). Three-year measurement of methane emission from an Indonesian paddy field. *Plant and Soil*, **181**, 287–293.

Nykänen H, Alm J, Lång K, Silvola J, Martikainen PJ (1995) Emissions of CH_4 N_2O and CO_2 from a virgin fen and a fen drained for grassland in Finland. *Journal of Biogeography*, **22**, 1149–1155.

O'Neill EH (1994) Responses of soil biota to elevated atmospheric carbon dioxide. *Plant and Soil*, **165**, 55–65.

O'Neill EG, Luxmoore RJ, Norby RJ (1987) Increases in mycorrhizal colonization and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched CO_2 atmosphere. *Canadian Journal of Forest Research*, **17**, 878–883.

Paterson E, Hall JM, Rattray EAS, Griffiths BS, Ritz K, Killham K (1997) Effect of elevated CO_2 on rhizosphere carbon flow and soil microbial processes. *Global Change Biology*, **3**, 363–377.

Pimentel D (1986) Biological invasions of plants and animals in agriculture and forestry. *Ecological Studies*, **58**, 149–162.

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104/105**, 77–97.

Regina K, Nykänen H, Silvola J, Martikainen PJ (1996) Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. *Biogeochemistry*, **35**, 401–418.

Reynolds JF, Kemp POT, Acock B, Chen JL, Moorhead DL (1996) Progress limitations and challenges in modelling the effects of elevated CO_2 on plants and ecosystems. In: *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch GW, Mooney H), pp. 347–380. Academic Press, San Diego, CA.

Reynolds JF, Thornley JHM (1982) A shoot:root partitioning model. *Annals of Botany*, **49**, 585–597.

Rice CW, Garcia FO, Hampton CO, Owensby CE (1994) Soil microbial response in tallgrass prairie to elevated CO_2. *Plant and Soil*, **165**, 67–74.

Rogers HH, Peterson CM, McCrimmon JM, Cure JD (1992a) Response of soybean roots to elevated atmospheric carbon dioxide. *Plant, Cell and Environment*, **15**, 749–752.

Rogers HH, Prioir SA, O'Neill EG (1992b) Cotton root and rhizosphere responses to free-air CO_2 enrichment. *Critical Reviews in Plant Science*, **11**, 251–263.

Rogers HH, Runion GB, Krupa SV (1994) Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution*, **83**, 155–189.

Ross DJ, Tate KR, Newton PCD (1995) Elevated CO_2 and temperature effects on soil carbon and nitrogen cycling in ryegrass/white clover turves of an Endoaquept soil. *Plant and Soil*, **176**, 37–49.

Rouhier H, Billès G, Billès L, Bottner P (1996) Carbon fluxes in the rhizosphere of sweet chestnut seedlings (*Castanea sativa*) grown under two atmospheric CO_2 concentrations: ^{14}C partitioning after pulse labelling. *Plant and Soil*, **180**, 101–111.

Rouhier H, Billès G, El Kohen A, Mousseau M, Bottner P (1994) Effect of elevated CO_2 on carbon and nitrogen distribution within a tree (*Castanea sativa* Mill.) – soil system. *Plant and Soil*, **162**, 281–292.

Rouland C, Ikhouane A, Nayalta N (1993) Etude biologique des populations d'*Ancistrotermes guineensis* présentes dans les plantations de la SONASUT (Tchad). *Act College of U I E I S*, **8**, 79–87.

Roy J, Guillerm JL, Navas ML, Dhillion S (1996) Responses to elevated CO_2 in Mediterranean oldfield microcosms: species community and ecosystem components. In: Carbon Dioxide, Populations and Communities (eds Körner Ch, Bazzaz FA), Physiological Ecology Series. Academic Press, San Diego, CA.

Rygiewicz PT, Andersen CP (1994) Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature*, **369**, 58–60.

Sadowsky MJ, Schortemeyer M (1997) Soil microbial responses to increased concentrations of atmospheric CO_2. *Global Change Biology*, **3**, 217–224.

Sallih Z, Bottner P (1988) Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biology and Fertility of Soils*, **7**, 67–70.

Sanford RL, Cuevas E (1996) Root growth and rhizosphere interactions in tropical forests. In: *Tropical Forest Plant Ecophysiology* (eds Mulkey SS, Chazdon RL, Smith AP), pp. 268–300. Chapman and Hall, New York.

Schapendonk AHCM, Dijkstra P, Groenwold J, Pot CS, Van de Geijn SC (1997) Carbon balance and water use efficiency of frequently cut *Lolium perenne* L. swards at elevated carbon doixide. *Global Change Biology*, **3**, 207–216.

Schimel JP (1995) Plant transport and methane flux from arctic wet meadow tundra. *Biogeochemistry*, **28**, 183–200.

Soussana JF, Casella E, Loiseau P (1996) Long-term effects of CO_2 enrichment and temperature increase on a temperate grass sward. II. Plant nitrogen budgets and root fraction. *Plant and Soil*, **182**, 101–114.

Spek L, Van Oijen M (1988) A simulation model of root and shoot growth at different levels of nitrogen availability. *Plant Soil*, **111**, 191–197.

Stulen I, den Hertog J, (1993) Root growth and function under atmospheric CO_2 enrichment. *Vegetatio*, **104/105**, 99–116.

Swift MJ, Andren O, Brussaard L, Briones M, Couteaux M-M, Ekschmitt K, Kjoller A, Loiseau P, Smith P (1988) Global change, soil biodiversity and nitrogen cycling in terrestrial ecosystems: three case studies. *Global Change Biology*, **4**, 729–743.

Thomas RB, Richter DD, Ye H, Heine PR, Strain BR (1991). Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium* (Jacq. Walp.) exposed to elevated CO_2 atmosphere. *Oecologia*, **8**, 415–421.

Torn MS, Chapin FS (1993) Environmental and biotic controls over methane flux from arctic tundra. *Chemosphere*, **26**, 357–368.

Van de Geijn SC, van Veen JA (1993) Implications of increased carbon dioxide levels for carbon input and turnover in soils. *Vegetatio*, **104/105**, 293–292.

Van der Putten WW, Van Dijk C, Peters BAM (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, **362**, 53–56.

Van Noordwijk M, Brouwer G (1993) Gas-filled root porosity in response to temporary low oxygen supply in different growth stages. *Plant and Soil*, **152**, 175–185.

Van Noordwijk M, Brouwer G, Harmanny K (1993) Concepts and methods for studying interactions of roots and soil structure. *Geoderma*, **56**, 351–375.

Van Noordwijk M, De Willigen P (1987) Agricultural concepts of roots: from morphogenetic to functional equilibrium. *Netherlands Journal of Agricultural Science*, **35**, 487–496.

Van Noordwijk M, Lawson G, Groot JJR, Hairiah K (1996) Root distribution in relation to nutrients and competition. In: *Tree–Crop Interactions — a Physiological Approach* (eds Ong CK, Huxley PA), pp. 319–364. CAB International, Wallingford.

Van Noordwijk M, Van de Geijn SC (1996) Root, shoot and soil parameters required for process-oriented models of crop growth limited by water or nutrients. *Plant and Soil*, **183**, 1–25.

Van Veen JA, Liljeroth E, Lekkerkerk LJA, Van de Geijn SC (1991) Carbon fluxes in plant-soil systems at elevated atmospheric CO_2 levels. *Ecological Applications*, **1**, 175–181.

Veen BW (1980) Energy cost of ion transport. In: *Genetic Engineering of Osmoregulation* (eds Rains DW, Valentin RC, Hollaender A), pp. 187–195. Plenum Press, New York, NY.

Watanabe A, Kajiwara M, Tashiro T, Kimura M (1995) Influence of rice cultivar on methane emission from paddy fields. *Plant and Soil*, **176**, 51–56.

Waterman PG, Mole S (1989) Soil nutrients and plant secondary compounds. In: *Mineral Nutrients in Tropical Forest and Savanna Ecosystems* (ed. Proctor J), pp. 241–254. Blackwell Scientific Publications, Oxford.

Watson A, Stephen KD, Nedwell DB, Arah JRM (1997) Oxidation of methane in peat: kinetics of CH_4 and O_2 removal and the role of plant roots. *Soil Biology and Biochemistry*, **29**, 1257–1267.

Whipps JM (1985) Effects of CO_2 concentration on growth carbon distribution and loss of carbon from the roots of maize. *Journal of Experimental Botany*, **36**, 645–651.

Young I, Blanchart E, Chenu C, Dangerfield M, Fragoso C, Grimaldi M, Ingram J, Monrozier LJ (1998) The interaction of soil biota and soil structure under global change. *Global Change Biology*, **4**, 703–712.

Zak DR, Pregitzer KS, Curtis P, Teeri JA, Fogel R, Randlett DL (1993) Elevated atmospheric CO_2 and feedback between carbon and nitrogen cycles in forested ecosystems. *Plant and Soil*, **151**, 105–117.