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Research review

The representation of root processes in models addressing the responses of vegetation to global change

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SUMMARY

The representation of root activity in models is here confined to considerations of applications assessing the impacts of changes in climate or atmospheric [CO₂]. Approaches to modelling roots can be classified into four major types: models in which roots are not considered, models in which there is an interplay between only selected above-ground and below-ground processes, models in which growth allocation to all parts of the plants depends on the availability and matching of the capture of external resources, and models with explicit treatments of root growth, architecture and resource capture. All models seem effective in describing the major root activities of water and nutrient uptake, because these processes are highly correlated, particularly at large scales and with slow or equilibrium dynamics. Allocation models can be effective in providing a deeper, perhaps contrary, understanding of the dynamic underpinning to observations made only above ground. The complex and explicit treatment of roots can be achieved only in small-scale highly studied systems because of the requirements for many initialized variables to run the models.

Key words: vegetation model, root, resources, water and nutrient uptake, allocation.

INTRODUCTION

This paper addresses those methods by which roots are generally represented in vegetation models and in particular considers the methods by which roots are considered in vegetation models simulating the effects of environmental changes, specifically changes in climate and/or atmospheric [CO₂]. Studies in this area are, at a minimum, generally concerned with the carbon (C) cycle and how it responds to changes in the environment (Cao & Woodward, 1998). However, the C cycle is dependent on other cycles such as those for water and nutrients, so models must, in some way, consider their interplay (Schimel *et al.*, 1997). There is a strong tendency in global-scale models to consider only, or primarily, the above-ground components of vegetation because these can be observed by satellites (Goward *et al.*, 1993), but this seriously restricts the capacity to understand any root-level controls on

vegetation responses. In addition, Jackson *et al.* (1997) estimated that as much as 33% of global annual net primary production (NPP) is used for fine-root production. Ignorance of such a large component of NPP, such as might occur by inferring total NPP from satellite observations alone, could therefore lead to significant errors in defining C fluxes through vegetation.

This paper describes a range of approaches taken in vegetation models that aim to include or define the roles of roots in determining vegetation responses to environmental changes. The component parts explicitly or implicitly contained in these models are shown diagrammatically in Fig. 1. Roots and mycorrhizas are concerned with the acquisition of water and nutrient resources from the soil and also the return of nutrients locked up in shoot and root litter. The energy requirements for acquisition are supplied by C allocated from the photosynthetic shoots, and both the photosynthetic supply and the C allocation are dependent on climate and C supply from the atmosphere.

The inclusion of root activity in vegetation models,

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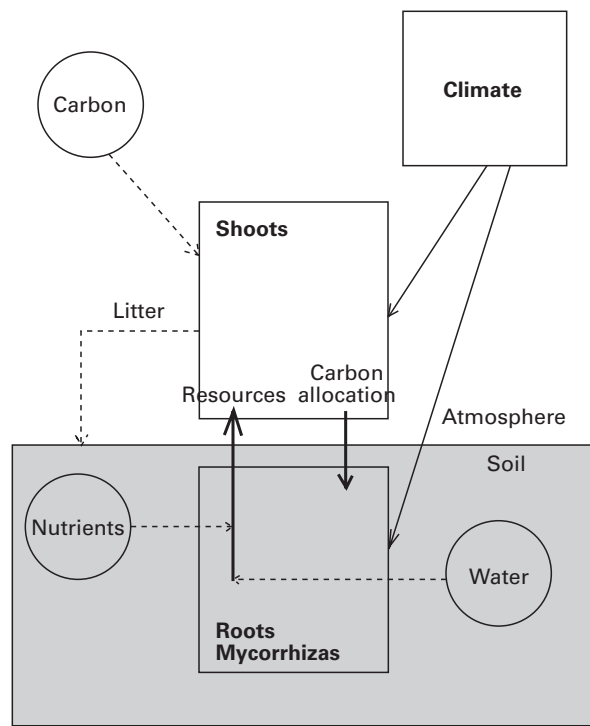


Fig. 1. Diagram of processes and influences on root activity as generally described in a range of vegetation models.

as outlined in Fig. 1, accrues from studies at the individual plant and root scale and also from understanding about soil processes, such as nutrient mineralization and water movement. Three major components to root activity have been recognized for inclusion in root models at the plant scale; these are nutrient uptake (Barber, 1995), allocation between above-ground and below-ground components (Brouwer, 1962), and root architecture (Lungley, 1973). Nutrient uptake is an essential component of whole-plant resource capture, and much research has investigated the dynamic nature of nutrient depletion zones around roots (Nye & Tinker, 1977) and, more recently, the interactions between nutrient and water availability in determining the dynamics of nutrient uptake (Ryel & Caldwell, 1998). However, the capacity for uptake of nutrients by plants has a direct energetic cost (BassiriRad, 2000) and, perhaps as a consequence, has an impact on the pattern of whole-plant allocation of resources (Barber, 1995). Allocation and uptake therefore require to be coupled in root simulations. The underlying philosophy of allocation is that allocation should occur so that there is a functional balance, or equilibrium, between shoots and roots (Brouwer, 1962). However, the underlying mechanism of allocation remains elusive (Farrar & Jones, 2000), and the notion that partitioning should, for example, maximize productivity is clearly not universally applicable (Reynolds & Pacala, 1993; Hunt *et al.*, 1998). The explicit inclusion of nutrient uptake in plant models could resolve the issue of whether

increasing atmospheric [CO_2] will, for example, change both the rates and the total quantities of nutrients taken up by plants. However, different models and experiments provide conflicting data on these responses (Hunt *et al.*, 1998), perhaps in part owing to uncertainty about allocation responses and costs. The loss of C from roots and associated mycorrhizal hyphae to the soil is a further component of allocation that is difficult to measure but might be a critical component of C sequestration by vegetation (Fitter *et al.*, 2000; Zak *et al.*, 2000). There is evidence that the degree of sequestration is not only dependent on C turnover in the soil but is also nutrient dependent (Wullschlegel *et al.*, 1994) and so model results are strongly dependent on the manner in which nutrients control allocation. This is clearly an area that requires further improvement and development, in terms of both modelling and experiment.

It is possible at the plant level to simulate the growth and development of root architecture (Lungley, 1973) and this emphasis can prove particularly fruitful. For example, it is often considered that root development is controlled primarily by temperature (Diggle, 1988; Jamieson *et al.*, 1998), but field observations (Fitter *et al.*, 1999) and model simulations that treat the growth in structure of the whole root system (Aguirrezabal & Tardieu, 1996) indicate that intercepted light rather than temperature dominates the control of root growth. This feature might prove to be a major failing of the many C-cycle models that model root growth as being controlled primarily by temperature.

Root dynamics are modelled simply in most regional and global-scale models concerned with the C cycle, usually within a compartmental model structure that also includes litter decomposition and nutrient mobilization. These models consider roots to be distributed in a small number of layers (from one to about five), which in some models are vegetation-specific and relate root activity to water depth and nutrient dynamics. Such models include CENTURY (Parton *et al.*, 1992), BIOME-BGC (Running & Coughlan, 1988), TEM (McGuire *et al.*, 1992) and NASA-CASA (Potter & Klooster, 1999). These models consider nutrient and water uptake by the vegetation and a fixed or variable allocation of production to above-ground and below-ground components of the vegetation. In these terms the models attempt to include the detail found in different plant-scale models of root activity but do not consider the impact of variations and development of root architecture.

The compartmental modelling approaches are here taken as the base from which increased realism, in considering root activity, is introduced in four specific examples of models investigating the impacts of this increased detail of root activity in modelling vegetation responses to climatic change.

ROOT PROCESS REPRESENTATIONS

Equilibrium approach

Table 1 indicates the basis of an approach (Schimel *et al.*, 1997) in which the C, water and nitrogen (N) cycles are considered to be in steady state, avoiding any considerations of dynamics and different response times of the cycles. Water availability is critical for plant growth and also for the mineralization and supply of nutrients, and therefore high and positive correlations are expected (Table 1) between evapotranspiration, NPP and the rate of N mineralization from the soil. In a similar fashion, high N inputs to ecosystems are also strongly correlated with high rates of evapotranspiration. These correlations (Table 1) indicate that, for example, increases in N deposition increase ecosystem NPP, whereas changes in climate that decrease water supply and evapotranspiration cause the reverse response. Such approaches often ignore interactive effects, such as those between [CO₂] and precipitation, even though it is well established that such effects occur.

Supply and demand

The equilibrium approach to root processes has no explicit treatment of roots or of their spatial extent. However, roots vary considerably in their depth

Table 1. *Correlations between evapotranspiration (ET) and net primary productivity (NPP) and components of the nitrogen cycle: N_{min}, N mineralization; N_{input}, N inputs to ecosystems; N_{gas}, trace gas losses of N; NO₃, nitrate leaching (from Schimel *et al.*, 1997)*

	NPP	N _{min}	N _{input}	N _{gas}	NO ₃
ET	0.71	0.76	0.96	0.71	0.33

(Canadell *et al.*, 1996) and therefore in their capacity to take up water and nutrients. Optimization theory would suggest that, at any location, plants should optimize the root depth such that an optimal balance is achieved between the allocation of NPP to roots, the capacity of these roots to provide water through the growing season and the attainment of a maximum NPP. This requires a certain balance of photosynthate allocation between shoot and root, which maximizes the balance of both water uptake and photosynthetic gain (Kleidon & Heimann, 1998). The approach taken by Kleidon & Heimann (1998) for estimating maximum rooting depth at the global scale depends on a simple balance between the supply of water from the soil and the demand for water loss to the atmosphere by transpiration (Table 2). The first drought factor indicates the basic philosophy of the approach, whereas the second drought factor indicates the variables that are calculated in the model. Whenever the drought factor $\alpha(D)$ declines, NPP is decreased because less of the absorbed photosynthetically active radiation is converted to NPP. The model responds by increasing root length to diminish this effect. As presented, the model needs to have a predetermined maximum root depth, but this could be calculated by explicit photosynthetic allocation responses between shoot and root.

Allocation approach

Fig. 1 shows the range of controls on the plant, and many observations indicate that plants adjust the allocation of photosynthate to different parts of the plant, with differing resources to capture, in a manner that maximizes growth (Iwasa & Roughgarden, 1984) or minimizes the effects of depleting resources (Sharpe & Rykiel, 1991). Table 3 describes the basic approach taken by Friedlingstein *et al.* (1999) to allocating NPP among the major resource capturing parts of plants and vegetation. The approach maximizes NPP by opti-

Table 2. *Equations used for calculating rooting depth (from Kleidon & Heimann, 1998)*

NPP calculation	$NPP(D) = \epsilon\alpha(D)PAR$
Drought factor 1	$\alpha(D) = \min\left[\frac{SUPPLY(D)}{DEMAND}; 1\right]$
Drought factor 2	$\alpha(D) = \min\left[\frac{cW(D)}{W_{max}(D)DEMAND}; 1\right]$

NPP(D), net primary productivity, limited by rooting depth (D); ϵ , light use efficiency; $\alpha(D)$, drought factor. In the first equation for calculating the drought factor, SUPPLY(D) is the soil water supply for transpiration and DEMAND is the atmospheric demand for transpiration. In the second equation for calculating the drought factor, c is the maximum rate of soil water supply, $W(D)$ is the plant-available water in the rooting zone and $W_{max}(D)$ is the maximum plant-available water in the rooting zone.

Table 3. Interactive allocation scheme for net primary productivity (NPP), based on resource type and availability (Friedlingstein et al., 1999)

Root allocation	$a_r = 3r_0 \frac{L}{L + 2\min(W, N)}$
Stem allocation	$a_s = 3s_0 \frac{\min(W, N)}{2L + \min(W, N)}$
Leaf allocation	$a_l = 1 - (a_r + a_s)$

$a_{r,s,l}$, the fractional allocation coefficients to root, stem and leaf; r_0 and s_0 , the fractional allocation coefficients to root and stem under non-limiting conditions; L , W and N , scalars of resource availability for light, water and nitrogen, ranging from 0.1 (severely limited) to 1 (readily available); $\min(W, N)$, the minimum of both W and N .

mizing the allocation of C to roots, stems and leaves, on the basis of the availability of the resources light, water and N. Light availability controls the allocation of NPP to stems, whereas the most limiting resource of either water or nutrients controls the allocation to roots. The leaves receive the residual amount of allocated NPP.

The explicit approach

The three approaches to representing roots in models so far discussed avoid explicit descriptions of root morphology, such as root density with depth, and of root architecture, such as the degree of root branching and the connection with mycorrhizal hyphae. Observations on plants (Aguirrezabal & Tardieu, 1996; Fitter *et al.*, 1999) indicate that including this detail is important, but it will be difficult to implement on the global scale for two reasons. The first is that the approach is particularly

complex for each location. The second is a measure of the usual problem at the global scale, a lack of information about the actual nature of root morphology and architecture in a wide range of vegetation types. However, including these components will have the greatest realism of the approaches described here. In addition this inclusion will permit more precise simulations of uptake zones through the whole root profile and indicate the costs to NPP of nutrient uptake by mycorrhizas, which are extensive and widespread on the global scale (Read, 1991).

The model selected for this section is that described by Grant (1998). The model simulates ecosystem energy exchange, canopy water relations, C fixation and phenology, nutrient uptake, plant growth and soil microbial activity. The approach is therefore very extensive, so only three of the components are outlined here (Table 4). The key point is that a particular process such as root growth is dependent on a wide range of interacting processes, such as root respiration, water relations and the supply and demand dynamics of the root and mycorrhizal mutualism. The rate of root growth is also determined by the rates of nutrient and C supplies to the growing area, whereas the flux of C to the mycorrhiza depends on the rate at which equilibration of C occurs with the mycorrhiza. C is usually transferred to the mycorrhiza, with N and P transfer occurring in the opposite direction. In addition to these processes, which are internal to the plant, the model also simulates nutrient flow in the soil and the depletion zones surrounding the roots. The model therefore includes processes that would typically be simulated in plant models (Barber, 1995) in addition to components that scale these responses to the canopy level.

Table 4. Basic equation of a model that integrates morphological dynamics of plant roots and mycorrhizal hyphae with a functional balance of allocation between roots and shoots (Grant, 1998)

Root growth/respiration	$R_{Ts,a,l,x,z} = \frac{R_R Z_{s,l,z,c} f_{Ts,l,z} f_{Os,l,z} \mathcal{J}_{s,a,l,x,z}}{\mathcal{J}_{s,l,z}}$
Root conductance	$\mathcal{J}_{s,a,l,1,r} = \frac{n_{s,a,l,1,r} r_{s,l,1,r}^A}{(d_{s,t} + d_{s,a,l,1,r})}$
Root: mycorrhiza transfer	$F_{s,l,r,m,k} = K_{s,m} F'_{s,l,r,m,k}$

In each equation the subscripts define the spatial resolution of the identifiers s , a , l , x and z , respectively, where s is species, a the shoot node from which the root axis originates, l the soil layer, x the order of root axis (primary or secondary) and z the 'root' type (r is root and m is mycorrhiza). $R_{Ts,a,l,x,z}$ is the total root respiration at maximum turgor, R_R is the maximum specific respiration and $Z_{s,l,z,c}$ is the storage C, N or P in the root or mycorrhiza. $f_{Ts,l,z}$ is a function for the effect of temperature on root activity, $f_{Os,l,z}$ is a function for the effect of oxygen transfer on activity and the \mathcal{J} variables are conductances of the roots to the storage components C, N or P. $n_{s,a,l,1,r}$ is the number of root axes of radius r and each of length d . $F_{s,l,r,m,k}$ is the actual flux of C, N or P between the mycorrhiza and root, and the F' is the equilibrium rate, with $K_{s,m}$ as a rate constant.

ROOTS AND ENVIRONMENTAL CHANGE

Equilibrium approach

In general, equilibrium approaches do not make explicit considerations of roots but, as shown in Table 1, root activity is implied by a calculation of evapotranspiration and consequent correlations with nutrient cycling. Smith *et al.* (1995) investigated the likely future responses of vegetation distributions to a range of future global circulation model (GCM) scenarios of climate (Table 5). The vegetation projections were based on Holdridge's climatic classification of vegetation types (Holdridge, 1967) in terms of temperature, precipitation and evapotranspiration. The GCMs differ in their range of climatological detail and spatial resolution but the OSU (Oregon State University) and GISS (Goddard Institute for Space Science) produce rather wetter future climates with a doubling in atmospheric $[\text{CO}_2]$. By contrast, the GFDL (Geophysical Fluid Dynamics Laboratory) and UKMO (UK Meteorological Office) models produce rather drier future climatic scenarios.

In the drier scenarios (Table 5) the area of mesic forest decreases and is replaced by dry forest; in the wetter scenarios the area of mesic forest increases, at the expense of drier vegetation such as grassland and dry forest. The essential differences in response

clearly relate to the capacity of the roots of mesic forest trees to take up and transpire the large quantities of water necessary for the survival of this vegetation type, which has a high leaf area index and corresponding evaporative loss (Woodward, 1987). It is interesting to note that the data in Table 1 also indicate that the high throughput of transpired water in this vegetation type will be related to high rates of N mineralization and NPP, both of which might be expected to fall under the drier scenarios.

Supply and demand

Kleidon & Heimann (1998) describe a simple approach (Table 2) to defining the volume of soil that roots can explore for water uptake. Rooting depth is clearly a difficult and variable component of vegetation to measure, but if the depth influences water uptake, then responses such as seen in the previous section, on equilibrium approaches, will also be affected. Field studies indicate rooting depths to at least 60 m (Stone & Kalisz, 1991), a depth that will rarely be measured in field campaigns. Jackson *et al.* (1999) have demonstrated water uptake to at least 18 m of depth below forests and consider that this capacity for deep uptake is critical when the surface availability of water, and perhaps nutrients, is small.

In many global-scale vegetation models, rooting

Table 5. Predicted changes in temperature, precipitation and the equilibrium distributions of major global vegetation types in response to global climatic change (from Smith *et al.*, 1995)

Model	Temperature (°C)	Precipitation (%)	Area (1000 km ²)			
			Tundra	Grassland	Dry forest	Mesic forest
OSU	2.8	7.9	-302	30	4	561
GISS	4.2	11.0	-314	694	487	120
GFDL	4.0	8.7	-515	969	608	-402
UKMO	5.2	15.0	-573	810	1296	-519

OSU, Oregon State University; GISS, Goddard Institute for Space Science; GFDL, Geophysical Fluid Dynamics Laboratory; UKMO, UK Meteorological Office.

Table 6. Influence of optimized rooting depth, at the global scale, on vegetation net primary production (NPP), evapotranspiration (ET) and runoff in response to current climate and a doubling of water-use efficiency (WUE) (a simple simulation of an increase in atmospheric $[\text{CO}_2]$) (from Kleidon & Heimann, 1998)

Model	Depth (m)	NPP (Gt C yr ⁻¹)	ET (mm d ⁻¹)	Runoff (mm d ⁻¹)
Standard, WUE × 1	1.0	60.0	1.0	1.2
Optimized, WUE × 1	6.9	69.6	1.2	1.0
Standard, WUE × 2	1.0	72.8	0.6	1.5
Optimized, WUE × 2	4.3	80.6	0.7	1.5

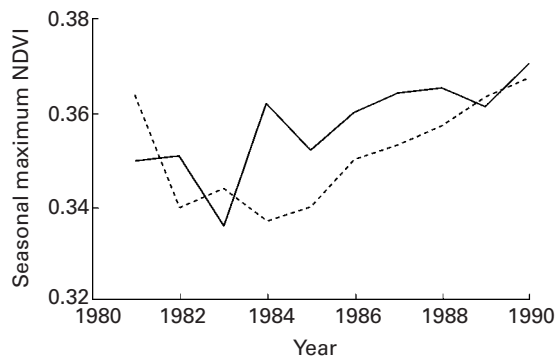


Fig. 2. Simulated changes in normalized-difference vegetation index (NDVI) by a vegetation model (broken line) (Osborne & Woodward, 2000), and observed by satellite (solid line) (Myneni *et al.*, 1997, 1998), for the Mediterranean region, where scrub is the dominant vegetation type.

depth is taken as a constant, typically between 1 and 2 m (Kleidon & Heimann, 1998). This means a limited volume of soil for the uptake of both water and nutrients. The question is then a matter of assessing how critical such an imposed limit might be on other components of vegetation activity, such as NPP and evapotranspiration. This was investigated by Kleidon & Heimann (1998) using the approach described briefly in Table 2 and applying it to two situations, the present climate and atmospheric $[\text{CO}_2]$ and a future situation in which vegetation water-use efficiency was doubled, such as might occur in response to an increase in atmospheric $[\text{CO}_2]$. A constant rooting depth of 1 m and an optimized rooting depth (Table 2) exert significantly different effects on NPP, evapotranspiration and runoff (Table 6). The optimized rooting depth was obtained by maximizing NPP (Eqn 1, Table 2) with respect to rooting depth (D , Table 2). In both the current and future simulations, optimized rooting depth is greater, and variably so with treatment, than the fixed depth of 1 m, and both NPP and evapotranspiration increase by between 11% and 18%. As a consequence, runoff decreases by between 5% and 16%. Models of vegetation with a constant, particularly shallow, rooting depth therefore tend to underestimate productivity and evapotranspiration and, as a consequence of the smaller volume of available water, are more subject to the effects of drought. Of course vegetation that is following a pathway of succession gradually increases its rooting depth towards an optimum and in this case the relative dynamics of leaf area and rooting depth increase have a major role in the responses to drought. Simulating the effects of increasing atmospheric $[\text{CO}_2]$, by an increase in water-use efficiency, reduces the difference between the standard and optimized cases and so it is feasible that a greater availability of NPP for allocation to above-ground growth might competitively favour a more shallow-rooted vegetation type.

Allocation approach

The allocation approach to defining root activity (Table 3) is the one most commonly found in vegetation models and is really an expansion of the supply and demand approach. This represents the ease with which models can be defined to measure the balance between NPP allocation and resource requirements. This is a feature that is difficult to achieve practically, because of the small dynamic changes in allocation and quantities of allocated NPP, which occur over critical periods of changing resources such as during drought (Luo *et al.*, 1994). Models have developed to high levels of complexity (e.g. Thornley & Cannell, 1997), perhaps too high for use outside intensely studied systems. However, the approach will indicate what is known and what is not known by experiment and observation.

The example chosen for this section addresses a question posed by observations from satellites. Myneni *et al.* (1997, 1998) analysed satellite time series of vegetation reflectance by using the normalized-difference vegetation index (NDVI). From 1981 to 1991 they observed significant increases in the NDVI of northern temperate vegetation, with the largest increases across the northern Mediterranean. This can be interpreted as indicating that vegetation is becoming more leafy (NDVI increases with vegetation leaf area index), and it was suggested that the trend was the result of higher temperatures and earlier spring growth. This would most probably be true at high latitudes, where growth is limited by low temperatures and snow cover (Myneni *et al.*, 1997). In the Mediterranean an increase in leaf area index and NDVI could also be caused by changes in the water balance of the vegetation (de Lillis & Fontanella, 1992). The likely environmental causes of the changes in the Mediterranean region can be investigated further by modelling.

Osborne *et al.* (2000) have described a process model of Mediterranean vegetation that has tested effectively against field observations. Carbon fixation, growth, allocation and water loss are incorporated in the model (a description of the model can be found at <http://www.shef.ac.uk/uni/academic/A-C/aps/medveg.pdf>). This model has been used to investigate the trends in NDVI for the Mediterranean region (Osborne & Woodward, 2000). In brief, the vegetation model (scrub and tree functional types) has been run with historical climatic data for the Mediterranean basin (New *et al.*, 2000). The leaf area index of the canopy and the fraction of bare ground are simulated and then their reflectivities in the red and far-red bands are used to calculate NDVI for comparison with satellite observations. Finally the changes in leaf area index are interpreted in terms of the vegetation response to changes in climate and atmospheric $[\text{CO}_2]$ (an

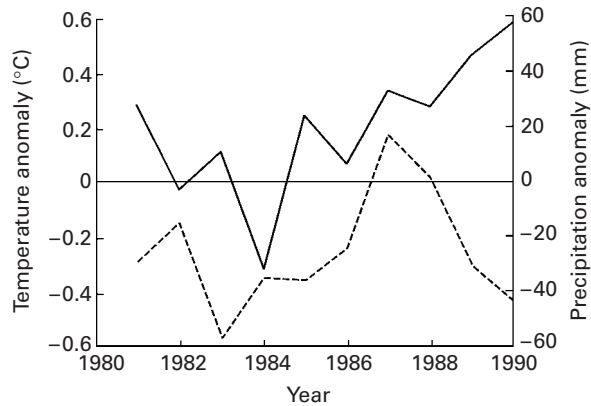


Fig. 3. Annual mean temperature (solid line) and total precipitation (broken line) anomalies from the long-term mean values from 1975 to 1995 and for the Mediterranean region.



Fig. 4. Simulated time series of annual maximum (typically achieved in May) leaf area index.

increase of 30 ppm by volume over the chosen time interval).

Over the period from 1981 to 1990, NDVI increased (Fig. 2). The same general trend was predicted by the vegetation model (Fig. 2), with some inter-annual differences. Thus the trend is repeated, also with an initial downturn in NDVI from 1981 to 1983. The climatic trends are rather more complex (Fig. 3), but there is a clear correspondence between temperature and NDVI. Simulated leaf area index (Fig. 4) is also closely correlated with NDVI, but in control runs with mean, rather than varying, temperature, the trends in leaf area index change rather little and the model yields no evidence of earlier spring growth. Therefore the notion that temperature is the major cause of the simulated change in leaf area index, and therefore NDVI, is rejected. However, precipitation exerts a significant effect on leaf area index in this evergreen vegetation type (Osborne & Woodward, 2000). Leaf area index is not equal in 1982 and 1990, when precipitation was broadly the same (Fig. 3) but both temperature and $[\text{CO}_2]$ (Osborne *et al.*, 2000) were higher. The increasing trend in leaf area index from 1985 is difficult to understand. However, essentially

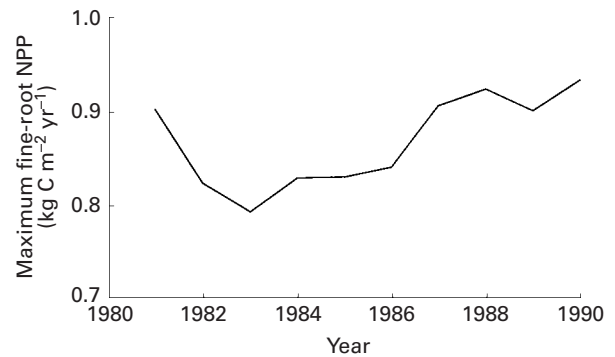


Fig. 5. Simulated changes in maximum annual fine-root net primary production (NPP).

the same trend is also seen for the fine-root NPP (Fig. 5). This indicates an increasing capacity of the plant to supply resources (primarily water in the Mediterranean climate) to support the higher rates of evapotranspiration associated with the higher leaf area index and higher temperatures. This response of the fine roots indicates a strong influence of increasing $[\text{CO}_2]$, which stimulates NPP and therefore root growth (Rogers *et al.*, 1994). This response is greatly diminished in simulations when $[\text{CO}_2]$ is maintained constant.

The simulations therefore support the observations of an increase in NDVI through the 1980s, although the impact of instrument drift cannot be discounted completely (Gutman, 1999). However, the increasing NDVI seems unlikely to be due to increasing temperature but rather to the combined effects of precipitation and atmospheric $[\text{CO}_2]$.

The explicit approach

The explicit approach to modelling root activity aims at defining growth and resulting morphological changes in root architecture and, in a complete simulation, changes in associated mutualistic mycorrhizal associations (Grant, 1998). The approach defined by Grant also incorporates a functional balance between roots and shoots in terms of C and nutrient allocation, indicating that this is a development from the widespread allocation approach. In addition, the fine detail and scale of the simulations also permit considerations of spatial and temporal variability in structure and function.

As indicated in the previous section, such a detailed approach must limit the general applicability of the model to well studied systems. Such a system and example are provided by the work of Grant *et al.* (1995) in interpreting the responses of wheat grown under two levels of irrigation within a free-air CO_2 enrichment (FACE) experiment. The FACE approach exposed wheat plants to two different values of $[\text{CO}_2]$ (370 and 550 ppm), but with no enclosure. The crop model of Grant was used to predict the effects of the different values of

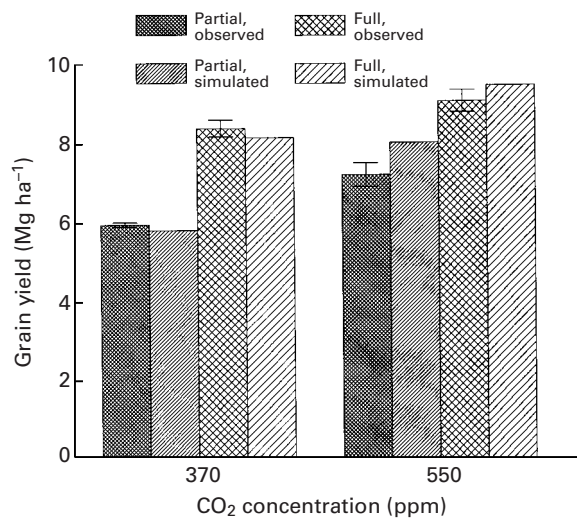


Fig. 6. Observed and simulated changes in wheat grain yield at two values of [CO₂] (370 and 550 ppm) and for full irrigation and partial irrigation. Observations are shown with one SE (from Grant *et al.*, 1995).

[CO₂] on wheat yield under treatments of high and low irrigation. Destructive growth analysis provided data for testing the model. Once the model had been initially parametrized it provided simulated results based entirely on current physiological understanding; any significant differences from observations indicated areas of uncertain knowledge, requiring further investigation.

Grain yield is the major product from growing wheat and its successful prediction has major economic benefits. Observed and predicted yields, under the two [CO₂] values and under two levels of irrigation, were very closely predicted by the simulation model (Fig. 6), indicating an adequate understanding of yield responses to both CO₂ enrichment and variations in irrigation. Unfortunately a large number of constants (24 for just CO₂ exchange (Grant *et al.*, 1995)) are required to initialize the model, indicating its highly specific use. There is also the possibility that interesting and novel effects of [CO₂] might actually be smoothed away by such a stiff selection of variables and that an imprecise definition of variables could lead to significant error propagation.

DISCUSSION

Quantifying roots in the soil is the hardest task by far when analysing the growth of plants and vegetation. There are global budgets of roots (Jackson *et al.*, 1996, 1997) but there are major underestimates of fine-root biomass, which is difficult to extract from soil (Hendrick & Pregitzer, 1993). This also creates major problems in measuring vegetation net primary production, as fine-root production might be a large fraction of NPP (e.g. up to 66% of NPP in *Abies* forest (Grier *et al.*, 1981)). No remote sensing

techniques are available to fill in the gaps between sparse measurements, such as are available for the above-ground component of vegetation. These distinctive features suggest a rich field for the application of root models to understanding their global characteristics and, in the chosen context of this paper, their responses to global change. A survey of the methods employed in simulating root behaviour in models indicates a rather restricted approach with no strong evidence that modelling is providing new ideas for experiments and observations to address. In comparison, above-ground modelling has often proved to be in advance of empirical understanding (Betts *et al.*, 1997). The explanation of such marked differences in development are not completely clear. However, very strong correlations between major root activities in terms of resource capture (Fig. 1) indicate that an efficient treatment of one characteristic, for example transpiration, inevitably leads to an adequate treatment of another, such as nutrient uptake.

Global scale models might, however, be too simplistic in their treatment of roots. Kleidon & Heimann (1998) indicate that the common, and unwarranted, consideration of root depth as a global constant of 1 m can lead to underestimates of primary productivity and evapotranspiration, in comparison with more realistic and variable root depths. However, even here the effects might only just exceed 10%, as for NPP (Kleidon & Heimann, 1998), which is itself known with even less accuracy.

In all environments conducive to growth there is an interplay and variability in the availability of resources for growth and development. Obvious examples are light, water and nutrients. Variation in the supply of any of these resources leads to changes in the allocation of growth to minimize shortages of resource supply (Sharpe & Rykiel, 1991). The effects of such changes in allocation are easy to simulate (Friedlingstein *et al.*, 1999) but are much more difficult to measure in experiments in which the status of resources can be changing continually. In addition, it is actually difficult to measure and to define the appropriate measurement quantity of, a resource. Whether plants actually do optimize their photosynthate allocation to equalize resource supply is a moot point (Friedlingstein *et al.*, 1999) and one worth investigation. Although the benefits of resource acquisition are well characterized, the costs are less clear. However, the continued and strong correlations between the major resource fluxes through leaves and roots (Gifford, 1992) indicate that the optimization approach always provides a reasonable simulation of plant response. Cannell & Thornley (1998) take a different line, indicating that simple ecosystem models are inadequate for simulating responses to [CO₂]. They show, for example, that when considering nutrient acquisition it is critical to consider all C inputs to the soil, the mass

and activity of soil microbial biomass, in addition to explicit and separate treatment of C and N substrates, transport and different pools. Cannell & Thornley (1998) champion the use and development of complex models, not because they simulate complex processes but because many simple processes must be simulated comprehensively. The same conclusion can be drawn from the models developed by Grant (1998), who also considered the importance of mycorrhizas in nutrient and C dynamics, a feature that seems to be absent, at least explicitly, from the model of Cannell & Thornley (1998), even in low-nutrient soils in which mycorrhizas are critical in nutrient cycles (Read 1991).

The approaches taken by Cannell & Thornley (1998) and Grant (1998) have proved successful in their particular applications. However, these are very restrictive because many variables need to be initially quantified before the simulations can proceed. This severely limits their application to small-scale, well characterized systems. At the global scale such approaches are impossible, but the moderate success of all approaches, even those that ignore roots completely, perhaps indicates that it is unlikely that root processes will be a major concern for future development at large spatial scales.

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