



Roots: evolutionary origins and biogeochemical significance

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Abstract

Roots, as organs distinguishable developmentally and anatomically from shoots (other than by occurrence of stomata and sporangia on above-ground organs), evolved in the sporophytes of at least two distinct lineages of early vascular plants during their initial major radiation on land in Early Devonian times (c. 410–395 million years ago). This was some 15 million years after the appearance of tracheophytes and c. 50 million years after the earliest embryophytes of presumed bryophyte affinity. Both groups are known initially only from spores, but from comparative anatomy of extant bryophytes and later Lower Devonian fossils it is assumed that, during these times, below-ground structures (if any) other than true roots fulfilled the functions of anchorage and of water and nutrient acquisition, despite lacking an endodermis (as do the roots of extant *Lycopodium* spp.). By 375 million years ago root-like structures penetrated almost a metre into the substratum, greatly increasing the volume of mineral matter subject to weathering by the higher than atmospheric CO₂ levels generated by plant and microbial respiration in material with restricted diffusive contact with the atmosphere. Chemical weathering consumes CO₂ in converting silicates into bicarbonate and Si(OH)₄. The CO₂ consumed in weathering ultimately came from atmospheric CO₂ via photosynthesis and respiration; this use of CO₂ probably accounts for most of the postulated 10-fold decrease in atmospheric CO₂ from 400–350 million years ago, with significant effects on shoot evolution. Subsequent evolution of roots has yielded much-branched axes down to 40 µm diameter, a lower limit set by long-distance transport constraints. Finer

structures involved in the uptake of nutrients of low diffusivity in soil evolved at least 400 million years ago as arbuscular mycorrhizas or as evaginations of 'roots' ('root hairs').

Key words: Devonian, endodermis, phylogeny, Silurian, weathering.

Introduction

The evolution of 'the root' has attracted much less attention than that of 'the shoot'. This is particularly true of the evolutionary origin of the root, where the limited economic significance of the lower vascular plants is one of the factors constraining consideration of this topic. Furthermore, roots may be less readily fossilized than shoots, and the fossil record is, as we shall see, not very helpful. The position was well put in the following quotation from Gifford and Foster. 'The differentiation between distinct root and shoot systems in most living vascular plants is of considerable interest from an evolutionary viewpoint. It is now rather generally agreed that this differentiation did not exist in such Devonian land plants as *Horneophyton* and *Rhynia*. In these archaic organisms portions of the underground system of stems apparently served physiologically as roots. It seems reasonable to postulate that roots were acquired later in the evolution of vascular plants. However, the steps in the evolutionary divergence of roots from primitive shoots, which led to the acquisition of a root cap, a prevalent internal or endogenous origin of roots, and the retention of a primitive type of vascular system, are unfortunately obscure today' (Gifford and Foster, 1987). More recently, Fitter and Moyersoen wrote, 'Complex root systems have

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been a feature of land plants for a long time, although the fossil record is unclear as to exactly how long' (Fitter and Moyersoen, 1996).

This review considers root evolution by attempting to define the root and, in so doing, delimiting its difference from the shoot, and by considering the functions of the roots of extant plants and cases in which 'root' functions are performed by non-root structures. The article then considers the fossil history of vascular plants and the environment in which they evolved, the time at which true roots first appear in the fossil record, and the role of roots and root-like structures which fulfil root functions in modifying global biogeochemistry and its influence on shoot evolution.

What is a root?

The anatomical and morphological material assembled here comes from many sources (Bell, 1991; Bierhorst, 1971; Cutter, 1971; Eames, 1936; Eames and MacDaniels, 1947; Esau, 1953; Fahn, 1974; Gifford and Foster, 1987; Goebel, 1930; Groff and Kaplan, 1988; Raven, 1977, 1984*a, b*, 1986, 1993, 1995*a*, 1997).

Roots are axial multicellular structures of the sporophytes of vascular plants which usually occur underground, have strictly (root cap notwithstanding) apical elongation growth, and generally have gravitropic responses which range from positive gravitropism to diagravitropism, combined with negative phototropism. Developmentally, the apical meristem of one (most lower vascular plants) to many (all seed plants) dividing cells produces a root cap acropetally and initials of the stele, cortex and epidermis basipetally. The branching of roots involves the endogenous origin of new root apical meristems in the pericycle or, in many ferns (e.g. *Marsilea*), the endodermis of the parent root. The lateral roots emerge from the pericycle through the endodermis or from the endodermis (when present, as it usually is), then pass through the cortex and the epidermis. Roots do not have superficial production of cells or tissues other than unicellular enations (root hairs). The primary stele of roots is generally a protostele (i.e. a solid cylinder of xylem, with or without parenchyma cells), often with convolutions of the stele-pericycle interface to produce an actinostele. There are roots which have a central pith with peripheral vascular tissue within the endodermis; examples are most monocotyledonous angiosperms. Roots do not have the segmentation of the axis between (superficial) leaves on the stem which is typical of shoots (\equiv stems plus leaves plus sporangia and their modifications such as strobili and flowers and their derivatives, seeds and fruits) to produce internodes between nodes. Roots arise from the embryonic axis, from other roots or stems; the latter is where all roots originate in non-seed vascular plants.

The root cap is thought to be a source of lubrication to the growing root apex, and a means of causing adherence of mature roots to soil particles via the production of mucilage, while living detached root cap cells (root border cells) may act as a means of manipulating the microbiota of the rhizosphere (McCully, 1999; Hawes *et al.*, 2000). The root cap is also involved in graviperception.

Shoots, which are the other organ system of vascular plants, contrast with roots by being typically above-ground and their gravitropism ranges from negatively gravitropic to diagravitropic. The shoot apical meristem does not produce a (root) cap. The branching of shoots, including the production of leaves, is superficial (exogenous). The primary vascular tissue is sometimes a protostele, more usually a siphonostele or dictyostele (i.e. both with a pith, and a more or less dissected hollow cylinder of vascular tissue). An endodermis is less frequently present in shoots than in roots. Shoots growing in air can (as can the much less common aerial roots) have intercalary as well as apical elongation growth since they do not have the buckling problems which below-ground organs with intercalary growth would have as they grow through a much more resistant medium than air (Gill and Tomlinson, 1975). Shoots with intercalary growth growing negatively gavitropically, or diagravitropically can have problems with posture maintenance since by definition an extension zone must rely on a hydrostatic rather than a rigid skeletal system; aerial roots which grow downwards have no such problems. Shoots can generally give rise to roots (as well as shoots); roots more rarely give rise to shoots (Groff and Kaplan, 1988).

The distinguishing features of the roots (as compared to the shoots) of vascular plants are thus the occurrence of a root cap, a more defined lineage of cells from the apical cell(s) to tissues in the more mature parts of the roots, the essentially universal occurrence of an endodermis, a protostele (sometimes with a pith) and endogenous origin of lateral roots from roots (Table 1). Many root systems show localized root proliferation in response to spatial variability in resource availability (Robinson, 1996; Robinson *et al.*, 1991, 1998; Zhang and Forde, 1998).

Groff and Kaplan, in their excellent critical review of the concept of roots versus shoots in vascular plants (Groff and Kaplan, 1988; see also Goebel, 1930), very wisely discourage the use of the term 'adventitious' as applied to roots, since it can imply that the production of roots by stems is always abnormal, whereas it is the norm in many plants. Similarly, the use of 'primary' is discouraged in the context of root systems, since it can mean either 'the first root' or 'the persistent root' (Groff and Kaplan, 1988). These authors also counsel that the production of shoots from roots is not to be regarded as anomalous.

In the context of production of shoots by roots, it is instructive to consider N₂-fixing leguminous root nodules; these are essentially shoot-like structures which are produced by the roots of many members of the Fabaceae in the presence of appropriate rhizobia (Sprent, 1989; Mathesius *et al.*, 1998; Gualtieri and Bisseling, 2000). The legume nodules develop from primordia that are initiated in the cortex and have peripheral vascular bundles and central symbiotic tissue. However, it is important to note that some legumes can form rhizobial nodules on shoot (stem) tissue as well as on roots (Parsons *et al.*, 1993, 1995). Furthermore, the same rhizobial signal molecules (Nod factors) can induce the production of N₂-fixing nodules on the roots of the non-leguminous angiosperm *Parasponia* (Ulmaceae); these nodules are root-like with central vascular tissue and peripheral (cortical) symbiotic tissue, although they have no root cap tissue (Gualtieri and Bisseling, 2000). These rhizobial nodules of *Parasponia* have developmental and anatomical similarities to the actinorhizal (*Frankia*-containing) N₂-fixing nodules of members of the Rosid 1 clade families Rosaceae, Eleagnaceae, Rhamnaceae, Betulaceae, Casuarinaceae, Myricaceae, Coriariaceae, and Datisceae (noting that the rhizobially nodulating families Fabaceae and Ulmaceae are also in the Rosid 1 clade): (Gualtieri and Bisseling, 2000). Thus, actinorhizal nodules have central vascular and peripheral symbiotic tissue, and originate from root pericycle tissue, but lack a root cap (Gualtieri and Bisseling, 2000).

These examples of the production of shoots by roots mean that the phylogeny and the ontogeny of roots do not abolish their potential to produce shoot tissue.

Finally, Groff and Kaplan (Groff and Kaplan, 1988) recall the concepts of allorhizy and homorhizy (Goebel, 1930). Allorhizy denotes the development of shoot and root at opposite ends of the embryonic axis, as in extant

seed plants, while homorhizy denotes root development which is lateral with respect to the longitudinal axis of the embryo, as in extant lower vascular plants. Later this study returns to Goebel's concepts in the context of the monophyletic or polyphyletic origin of roots (Goebel, 1930).

The functions of roots in extant plants in relation to the capabilities of other below-ground plant structures

What do roots do in extant plants?

In addressing this question it is necessary to examine the occurrence of roots in extant plants, and of how the functions of roots are fulfilled in rootless plants in habitats where root functions are needed. The traditionally recognized root functions are anchorage (Niklas, 1992; Ennos, 1993; Ennos and Fitter, 1992; Berntson, 1994), and the uptake and longitudinal movement of water and mineral nutrients (Clarkson, 1985; Varney and Canny, 1993; Marschner, 1995). Even when roots are well developed some of these root functions may be partly performed by other structures. Thus, in rhizomatous plants, the below-ground rhizome may have had a role in anchoring the plant, while the fungal components of mycorrhizas may supplement or replace root hairs as the root components which increase the area of absorptive surface per unit of below-ground biomass (see below) (Clarkson, 1985; Caldwell and Richards, 1986; Fitter, 1987, 1996; Moteetea *et al.*, 1996; Smith and Read, 1997; Blackwell, 2000; Redecker *et al.*, 2000).

There are clearly constraints on the optimization of the various functions of roots in relation to the resource costs of producing and maintaining the roots as a function of their structure and, especially, their diameter. Thus, the

Table 1. Relationships of characteristics among the 'original axis' (above- and below-ground) of early vascular plants, and the shoots and roots of extant plants

Data from Bell (1991), Cutter (1971), Damus *et al.* (1997), Duckett *et al.* (1996), Eames (1936), Eames and MacDaniels (1947), Esau (1953), Fahn (1974), Gifford and Foster (1987), Goebel (1930), Groff and Kaplan (1988), Raven (1977, 1984a, 1986, 1993, 1995a, 1997), and Schneider (1996).

Characteristic	Shoot of extant plants	'Original axis' of early vascular plants	Root of extant plants
Primary xylem	Protostele in some pteridophytes; pith present in other vascular plants	Protostele	Non-medulated protostele (except some monocotyledons with central pith, i.e. medullated)
Root cap	Absent	Absent	Present
Hairs	Varied 'shoot hairs' usually present	'Axis hairs'; mycorrhizas on below-ground parts	'Root hairs'; often supplemented by mycorrhizas
Origin of branches	Superficial origin of branch shoots. Roots originating from shoots can be endogenous or exogenous	Superficial origin	Endogenous origin of branch roots. Shoots originating from roots can be endogenous or exogenous
Endodermis in organs lacking secondary thickening	Usually absent; present in many pteridophytes, some spermatophytes	(Apparently) absent	Present in almost all cases; sometimes supplemented by an exodermis (endodermis-like hypodermis)

absorptive (and anchorage) functions are maximized per unit of root biomass by small root diameter (Silberbush and Barber, 1983; Boot, 1989; Clarkson, 1985). However, the analysis of Silberbush and Barber showed that an even more important root attribute in maximizing the uptake of slowly-diffusing solutes is root elongation rate (Silberbush and Barber, 1983). Thus, for a nutrient such as phosphate in well-aerated soil, with phosphate binding to oxidized iron minerals, and a very low diffusion coefficient for the solute in soil, root elongation rate is very important in determining uptake of phosphate since it determines access to unexploited volumes of soil. However, Table 2 shows that, for the range of diameters of below-ground roots for which data are available, the larger diameter roots have the most rapid elongation rate. While there seems to be no mechanistic basis for this correlation, its existence shows that root diameter and root elongation rate are not independent variables, at least for the plants (all cultivated grasses) in Table 2. It is of interest that the correlation of extension rate and root diameter for cereals in Table 2 contrasts with hypotheses and data on slow-growing 'magnolioid' roots with a diameter up to 1.5 mm in the absence of secondary thickening and with a great dependence on mycorrhizas in the flowering plants (Baylis, 1975; St John, 1980). These are contrasted with faster-extending, smaller-diameter 'graminoid' roots with a greater potential to produce root hairs and less dependence on mycorrhizas (Baylis, 1975).

A further correlation with root diameter is that roots of smaller diameter may have higher construction costs and maintenance costs on a unit biomass basis than do larger diameter roots (Eissenstaadt and Yanai, 1997). This adds to the costs of producing and maintaining small diameter roots to set against the benefit, in nutrient-uptake terms, of a large surface area per unit biomass and the constraint on nutrient-uptake capacity due to their

lower growth rate. Smaller diameter roots are also more likely to be determinate in their growth and to live for a shorter time than is the case for roots of larger diameter (Eissenstaadt and Yanai, 1997; Skene, 1998, 2000). This also impacts on the mechanical effectiveness of roots, with the increased surface area for functional contact per unit biomass of smaller roots offset, in terms of mechanical benefit per unit construction cost, by their shorter lifespan.

After absorption of nutrient solutes and water by a root zone, the major fraction of the nutrients and water is transported axially toward the shoot in the xylem. Growth and maintenance of roots requires that photosynthate moves to them in the phloem. In both xylem and phloem mass flow of solution occurs along the conduits, and the Hagen-Poiseuille equation shows that the flux of solution along a conduit under a given hydrodynamic driving force is proportional to the fourth power of the radius of the conduit (Fitter, 1987; Varney and Canny, 1993; Varney *et al.*, 1991; Raven, 1999a, b). This constraint on axial flow in very small conduits imposes a lower limit on the diameter of roots, in that a root functional in axial conduction must have at least one xylem element and one phloem element, each with more than a certain minimum radius (Raven, 1999a, b).

Roots must also (with very few exceptions) have living cells in the stele associated with the xylem and phloem conducting elements, an endodermis, one or more layers of cortex, and an epidermis (Peterson, 1992; Damus *et al.*, 1997; Aloni *et al.*, 1998; Peterson and Cholewa, 1998; Raven, 1999a, b). In addition to these constraints on the minimum *number* of living cells in the radius of a root, there are also constraints on the minimum *size* of each of these living cells imposed by cost-benefit and other considerations (Raven, 1999a, b). Taken together, these constraints mean that the smallest radius of indeterminate roots of extant plants (20–25 μm ; Fitter, 1987; McCully,

Table 2. Linear elongation rate of roots, root hairs, fungal hyphae and other structures as a function of the diameter of the organ and the medium (soil, air) in which elongations occurs

Determinants of the elongation rate of roots are discussed by Barlow (1973), Canny (1973), Lyndon (1973), Passioura and Ashford (1974), Cahn *et al.* (1989), Varney *et al.* (1991), Bret-Harte and Silk (1994), and Pritchard (1994). The very rapid elongation of aerial roots of *Cissus* can be related to the large number of enlarging cells in the 1 m long elongation zone. This long elongation zone is permitted in aerial structures where buckling, such as would occur in below-ground structures with a long elongation zone, is not a consideration.

Structure	Diameter	Extension rate	Reference
Main root axis of small-grain cereal	0.4–0.7 mm	20 mm d ⁻¹	Scott (1977)
First order lateral root axis of small-grain cereal	0.2 mm	5 mm d ⁻¹	Scott (1977)
Second order lateral root axis of small-grain cereal	0.05–0.1 mm	1 mm d ⁻¹	Scott (1977)
Main root axis of the large-grain cereal <i>Zea mays</i>	1 mm	60 mm d ⁻¹	Scott (1977)
Root hairs	10–15 μm	2 mm d ⁻¹	Scott (1977); Sievers and Schnepf (1981)
Arbuscular mycorrhizal hyphae	2–27 μm	3 mm d ⁻¹	Smith and Read (1997)
Ectomycorrhizal hyphae	2–3 μm	2–4 mm d ⁻¹	Smith and Read (1997)
Free-hanging aerial roots of <i>Cissus</i> spp.	1 mm over length of 8 m; elongation zone 1 m long	240 mm d ⁻¹	Gill and Tomlinson (1975)
Underground stem (rhizome) of <i>Pteridium</i>	3 mm	3 mm d ⁻¹	Harper (1977); Page (1982)

1999; Varney and McCully, 1991) can be rationalized, in functional terms, with roots of rather smaller radius possible if there is no endodermis (Damus *et al.*, 1997).

While endodermis has been cited as an essential functional feature of roots, it is noted that the extant *Lycopodium* lacks an endodermis in its roots (but not in its shoots) (Damus *et al.*, 1997), and that well-preserved fossil sporophytes of vascular plants (and other polysporangiate plants) do not have identifiable endodermis until the Carboniferous (Walton, 1940; Raven, 1984b, 1994b). Furthermore, such physiological work as has been performed on *Arabidopsis thaliana* mutants lacking a root endodermis (e.g. with mutation in the *SHORT-ROOT* (*shr*) gene) shows no significant functional impact on Ca transport to the shoot (Benfey *et al.*, 1993; Scheres and Benfey, 1999; White *et al.*, 2000).

This argument, as to the minimum size of multicellular underground absorptive and anchoring organs, has been couched in the context of the functional anatomy of roots. However, there seems to be no reason why stem (i.e. shoot components) structures could not be miniaturized to the same extent as the smallest extant roots, provided that they had a protostelic structure of their vascular tissue (Raven, 1999a). Clearly, an endodermis could be accommodated in such a small shoot radius just as is the case for roots. However, there seem to be no known below-ground shoot structures with as small a radius as these very small-radius roots. Any such small-radius stems with an endodermis occurring below ground could only with difficulty be distinguished from roots except for the absence of a root cap (Table 1), since these very small-radius structures are probably too small to branch, and thus be distinguished by exogenous rather than endogenous branching. Such small-radius stems would certainly have to be protostelic (Table 1).

Structure and function of root hairs and mycorrhizas

There are potential advantages in having diameters of nutrient-absorbing structures which are less than that consistent with the structure of roots. The argument here is an extension of that used above for roots. The uptake of a nutrient with low concentration and low diffusion coefficients in soil (e.g. phosphate in aerobic soils) has a higher uptake rate per unit biomass if that biomass is allocated to structures of smaller diameter (Silberbush and Barber, 1983; Clarkson, 1985; Boot, 1989; Harrison and van Buuren, 1995; Allaway and Ashford, 1996; Ashford *et al.*, 1996; Eissenstadt and Yanai, 1997; Gilroy and Jones, 2000; Hodge *et al.*, 2000; von Wirén *et al.*, 2000).

Based on the orders of magnitude of the diameters of roots, root hairs and mycorrhizal hyphae in Read (Read, 1999; p. 171) a 2 µm diameter mycorrhizal hypha would have a 100 times greater surface area per unit biomass

Table 3. Cytoplasmic streaming speed in relation to the diameter of the spherical or cylindrical cells in which it occurs; temperature 20–25 °C

Organism, cell	Cell diameter (µm)	Streaming speed (µm s ⁻¹)
<i>Chara braunii</i> cylindrical internodal axial or 'leaf' cells	400	105
	150	67
	80	50
<i>Acetabularia calyculus</i> cylindrical 'shoot' cell	500 µm	2.5–6.0
<i>Elodea canadensis</i> spherical leaf cells	30 µm	3–10
Higher plant root hairs	10–15 µm	4–10

References: Raven (1984c); Stebbins and Hyams (1979); Amos and Amos (1991); Table 2.

(volume), and a 20 µm diameter root hair 10 times greater surface area per unit biomass (volume), than a 200 µm diameter root. While these very small diameter 'unicellular' structures have advantages in terms of acquisition of resources such as phosphate by their increased surface area per unit biomass, they may have corresponding costs. One is that axial fluxes of solutes by cytoplasmic streaming may scale with cell diameter (Table 3). Another is that root hairs and mycorrhizas have a slow elongation rate (and thus a slow rate of exploitation of unexplored volumes of soil) (Table 2) and (at least for most root hairs) a short life-span, thus limiting the quantity of nutrient acquired per unit resource allocated to the structure (Eissenstadt and Yanai, 1997), at least as far as components (e.g. walls of root hairs) which cannot be recovered by the plant by disassembly and translocation to the longer lived parts of the plant are concerned (see below).

Rootless rhizophytes: the function of roots performed by non-root structures in rootless organisms

Putting anchoring and absorbing structures into a wider context, it is important to remember that vascular plants rooted in soil on land belong to the large life form category known as rhizophytes (Raven, 1981, 1983, 1984a, b, 1986; Raven *et al.*, 1998). These organisms, with plant structures in the soil or sediment which are large relative to the grain size of the soil or sediment, include a wide range of structures produced by photosynthetic organisms other than the roots (and root hairs and mycorrhizas) of terrestrial sporophytes of vascular plants. Even among the extant sporophytes of terrestrial vascular plants some (*Psilotum*, *Tmesipteris*) lack roots despite living in soil or epiphytically; here shoot structures with 'root hairs' and mycorrhizas are functional replacements for roots.

Roots are retained by most vascular plant sporophytes after they have moved back to live in water, even when

they cease to be rhizophytes. Thus, while *Utricularia* and *Ceratophyllum* lack roots, the Lemnaceae usually retain roots despite being much-reduced pleustophytes (free-floating plants: Raven, 1981, 1999a), while the freshwater Podostemaceae and certain seagrasses (*Phyllospadix* spp.; some specimens of *Amphibolis* spp.) are haptophytes, with their roots modified as holdfasts with no special role in nutrient uptake, since haptophytes are benthic plants attached to substrata of a grain size much larger than the attaching organ, and often larger than the whole organism (Raven, 1981, 1999a). Among these extant vascular plant sporophytes the absence of roots is apparently a derived condition.

The free-living gametophytes of the homosporous free-sporing vascular plants are also rhizophytes, with the anchoring and absorptive structures comprising just the rhizoids (analogous to root hairs) of photosynthetic representatives, while non-photosynthetic taxa have fungal associates analogous to mycorrhizas (Raven, 1981, 1986, 1999a). No multicellular below-ground structures have been found in the gametophytes of now extinct Lower Devonian vascular plants (or of close, now extinct, polysporangiophyte relatives of the early vascular plants) with many homiohydric features, i.e. an endohydric conducting system, cuticle, stomata and intercellular gas spaces (Taylor and Taylor, 1993; Remy *et al.*, 1997).

The vascular plants (tracheophytes) are embryophytes; the other extant embryophytes are at the bryophyte grade of organization, and include the mosses, liverworts and hornworts (Gray, 1985; Kenrick and Crane, 1997). Here the sporophyte phase retains its early parasitism on the gametophyte phase throughout its life, so anchoring to, and absorption from, non-living substrata is essentially a gametophyte function in bryophytes.

While many aquatic, and some terrestrial, bryophytes are haptophytic, a majority are rhizophytic. The gametophyte phase of bryophytes often comprises multicellular structures on the land surface, with below-ground structures (rhizoids) comprising cylindrical evaginations of cells of the lower epidermis (sometimes with transverse walls). However, the Polytrichaceae and some other mosses have diageotropic rhizomes at or just below soil level as parts of axes continuing as leafy aerial shoots; the rhizomes bear rhizoids. Furthermore, the occurrence of below-ground positively gravitropic multicellular (parenchymatous) cylindrical branched structures in *Takakia* and *Haplomitrium* has been demonstrated (Grubb, 1970). While both genera were formerly regarded as liverworts, *Takakia* is now considered to be a moss (Smith and Davison, 1993; Kenrick and Crane, 1997). These 'roots' of bryophyte gametophytes lack a root cap, although the 'roots' become mucilage-covered in dry conditions (Grubb, 1970). *Takakia* and *Haplomitrium* 'roots' have a central cylinder of elongate cells, but, unlike the corresponding cells in the shoots of these plants, the central

elongate 'root' cells are alive at maturity (Grubb, 1970) and so do not strictly function in the endohydric conducting system of these organisms. Grubb suggests that the superficial origin of branches in these 'roots' of bryophytes resembles that of the rhizospheres in the sporophyte phase of the vascular plant *Selaginella*, and that endogenous origin of branches is not a good criterion of the 'root' rather than 'shoot' nature of a structure (Grubb, 1970). The occurrence and roles of mycorrhizas in embryophytes of the bryophyte grade of evolution have been discussed; arbuscular mycorrhizas are common in the gametophytes of extant liverworts (Read *et al.*, 2000).

Among the algae, the extant class of the Chlorophyta which is most closely related to ancestors of the Embryophyta is the Charophyceae. While probably not the nearest extant relatives of the embryophytes, the Characeae (*Chara*, *Nitella*, etc.) are rhizophytic aquatic plants which can have shoots up to 1 m long and have rhizoids penetrating several mm into sediments. These rhizoids are only one cell wide by one to several cells long, and are clearly involved in nutrient uptake (Raven, 1981, 1991). Many marine green macroalgae in the class Ulvophyceae, and some freshwater members of the Chlorophyceae, are also rhizophytes, usually with unicellular rhizoids. Most other benthic macroalgae are haptophytes. Many lichens are also, via the rhizines of the mycobiont, rhizophytes (Raven, 1981, 1986).

Julian *et al.* have used the term 'root' to denote a structure of the vestimentiferan *Lamellibrachia* which is embedded in anoxic sediments, and which seems to be involved in uptake of hydrogen sulphide by this animal with its chemolithotrophic symbionts (Julian *et al.*, 1999).

These comparative analyses of the 'rooting' structures of rhizophytes (and quasi-rhizophytes such as *Lamellibrachia*) show that at least some of the classic root functions of the roots of sporophytes of terrestrial vascular plants are shared with the rhizoids or more complex structures of other phases in the tracheophyte life cycle, or other (non-tracheophyte) higher taxa of plants. The special role of rooting structures in water uptake is less significant in submerged aquatic plants where there is no transpiratory water loss, which accounts for up to 97% of the water taken up from the soil by C₃ plants on land. Furthermore, some specialized functions of roots demand the complexity of roots, or at least (parenchymatous) structures which are at least three cells in diameter. Examples are cluster roots (Marschner, 1995; Skene, 1998), epidermal transfer cells related to the external Fe³⁺ reduction mode of Fe acquisition found in almost all vascular plants tested (grasses are an exception) (Marschner, 1995), and the production of N₂-fixing nodules involving rhizobia or *Frankia* which need a minimal size for the required plumbing (carbohydrate input; organic N removal) and O₂-protective structures (Raven *et al.*, 1994; Thumfort *et al.*, 1994).

However, some important attributes of resource acquisition by higher plant roots can apply to morphologically simpler, and smaller-radius, absorptive structures, including rhizoids, root hairs and mycorrhizas. An example is apical alkalization (increasing Mo availability and decreasing Al toxicity) and more basal acidification (favouring P and Fe availability) resulting from longitudinally and radially circulating currents carried by (buffered) H^+ (Raven, 1989, 1991, 1995*b*, 1998, 2000*a*; Plassard *et al.*, 1999). This could not directly apply to marine ulvophycean green algae with their currents carried by Cl^- (Raven, 1991). Furthermore, acidification of the whole rhizosphere by production of intracellular organic acids followed by K^+/H^+ exchange across the plasmalemma, or by organic acid (and, to a much smaller extent, amino acid) secretion across the plasmalemma, can occur even when NO_3^- is the N source and the expectation from N assimilation alone is for rhizosphere alkalization (Bertrand *et al.*, 1999; Darrah, 1993; Jones and Darrah, 1993; Jones *et al.*, 1994; Kirk *et al.*, 1994; Neumann and Römheld, 1999; Raven *et al.*, 1980, 1990; Raven, 1995*a*, 2000*a*). Such acidification can aid P and Fe acquisition (Raven, 2000*a*). This organic acid excretion and H^+ excretion (paralleling organic anion retention by roots) in more mature root zones accentuates the H^+ efflux from circulating currents, just as alkalization resulting from the organic anion efflux from root apices (related to offsetting Al toxicity) accentuates the alkalization resulting from the H^+ influx due to circulating currents carried by (buffered) H^+ . Kochian notes that alkalization of the rhizosphere around the root apex does not invariably reduce Al toxicity (Kochian, 1995; cf. Raven, 2000*a*).

Finally, and as a link to the next section of this paper, the role of (aerial) shoots in nutrient acquisition (and release) must be mentioned. There has been a comprehensive review of land plant mineral nutrient acquisition from outside the pedosphere (Clarkson *et al.*, 1986), including uptake of nutrient solutes by aerial shoots and other above-ground structures (Parsons *et al.*, 1993, 1995). While not generally as important as the uptake of nutrients by the shoots of submerged rhizophytes, such uptake by land plants can be significant. This uptake by extant land plants often involves air-borne nutrients resulting from the activities of other land biota (or biota which evolved on land), for example, solutes leached from plant structures higher in the canopy in the case of understorey bryophytes, and uptake of gaseous NH_3 from seabird colonies or (anthropogenically) intensive animal production units (Raven and Yin, 1998). Accordingly, the earliest terrestrial biota would not have had access to the range and quantity of air-borne nutrients that are found today (Raven and Yin, 1998).

It is of interest that nutrient solutes which run off the canopy can induce rooting (Herwitz, 1991; Atger and Edelin, 1994).

The biogeochemical context of the early embryophytes

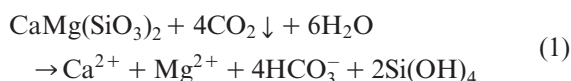
Embryophytes evolved from charophycean green algae possibly as much as 510 million years ago (Gray, 1985; Edwards *et al.*, 1998; Kenrick and Crane, 1997; Edwards, 2000; Strother, 2000; Wellman and Gray, 2000). The earliest (mid-Ordovician) fossil evidence as to the structure of the early embryophytes consists entirely of spores which were probably aurally dispersed (Gray, 1985; Edwards *et al.*, 1998) and it appears that embryophytes evolved on land, possibly on the margins of drying pools, from relatively small algal ancestors (Stebbins and Hill, 1980; Graham, 1993).

The land surface inhabited by the earliest embryophytes was one that was already inhabited by photosynthetic organisms and by organisms which consumed, pre- and post-mortem, these photolithotrophs. There is geochemical evidence consistent with organisms living on land back to 1.2 billion years ago, i.e. in the Mesoproterozoic (Horodyski and Knauth, 1994; cf. Keller and Wood, 1993; Shear, 1991; see also Rye and Holland, 2000). The argument here is based on the weathering of rock surfaces. The rate of weathering depends on temperature, the presence of water, and the concentration of CO_2 in this rock-surface water. The rate of weathering on land surfaces between 800 and 1200 million years old is said (Horodyski and Knauth, 1994), to have exceeded the rate expected from the likely atmospheric CO_2 concentration equilibrated with surface water, with the atmospheric CO_2 estimated from the greenhouse considerations and the lower radiation output from the sun 800–12000 million years ago than is the case today. While there are no fossils of the actual organisms involved, evidence from marine deposits shows that cyanobacteria and (prasinophycean) green algae were present in the sea, and could have been primary producers on land as well (Raven, 1995*a*, 1997, 1998; Golubic and Seong-Joo, 1999). Parasites, grazers and decomposers could have been viruses, bacteria, archaea, and (possibly) fungi; Raven (1997).

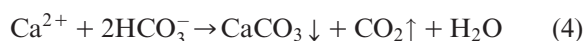
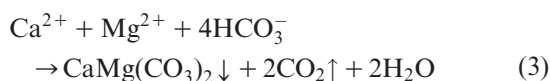
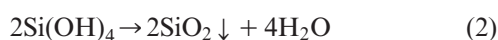
The biological 'CO₂ pump' from the atmosphere to water in fissures in the rock surface would have taken the form of primary producers (cyanobacteria; green algae?) on the rock surface where light supply was sufficient to allow photosynthesis. Transport of organic material into the fissures on the rock could have occurred as particles (dead cells gravitationally falling into crevices, motile protists, or fungal filaments, moving into the crevices; and soluble organic material released from dead, including virally lysed, cells percolating into crevices). Subsequent metabolism, with respiratory or fermentative CO_2 -production, could have led to a CO_2 build-up as diffusive CO_2 movement to the atmosphere only equals net CO_2 production in the rock crevices when a significant

concentration difference is established between the sites of CO₂ generation and the water-atmosphere interface. This build-up of CO₂ means that CO₂ consumption in rock weathering becomes an increasingly significant competitor with diffusive CO₂ loss to the atmosphere. The impact of cyanobacteria and algae in the weathering of mineral surfaces today has been discussed (Vestal, 1993; Walton, 1993; Wynn-Williams, 1993).

The chemistry by which CO₂ is removed in weathering of silicates can be represented as (equation (1)):



The HCO₃⁻, Si(OH)₄, Ca²⁺, and Mg²⁺ dissolve in the soil water which becomes groundwater, lakes and rivers and ultimately reaches the sea. Here the Si(OH)₄ is precipitated (with much biological participation) as SiO₂, and Mg²⁺ and (especially) Ca²⁺ is precipitated as MgCa(CO₃)₂ (dolomite) and CaCO₃ (calcite) according to equations (2–4):



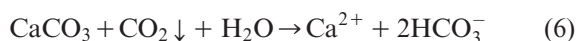
Overall, equations (1)+(2)+(3) sequester 2CO₂ (ultimately from the atmosphere) as 2 sedimented CO₃²⁻.

Equations (1–4) occur over time scales of millions to tens of millions of years. The exogenic C cycle is completed by magmatic and volcanic processes in the Earth's crust. Here CaMg(CO₃)₂, CaCO₃ and SiO₂ produced in equations (2–4) are converted to the starting points (other than H₂O) for equation (1) as follows:



This part of the cycle takes of the order of hundreds of millions of years.

Any CaCO₃ which reaches the surface of the land is weathered according to equation (6):



This, with equation (4), shows that CaCO₃ weathering on land and production in the sea is CO₂-neutral over times of tens to hundreds of millions of years. The time scale here relates to the predominant deposition of CaCO₃ in continental shelf sediments, i.e. above the lysocline. It also concerns the long time taken for shelf CaCO₃ to be weathered; the shelf deposits are generally not subducted and subject to equation (5) reactions, but follow equation (6).

Weathering of rocks of varying mineralogy has a very wide range of chemical effects (Berner and Berner, 1996), but it generally increases the solubility of many of the plant nutrients found in rocks, for example, potassium, magnesium, calcium, phosphate, and sulphate among the macronutrients. The atmosphere 1200 million years ago contained oxygen (all from photosynthesis in the sea) at perhaps 1% or more of the present level, and would have immobilized the micronutrient iron as ferric oxides, hydroxides and carbonates; the ferric oxides, with aluminium oxide also produced by weathering, immobilize phosphate. Iron and phosphate could be remobilized by organic acids and reductants produced by biota and, in the case of iron, by siderophores produced by many bacteria (including cyanobacteria) (Raven, 1997). In addition to sources from weathering on land, sulphur could have been supplied via the atmosphere from oxidation products of dimethylsulphide produced by marine biota (Lovelock *et al.*, 1972).

Nitrogen is a plant nutrient present in very small amounts from rock weathering relative to other nutrient elements when viewed in the context of the ratio of elements found in optimally nourished plants. The large pool of N₂ in the atmosphere can only be accessed biologically by prokaryotes; there is the possibility that bacteria (including cyanobacteria) and archaea could have been fixing N₂ on land in the Proterozoic (Raven and Yin, 1998; Golubic and Seong-Joo, 1999). The co-occurrence of N₂ and O₂ in the Meso- and Neo-Proterozoic atmosphere permitted the generation of biologically significant quantities of oxidized combined nitrogen in electrical storms (Raven and Yin, 1998).

Work on extant terrestrial cyanobacteria, algae and chemo-organotrophic microbes on rocks (Vestal, 1993; Walton, 1993; Wynn-Williams, 1993) suggests that their influence on weathering is less than that caused by lichens. However, lichens were not present in the Proterozoic; the earliest known fossil lichen is from the Rhynie Chert (Lower Devonian) in the form of a lichen with a cyanobacterial photobiont and a glomalean mycobiont with no present-day analogues (Taylor *et al.*, 1997). The ascomycetes and basidiomycetes, which are the fungal components of extant lichens, are not known as fossils until the Upper Silurian (based on microfossils: Sherwood-Pike and Gray, 1985; Taylor, 1994) and the Carboniferous-Permian, respectively, although molecular-genetic evidence, combined with zygomycete fossils, suggests an origin of filamentous fungi 600 million years ago (Simon *et al.*, 1993; Simon, 1996; Blackwell, 2000; Redecker *et al.*, 2000). The present form of lichens probably evolved in the Permo-Triassic as peltigeralean lichens (Hawksworth, 1988) although the earliest known fossils of lichens involving fungi other than zygomycetes are only 50 million years old.

These considerations suggest that a skeletal soil could have been present as much as 1.2 billion years ago. The

presence of O₂ in the atmosphere at this time would have had direct (metabolism, including respiration and active oxygen species production) and indirect (UV-B screening via stratospheric O₃, and restrictions on P and Fe availability) effects on land biota.

The authors do not wish to over-emphasize the extent to which the marine biota and the microbial terrestrial biota had modified the terrestrial habitat in ways which might have facilitated the establishment of a rhizophytic terrestrial embryophyte flora. However, it is likely that the land surface was preconditioned to some extent as a habitat which the early embryophytes could further modify upon their evolution perhaps 510 million years ago. The use of geochemical proxies (in this case the Fe(CO₃)OH content of goethite) to estimate the rock surface ('soil') CO₂ concentration (Yapp and Poths, 1992, 1994) on land 440 million years ago is consistent with high primary productivity, which at once permits (via CO₂ input) and requires (to support productivity) high rates of weathering or, at least, of recycling of nutrients from biota. The high productivities suggested (Yapp and Poths, 1994) requires quite complex plant structures (Raven, 1997, 1998), for which the only fossil evidence is the aerielly dispersed spores (Gray, 1985). Suggestions that spores of potentially mycorrhizal glomalean fungi occur in Ordovician deposits (Blackwell, 2000; Redecker *et al.*, 2000) require reconsideration in view of the mineralogical context.

A further point about the high productivities suggested (Yapp and Poths, 1994) in the Ordovician concerns the impact on atmospheric CO₂. Increased weathering rates tend to draw down atmospheric CO₂, depending on the land area covered by these high-productivity plants. This has implications for the later discussion on the role of deeper rooting in the Devonian CO₂ drawdown shown by the Geocarb II model of Berner (Berner, 1994), since one of the inputs to the model is the plant-induced CO₂ drawdown (Raven, 1998).

The early (Palaeozoic) evolution of embryophytes and the origin of roots

Silurian

Edwards *et al.* (Edwards, 1993, 1994; Edwards *et al.*, 1998) discuss the evidence as to the vegetative morphology and anatomy of the earliest embryophytes known from remains other than spores (Banks, 1970; Chaloner, 1970; Spicer, 1989; Kenrick and Crane, 1997; Bateman *et al.*, 1998; Shear, 1991). These Silurian fossils are generally composed of branching parenchymatous axes, and appear to represent the sporophyte phase of the life cycle, based on the occurrence of sporangia or, where these are not present, the absence of antheridia and archegonia, or of a structure representing a young

sporophyte parasitic on a gametophyte, as is always the case for bryophytes and homosporous free-sporing tracheophytes. That these two latter indicators of the gametophyte nature of a fossil can be preserved is shown by Lower Devonian fossils with well-preserved antheridia and archegonia or vegetative structures which are more complex than any extant gametophyte (see below) (Taylor and Taylor, 1993), and a liverwort-like fossil with gametophyte and (possibly) an attached sporophyte (Edwards *et al.*, 1995).

The clearly sporophytic (i.e. sporangia-bearing) fossils from the Silurian have, in many of the cases where preservation is adequate to show the structures if indeed they were present, one or more of the four essential attributes of homoiohydry, i.e. an endohydric conducting system, cuticle, stomata, and some underground structures. Preservation of Silurian fossils examined so far is never adequate to show if the fifth attribute of homoiohydry, i.e. intercellular gas spaces, occurred. The full suite of five structures permits water (and nutrient solute) supply to aerial axes when enough soil water is available to supply the transpiring surface with liquid water at a rate sufficient to support the transpiratory loss of water vapour found during rapid photon and CO₂ absorption in photosynthesis. By stomatal closure organisms with these attributes can maintain cellular hydration for shorter or longer periods (depending on, for example, the water conductance of the cuticle plus epicuticular wax) when soil water supply is inadequate to make good the transpiratory water vapour loss when stomata are open. Stomatal closure prevents net CO₂ fixation, and thus trades death from thirst for the potential of death by starvation, but by tiding the plant over periods of limited soil water supply as a hydrated vegetative entity the plant can grow on land and yet not be tolerant of desiccation in the vegetative state. For as yet imperfectly understood reasons the combination of homoiohydry and vegetative desiccation intolerance seems to be essential for any terrestrial plant which has structures more than about a metre above ground level (Raven, 1993, 1995a, 1997, 1998).

It must be emphasized that in most of these Silurian sporophytes the occurrence of all of the attributes of homoiohydry in a given (form) genus or species is very much the exception rather than the rule. Even for one of the most complex known (Upper) Silurian sporophytes, the (probable) lycophyte *Baragwanathia*, cuticle, stomata, tracheids, and (probably) intercellular gas spaces are known from above-ground structures in Lower Devonian specimens (but not so far from the less well preserved Upper Silurian fossils) (Hueber, 1983), but we have little knowledge of the underground structures which, it is widely believed, such plants must have possessed if they were to have been adequately anchored, and to have had a sufficient capacity for uptake of water and soil-derived

nutrients (Driese and Mora, 2001). The aerial shoot of *Baragwanathia* had microphyllous leaves, with sporangia whose mode of attachment (to the upper leaf surface or to the axis just above leaf insertion with no evidence of any consistent relation between microphyll and sporangium) is still enigmatic. Any below-ground axes of *Baragwanathia* would be expected to lack the stomata, microphylls and sporangia as well as the overt cuticle. Without these features, and with generally imperfect preservation of the anatomy of *Baragwanathia* (at least in comparison with the Rhynie Chert fossils), how would such an axis system be recognized as being from *Baragwanathia*? It is clear from the size of the erect aerial axes of *Baragwanathia* that substantial below-ground structures would be needed.

Lower Devonian

In the Lower Devonian there are fossil localities with exceptional preservation, for example, the Rhynie Chert, and also localities with important evidence of the earliest rooting structures (Driese and Mora, 2001; Gensel *et al.*, 2000; Hotton *et al.*, 2001). Here a range of embryophyte sporophytes and gametophytes is found. The sporophytes have branched aerial axes (i.e. are polysporangiophytes: Kenrick and Crane, 1997) which are endohydric, but do not always have true xylem (i.e. water conducting cells with unevenly but regularly thickened walls typical of tracheids); an example of an endohydric plant without true xylem is *Nothia aphylla* (Kerp *et al.*, 2001). Regardless of whether they have true xylem, these sporophyte axes have intercellular spaces, cuticle and stomata, and sporangia. Among those with true xylem are representatives with smooth axes (*Rhynia gwynne-vaughanii*) and, with microphylls, the lycophyte *sensu lato* *Asteroxylon mackiei*. *Aglaophyton* (and some other Rhynie plants) have underground axes bearing rhizoids; these axes have arbuscular mycorrhizas, but mycorrhizas also occur on above-ground axes (Nicolson, 1975; Pirozynski and Malloch, 1975; Pirozynski and Dalpé, 1989; Simon *et al.*, 1993; Taylor *et al.*, 1995; Simon, 1996; Smith and Read, 1997). The occurrence of rhizoids may not always be an indicator of the subterranean nature of axes, since rhizoids of *Rhynia* are borne on hemispherical projections near the base of presumed aerial axes (Edwards, 1993). Edwards also points out that *Asteroxylon* sporophytes have anatomical differences (e.g. in the shape of the stele) between leafy aerial and smooth subterranean axes, but that distinction of the smooth axes as roots is not possible on the basis of endogenous branching, since the frequent branching by the smooth axes is always exogenous (Edwards, 1993). In the single known example of an *Asteroxylon* leafy shoot with endogenous branching it is not clear whether the branch is leafy or smooth (Edwards, 1993). In any case there is Grubb's warning about the

use of endogenous branching as an infallible test of the root nature of an organ (Grubb, 1970), although his tracheophyte example, i.e. the extant *Selaginella*, is perhaps contentious (Bierhorst, 1971; Gifford and Foster, 1987; Lu and Jernstedt, 1996).

Fossils of other Lower Devonian embryophyte sporophytes, i.e. those from sites other than the Rhynie Chert, also have strong indications of the occurrence of roots, or at least structures with considerable similarity to roots. Thus, Rayner (Rayner, 1984) has suggested that the lycophyte (*sensu lato*) *Drepanophycus spinaeformis* had roots on the basis of the branching pattern and the attitude in the sediment of the smooth axes in relation to the bedding plane (Schweitzer, 1980). However, there is no anatomical evidence (e.g. endogenous branching) to support this view. Li and Edwards have re-investigated *Drepanophycus spinaeformis* from the Lower Devonian of Yunnan Province, southern China (Li and Edwards, 1995). This material, now named *Drepanophycus qujingensis* (Li and Edwards, 1995), was shown to have roots, i.e. structures borne by both fertile and sterile leafy shoots, which branch dichotomously at least five times. The roots appear to be inserted randomly, and the largest branching root system extends up to 30 mm from the stem. The diameter of the roots is about 3 mm at their attachment and rapidly decrease with branching; the smallest branches recovered have a diameter of less than 0.7 mm (Fig. 37D of Li and Edwards, 1995), and it is likely that the unpreserved, more apical, portions had an even smaller diameter. It is of interest that these roots were borne on leafy axes which were presumably above-ground but were probably prostrate, as the rooting system itself extends down into the rock, at an angle to the bedding plane in which the leafy axes were exposed.

The published information on roots or root-like structures in the early Devonian (Pragian-Emsian) (Gensel *et al.*, 2001) has been reviewed, and new data presented on Lower Devonian fossils from Bathurst Island, Arctic Canada, and from New Brunswick and Gaspé, Canada. These plants with root-like structures are zosterophyllophytes or lycophytes *sensu lato*. Rooting structures in these fossils were identified by the following five characteristics granted that the aerial axes that bear the rooting structures have emergences or microphylls (Gensel *et al.*, 2001). (1) The rooting structures are attached to aerial ones, but have no emergences or microphylls. (2) The rooting structures are generally much narrower in diameter, and shorter, than are the aerial axes that bear them. (3) The rooting structures are either unbranched or are irregularly branched; this contrasts with the more predictable branching of the aerial axes. (4) The rooting structures may have a sinuous or delicate appearance. (5) The rooting structures proceed in a direction opposite to that in which the aerial axes grow. These authors point out that characteristics 2–5 are also applicable to plants with naked

axes, and that the rooting structures show no evidence of root caps or indisputable root hairs; furthermore, the anatomy of the rooting structures is not yet known.

The Bathurst Island fossils (Gensel *et al.*, 2000) comprise *Drepanophycus* and *Bathurstia* spp. with aerial axis-borne rooting structures scattered along what appear to be trailing or rhizomatous structures, or forming parts of the so-called 'K-branching' structures, and *Zosterophyllum* sp. nov. with tufted rooting structures which occur as descending naked axes from plants with dense aggregations of branching aerial shoot systems. The Quebec and New Brunswick fossils comprise *Crenaticaulis verruculosus* and *Sawdonia ornata*: *C. verruculosus* has smooth, spinous, slender (0.5 mm wide) rooting structures departing at right angles to aerial or rhizomatous axes in regions where there are otherwise no branches (Gensel *et al.*, 2001). *Sawdonia ornata* fossils have structures like the putative rooting structures of *C. verruculosus* in close association to aerial axes, but not attached to the *S. ornata* aerial axes. The association of the root-like structures with *S. ornata* is rendered more likely because *S. ornata* is essentially the only species present at that level in the bedding sequence. Furthermore, Rayner interprets structures associated with H-shaped branching Scottish Emsian specimens of *Sawdonia ornata* as root-like or as rhizophores (Rayner, 1983). These *S. ornata* specimens have one of the usually basipetally directed, smooth laterals produced at H-shaped branching which differs from the usual spiny branches; sometimes there is a short spineless projection in the position normally occupied by this longer structure (Rayner, 1983).

The discussion above shows that the evidence for roots in Lower Devonian fossil sporophytes is based on the occurrence of smooth subterranean axes with branching patterns similar to extant roots, and with a simpler xylem morphology (protostele) than the actinostele in aerial parts of plants such as *Asteroxylon*. Where the origin of branches in these underground axes is known, it is superficial. There is no evidence of a root cap, although this is not a commonly fossilized structure; an exception is the well-preserved root cap of the Pennsylvanian (Upper Carboniferous) marattaceous fern *Psaronius* (Stewart and Rothwell, 1993). Furthermore, these smooth axes apparently lack an endodermis (which can be found in Carboniferous and later vascular plants, for example, in roots of *Equisetites*, *Tempskyia* and *Rhizopalmoxylin*: Walton, 1940; Raven, 1984*b*, 1994*b*; Tidwell, 1998). However, there is no evidence of an endodermis in aerial axes of those Lower Devonian plants, and the extant *Lycopodium* sporophytes also lack a root (but not a shoot) endodermis (Damus *et al.*, 1997; Raven, 1983, 1984*a, b*, 2000*a, b*; Edwards *et al.*, 1996; Epstein, 1999), as do leafy endohydric gametophytes of extant bryophytes (Grubb, 1961).

It would seem that the Lower Devonian sporophytes had below-ground parenchymatous structures which performed the functions of roots, but which do not necessarily have all of the features by which the roots of extant vascular plants are recognized. Furthermore, the zosterophyllophyte-lycophyte *sensu lato* clade possessed root-like structures in the Lower Devonian, although there is no corresponding evidence for root-like structures on euphyllophytes at this time. The earliest convincing euphyllophyte roots occur in the Middle Devonian cladoxylalean *Lorophyton goense*, thought to derive from trimerophytes (Fairon-Demart and Li, 1993) where bifurcating structures arise in tufts from a swollen stem base. This is consistent with the polyphyletic origin of roots, a point considered in more detail below.

Upper Devonian and Carboniferous

In Upper Devonian, and, especially, Carboniferous deposits, root structures with a protostele, endogenous branching and an endodermis can be distinguished from shoots of the same plant with (often) a more complex anatomy of the stele in primary growth, exogenous branching and (often) an endodermis (Taylor and Taylor, 1993; Meyer-Berthaud *et al.*, 1999). The most parsimonious explanation of these data is that endodermes, like roots, are not monophyletic in origin. The same conclusion applies to the origin of the exodermis, which is found in 90% of the 200 extant angiosperm species so far examined, but in none of the extant gymnosperms examined, and in only a few of the extant non-seed vascular plants investigated (Damus *et al.*, 1997).

An interesting case is the arborescent lycophytes. The embryo of the Upper Carboniferous lepidodendrid *Lepidocarpon* produces a 'root-like' organ by dichotomy of the embryonic shoot; this recalls the way in which root-like structures of Lower Devonian zosterophyllophytes and lycophytes *sensu lato* originated (Gensel *et al.*, 2001). This root-like organ develops into the 'stigmarian root system' bearing 'stigmarian rootlets', and the stigmarian axis and its rootlets is considered homologous to the shoot system (Rothwell, 1984; Rothwell and Erwin, 1985). This view is supported by the presence of a pith cavity in the stigmarian root system, and by the exogenous production of lateral organs (stigmarian rootlets) (Stewart and Rothwell, 1993; Taylor and Taylor, 1993). The 'stigmarian rootlets' have thus been interpreted as morphologically equivalent to leaves, and are closely similar in anatomy to the roots of the extant *Isoetes* spp. where, as one might expect of modified leaves, the roots have a major role in CO₂ uptake by the plant (Raven, 1970; Sand-Jensen *et al.*, 1982; Richardson *et al.*, 1984; Keeley *et al.*, 1984; Raven *et al.*, 1988). However, such an origin of roots is not a prerequisite for a major role in CO₂ uptake, for example, in flowering plants of the

isoetid life form (Raven *et al.*, 1988). The absence of root hairs on 'stigmarian rootlets' is also consistent with their origin from leaves.

Fossil and other evidence bearing on monophyly or polyphyly of roots

Aside from the 'stigmarian rootlets', it is necessary to address the question of the occurrence of a single evolutionary origin as opposed to multiple origins of roots (Groff and Kaplan, 1988). The question can be posed as the difference between a single origin before lycophytes and euphyllophytes diverged, and independent origins in each of these two clades.

The lycophyte clade (in the form of the putative lycophyte *Baragwanathia*) can be seen as separate from other tracheophytes by the Late Silurian (~400–420 million years ago), with the rhyniophytes related more closely to the ancestors of the extinct trimerophytes and other fossil and extant euphyllophytes which include all extant vascular plants other than lycophytes (Kenrick and Crane, 1997; Dolan and Scheres, 1998). The presence of clearly defined root-like structures in fossils of lycophytes in the Lower Devonian (see above), but their absence from equally well-preserved Lower Devonian fossils of other vascular plants (e.g. in the Rhynie Chert) suggests independent origins of roots in the lycophytes and the euphyllophytes. The alternative explanation is that roots existed in both clades in the Lower Devonian and the Upper Silurian, and in their common tracheophytic ancestor and that the absence of roots from the late Silurian fossil record, and in non-lycophytes in the Lower Devonian is a result of poor preservation of roots relative to other axial structures, including sporangia. This is possible for Late Silurian specimens of *Baragwanathia* (see Edwards, 1993, 1994 for discussions on the preservation potential of roots lacking secondary thickening), but is perhaps unlikely as a general explanation. The first possibility, i.e. an independent origin of roots in lycophytes and (later) in euphyllophytes, requires that such features of roots as a root cap, and endogenous origin of laterals evolved independently from the original relatively undifferentiated axis of the lycophytes and the euphyllophytes. Certainly the selective advantages of a root cap in an organ growing through soil seem clear and could account for two independent evolutionary origins. The endodermis is also found in many extant shoots (especially among organisms of the pteridophyte grade of organization) as well as in almost all extant roots (*Lycopodium* spp. being an exception). As for the simpler and less diverse morphology of the steles of roots (medullated or non-medullated protostele or actinostele) than of shoots (all categories of stele morphology occur in shoots), the root situation is closer to that of the ancestral axis.

A further line of evidence comes from the embryology of extant vascular plants. Goebel distinguishes *allorhizic* plants, where shoot and roots are at opposite ends of the embryonic axis, from *homorhizic* plants, where the root is lateral with respect to the longitudinal axis of the embryo (Goebel, 1930). All extant seed plants are allorhizic, while all extant free-sporing vascular plants are homorhizic. If this is a fundamental evolutionary distinction, then extant vascular plants (and their progymnosperm and (?) trimerophyte ancestors) can be distinguished from the lycophytes and extant euphyllophytes (*Equisetum*; ferns). This suggests the possibility of three origins of roots, yielding the allorhizic seed plants and their root-bearing vascular ancestors, the homorhizic lycophytes, and the homorhizic euphyllophytes other than seed plants (e.g. ferns and horsetails) and any of their ancestors from which they inherited roots.

A further, and much more recent, approach to the origin of roots comes from molecular genetic studies of shoot and root development in the (allorhizic) flowering plant *Arabidopsis thaliana* (Dolan and Scheres, 1998). These authors investigated the propagation of root pattern, formed in the embryo, through subsequent growth and development of the seedling root meristem. The root pattern is maintained by positional cues, and to some extent by local cell interactions. These cell interactions are involved in maintaining the balance between cell division and differentiation in cells close to the quiescent centre. This balance is also maintained in shoots, where the genetic basis of the phenomenon is now understood. They also point out that patterned cell differentiation in the epidermis of roots has a similar genetic basis to that in shoots (Dolan and Scheres, 1998).

Dolan and Scheres point out that the developmental similarities of shoots and roots in *Arabidopsis* could indicate that roots are derived from whole shoot structures (Dolan and Scheres, 1998). An alternative possibility (Dolan and Scheres, 1998) is that a suite of genes involved in shoot structure determination could have been co-opted into a similar role in roots derived from a lateral appendage of the shoot (other than a branch shoot), such as is likely to be the case for at least some (homorhizic) lycophytes, i.e. the isoetalean clade with roots derived from the leaf-like structures of stigmarian rootlets. The stigmarian roots on which the stigmarian rootlets are borne are derived by dichotomy of a shoot (see above). Dolan and Scheres acknowledge that this sort of molecular genetic work should be extended to other vascular plants, including free-sporing plants (Dolan and Scheres, 1998).

It was concluded from these lines of evidence that roots are probably (at least) diphyletic. Further genetic approaches to root morphogenesis in lycophytes and euphyllophytes should give a more definitive answer.

The diameter of the earliest roots

In view of the functional significance of root diameter in extant plants (see above) it is important to know the diameter of the earliest roots, both in the fossil record and in each major grade of embryophytes.

The earliest roots in the fossil record have diameters ranging from 3 mm at their attachment to less than 0.7 mm in the smallest branches recovered (Li and Edwards, 1995; see above). It is possible that roots of even smaller diameter occurred in these Lower Devonian lycophytes, but have not been preserved and recovered; the fossil record is likely to be biased in favour of the larger rather than the smaller diameter axes of roots lacking secondary thickening (Li and Edwards, 1995).

For extant embryophytes, the data for free-sporing polysporangiophytes suggest that the smallest lycophyte roots can be 330 μm (*Lycopodium*)–370 μm (*Isoetes*) in diameter, while among the euphyllophytes *Equisetum* has a root diameter of 370 μm or more, while fern roots range from 140 μm (*Azolla* and *Hymenophyllum*) to 830 μm (*Ophioglossum*) (Smith, 1938; Schneider, 1996). *Azolla* and *Hymenophyllum* are clearly relatively derived ferns (Rothwell, 1996). All known extant and extinct gymnosperms have secondary thickening and are mycorrhizal, although the finest branches of roots without secondary thickening have diameters of only a few hundred μm (Smith and Read, 1997). Among flowering plants, the roots of those considered, on molecular phylogenetic grounds, to be the closest living relatives of the ancestral angiosperms have roots of relatively large diameter (Baylis, 1975; St John, 1980; Qui *et al.*, 1999; Soltis *et al.*, 1999). Such roots may have low elongation rates and (except in aquatics such as the Nymphaeales) have a great dependence on mycorrhizas.

Implications for plants and for their environment of increased rooting depth by vascular plants during the Palaeozoic

The discussion of the biogeochemical content of the early embryophytes suggested that pre-embryophytic photosynthetic organisms on land, and associated microbial food webs, had significant effects in increasing the rate of weathering and the mobilization of plant nutrients from rocks, and in N_2 fixation, leading to the production of a surface layer resembling soil. The evolution of embryophytes with roots (or with the antecedents, or functional analogues, of roots) increased this weathering activity. The larger and more structurally complex below-ground structures, involved in anchoring the plant and in taking up water and nutrients, were simultaneously permitted and required by larger and more structurally complex above-ground structures absorbing photons and CO_2 .

Chaloner and Sheerin show, in their text—Fig. 5 (see also Fig. 6.15 of Niklas, 1997) the maximum observed aerial axis diameter of vascular plant fossils from the late Silurian to the Devonian-Carboniferous boundary (Chaloner and Sheerin, 1979). The increase is from some 3 mm diameter in the latest Silurian, via an approximately linear increase in the logarithm of diameter with time, to almost 2 m at the end of the Devonian in the progymnosperm *Archaeopteris* (*Callixylon*). This progymnosperm has secondary thickening; the use of the relationships between height and basal stem diameter for organisms with secondary thickening (Fig. 5.9, Niklas, 1994; Figs 6.14, 6.15, Niklas, 1997) suggest a height for *Archaeopteris* of 10–30 m.

Corresponding to this increase in height is an increased plant biomass per unit land area and depth of penetration of roots *sensu lato*. While not suggesting that the depth and mass of below-ground parts of the plant increase in direct proportion to the height and mass of above-ground parts of the plant, there is independent evidence of an increasing depth of penetration of roots (Algeo *et al.*, 1995; Algeo and Scheckler, 1998; Berner, 1990, 1993, 1994, 1997, 1998; Retallack, 1997; Elick *et al.*, 1998) during the Devonian. Thus, dichotomous root traces up to 2 mm in diameter and up to 0.9 m long in the Emsian (late Early Devonian) have been found (Elick *et al.*, 1998). An increasing area of land occupied by tracheophyte vegetation, and an increasing rooting depth in vegetated areas, meant an increasing volume of rock weathered throughout the Devonian. This permitted the ‘mining’ of more rock-derived nutrients which supplied the increasing biomass of plants, although the need per unit of added biomass for P, K, Fe and Mg does not increase in proportion to biomass in plants with extensive secondary thickening, since much of the biomass comprises non-living xylem which has much lower P, K, Fe and Mg (and N) content relative to the peripheral living tissue. This argument on mineral requirements requires that the P, K, Fe, Mg and N released can be recycled to growing peripheral tissue. A similar consideration applies to the recycling of P, K, Fe, Mg and N from relatively short-lived photosynthetic structures and nutrient and water-acquiring below-ground structures in long-lived plants (Addicott, 1982; Atkinson, 1992; Raven, 1986; Jackson *et al.*, 1997; Robinson, 1990). Internal recycling from senescent short-lived structures into the perennial plant structures avoids the loss of these resources which have not been transported into the living core of the plant when the short-lived organ dies, regardless of whether it is abscised. There are also considerations of how rapidly these mineral elements are recycled from dead plants (or abscised or otherwise removed dead parts of plants) to the soil and hence to growing plants.

It has been pointed out that the increased weathering rate, as the volume of land surface impacted by root

systems increased during the Devonian, was probably transient (Algeo and Scheckler, 1998). The argument contrasts to the high atmospheric CO₂ with minimal (see above) biological pumping of CO₂ into the land surface before the deep 'rooting' of embryophytes in the Devonian radiation with the low atmospheric CO₂ (due to increased weathering on land) with higher CO₂ in the land surface due to increased biological pumping as the volume of land surface impacted by root systems from the Carboniferous onwards. These two situations yield essentially identical rates of weathering (averaged over millions of years) before and after the Devonian radiation (Algeo and Scheckler, 1998). To recapitulate, the pre-Devonian high atmospheric CO₂ and minimal biological CO₂ pumping gave way to a post-Devonian lower CO₂ atmospheric level with substantial biological CO₂ pumping into the land surface and both scenarios are suggested to yield similar weathering rates. In the Devonian, as the area, and even more, the volume of biologically weathered land surface increased very significantly. This rapid weathering removed CO₂ from the atmosphere and was maintained by the increased volume of land surface impacted by high CO₂ produced from the biological pump. It has been suggested that CO₂ in the land surface built up relative to the (decreasing) atmospheric CO₂ in the Devonian so that the weathering rate was higher than before or after (Algeo and Scheckler, 1998). The argument of these authors suggests that there was a pulse of weathering of the land surface in the Devonian, whose extent has not been matched before (when weathering was predominantly a result of high atmospheric CO₂) or since (when weathering was predominantly a result of high land surface CO₂) (Algeo and Scheckler, 1998). It is possible that Algeo and Scheckler somewhat underestimated the pre-Devonian role of non-vascular terrestrial photosynthetic and other organisms in enhancing weathering (Algeo and Scheckler, 1998; Horodyski and Knauth, 1994; Yapp and Poths, 1992).

A further effect of increased weathering and the production of soil concerns the increased storage capacity for water near the surface. This helps to tide homoiohydric plants over between stochastic rainfall events as photosynthesizing organisms rather than just permitting them to stay alive, as would be the case for poikilohydric, desiccation-tolerant organisms. This water storage, together with the moderating effect on rainfall of the above-ground plant canopy and the more extensive root system, can reduce soil erosion during rainstorms.

These effects of the increased rock weathering as a result of an increased volume of rock available to weathering by plants have been viewed until now as having essentially a positive feedback in plants, i.e. increasing the quantity and/or continuity of resource (water, pedosphere-derived nutrients) availability. However, plant-increased weathering also has an effect on

the aerial environment of plants (discussed above in relation to the transitory increase in weathering rate) which can be considered as a negative feedback on the capacity for the rate of biomass increase. This relates to the removal of atmospheric CO₂ in weathering of silicate minerals.

The mechanism whereby photosynthesis at the (rock or) soil surface and respiration below the photic zone (a concept borrowed from aquatic ecology) increase CO₂ use in weathering, which was outlined earlier for algal mats as part of microbial food webs, is quantitatively accentuated for tracheophytes, and especially for deeper-rooting tracheophytes. The increased external (via a leaf area index in excess of one) and internal (via intercellular gas spaces in leaves) area involved in CO₂ uptake permits the canopy-top photon flux density of up to 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ to be used effectively in photosynthesis, noting that the potential for CO₂ fixation could be constrained with less appropriate geometry by diffusion of CO₂ in solution to the carboxylase. This latter constraint might, with geometry of photosynthetic structures similar, in principle, to those of extant plants, in the Silurian and early Devonian with CO₂ at 10–20 times the present level, permit C₃ photosynthesis to occur at up to 6 $\mu\text{mol CO}_2$ per m² of area over which CO₂ passes from the gas to the solution phase per second. This, with a photon yield of C₃ photosynthesis in high CO₂ of 0.1 mol CO₂ fixed per mol photons absorbed or 0.08 mol CO₂ fixed per mol incident photons (assuming an absorbance of 0.8), would permit a fixation of up to 75 $\mu\text{mol CO}_2 \text{ m}^{-2}$ gas exchange surface s⁻¹; this requires a gas-exchange surface area of 27 times the land area to effectively use 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ incident photon flux density. This could be accomplished by a leaf (axis) area index of three and an internal area exposed to a gas phase nine times the external (projected) area (see Raven, 1977, 1993, 1995a, 1997, 1998; Konrad *et al.*, 2000).

Up to half of this productivity could be transported in phloem (or analogous) tissues to roots, where up to half of the transported organic carbon could be respired to CO₂ by living plant cells. Dead roots, plus aerial plants parts mixed into soil by animals, could be respired by animals and, especially, microbes to produce CO₂. This CO₂ has two possible sinks. One sink is diffusion from the soil solution, via the soil gas phase to the atmosphere. The other sink is consumption in weathering. The low conductance for CO₂ via the soil gas spaces resulting from the long linear diffusion path and tortuosity of the diffusion path, and the small fraction of the area parallel to the soil surface which is occupied by gas spaces, result in the build-up of CO₂ in the rock/soil surface layers. This CO₂ build-up increases the rate of weathering. The balance between CO₂ evasion to the atmosphere and CO₂ consumption in weathering as CO₂ output into the rock/soil surface layers involves an increased rate of

weathering with an increased rate of respiratory CO₂ injection into the rock/soil surface. It is of interest that CO₂ arises not only from respiration by below-ground plant organs, and by heterotrophs living on live or dead particulate plant material, but also from respiration of soluble organic solution. These organic acids can, before their conversion to inorganic carbon, increase the rate and pathway of weathering of silicates (Berner and Berner, 1996).

The occurrence of an increasing fraction of the area of the land surface colonized by tracheophytes, and an increasing depth of (rock) soil exploited by tracheophyte roots, tends to speed up the reactions in equation (1) relative to those of equation (3), but has a negligible effect on the rate of equation (5) (see above under The biogeochemical context of early embryophytes). This means that the expansion of tracheophytes, including the activities of their root systems, removes CO₂ from the atmosphere. While the build-up of organic matter in biomass also removes CO₂ from the atmosphere, the much more rapid turnover of the great majority of this material to regenerate CO₂ (months to thousands of years, depending on the chemistry and structure of the material: Schlesinger, 1991; Berner and Berner, 1996) means that the impact on atmospheric CO₂ over millions of years and longer comes more from the sedimentation, weathering and vulcanism of inorganic carbon than of organic carbon.

The increased weathering due to more widespread and deeper-rooting tracheophytes is thought to be a major cause of the decrease in atmospheric CO₂ during the Devonian to a minimum (until the recent Pleistocene glacial maxima) value in Carboniferous (Berner, 1990, 1993, 1994, 1997, 1998; Berner and Berner, 1996). However, it is noted that the enhanced weathering due to tracheophytes is (rightly) incorporated in the biogeochemical models which predict atmospheric CO₂ levels, so that these values of atmospheric CO₂ are not obtained independently of assumptions about plant behaviour in increasing the rate of weathering.

This largely vascular land plant-induced decrease in atmospheric CO₂ in the Devonian had important implications for performance of the aerial shoots in photosynthesis. Lower CO₂ partial pressures decrease the rates of C₃ photosynthesis over a range of photon flux densities if the anatomical and biochemical characteristics of the shoot are not modified and the near-extant O₂ partial pressures in the Devonian is considered (Beerling *et al.*, 1998). Increased stomatal indices and/or densities with decreasing CO₂ partial pressures, as a result of adaptive or acclimatory processes, can partially offset the decreased CO₂ fixation rate, but at the expense of an increased rate of H₂O loss in transpiration per unit CO₂ fixed.

What evidence is there as to evolutionary changes in plant shoots in the Devonian in parallel with the

tracheophyte (root)-induced drawdown of atmospheric CO₂? One change in shoot morphology through the Devonian which may be related to the decreased atmospheric CO₂ level (Chaloner, 1999) is the evolution of planate branch systems, and of 'webbing' of photosynthetic tissues between the ultimate ramuli of the branches (Gensel and Andrews, 1984; Stewart and Rothwell, 1993; Taylor and Taylor, 1993). Chaloner suggests that the decrease in mean diffusion pathlength for CO₂ in the gas phase of the intercellular gas spaces in the planate webbed structures than in the cylindrical photosynthetic structures can be related to the decreasing atmospheric CO₂ level through the Devonian (Chaloner, 1999). This could be related to the mechanical constraints on the dimensions of cylindrical as opposed to planar structures with a density of $\sim 10^6 \text{ g m}^{-3}$ in atmosphere with a density of $\sim 10^3 \text{ g m}^{-3}$. At all events, the radius of cylindrical plant structures is greater than the smallest half-thickness of a laminar organ, a comparison which relates the maximum possible CO₂ diffusion pathlength from stomata to photosynthetic cells in the smallest diameter of cylindrical organ with that of the shortest CO₂ diffusion pathlength from stomata to photosynthetic cells in an amphitomatous planar structure. The decreased capacity for use of light energy in CO₂ fixation per unit projected area in a thin laminar structure relative to a small-diameter cylindrical organ can be countered at a whole-canopy level by increasing the number of layers (leaf area index: Raven, 1997, 1984a, b, 1993, 1994a, b, 1995a, 1997). Constraints on the structure of laminar organs in relation to the maximum possible distance between vascular tissue and the most distant photosynthetic cells have been discussed previously (Raven, 1994a). Clearly there are vascular plants today (when CO₂ levels in the atmosphere are similar to the lowest values seen in the Palaeozoic (Carboniferous)) which have cylindrical photosynthetic structures, frequently co-existing with tracheophytes with laminar photosynthetic structures so, as with so much in biology, there may be more than one structural type working well in performing a given function.

The other evolutionary change which occurred between the Silurian and the Carboniferous is an increase in stomatal density (Chaloner and Collinson, 1975; McElwain and Chaloner, 1995, 1996; Chaloner, 1999). The very wide genotypic range in stomatal densities among extant plants (Chaloner and Collinson, 1975), as judged from the wide stomatal density range for organisms all living in the same CO₂ environment means that extant comparators (NLE or nearest living equivalents) are needed in interpreting the fossil stomatal density values. This question has been addressed (McElwain, 1998; McElwain and Chaloner, 1995, 1996). This problem of NLEs occurs even for the recent past (Tertiary, and even the Mesozoic) when there were fossil plants with close phylogenetic similarity to extant plants (even extending to con-generics such as

Ginkgo species from the recent and Mesozoic) as well as life-form and habitat similarities. For the Palaeozoic, close phylogenetic similarities do not occur, so the NLE comparators are largely those organisms with similar life forms and habitats.

With these provisos in mind (Edwards, 1998; McElwain, 1998; McElwain and Chaloner, 1995, 1996) a number of Palaeozoic plants have been analysed and a very significant decline in stomatal density between the Silurian and the Carboniferous shown. This is consistent with the decrease in CO₂ suggested by the Geocarb II model (Berner, 1994) and the theoretical and observed acclimatory effects of growth CO₂ on stomatal density in extant plants (Woodward, 1987; Woodward and Bazzaz, 1988; Woodward and Kelly, 1995; Beerling *et al.*, 1998). The stomatal density changes over geological time have also been used to hindcast CO₂ levels (McElwain, 1998); this contrasts with the way they are used here.

These two examples, i.e. the evolution of laminar photosynthetic structures and of decreasing stomatal density in the Devonian, show the likely feedback of root activities, via atmospheric CO₂ drawdown, on shoot evolution.

Conclusions

An understanding of the evolution of roots based on fossil evidence is only being obtained slowly. This fossil evidence does not support a monophyletic origin of roots in polysporangiophytes. Molecular genetic studies on root development in extant lycophytes and euphyllophytes (including seed plants) should give further information on this point.

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