

1 Constraints on the Form and Function of Root Systems

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1.1 Introduction

This chapter sets the scene for many of the topics covered in detail later in this volume. We discuss first the basic problems that plants face when growing on land. These problems reflect the many physical, chemical and biological constraints that soil imposes on the functioning of roots in terms of growth and resource capture.

Second, we consider how these constraints are overcome or minimised by fundamental structural and physiological features of root systems. Such features include a capacity to penetrate soil pores, to branch hierarchically, to absorb and transport unpredictably available water and solute supplies, and to maintain and replace their constituent parts.

We then explore the ecologically important properties of root systems that emerge as a consequence of their 'primary' features. Some of the most important of these 'emergent properties' are the topology of the root system, its size and capacity for anchorage, and its relations with rhizosphere microbes, symbiotic or otherwise.

Little of what we discuss involves mechanisms. Much new information about the physiological and developmental control of root system form and function is being discovered for a few model species, e.g. *Arabidopsis thaliana* (Zhang et al. 1999; Forde and Lorenzo 2001; Williamson et al. 2001) and *Zea mays* (McCully 1999). Likewise, the molecular interactions between roots and soil microbes have been well documented for particular processes, e.g. rhizobia-induced nodulation of legume roots (Heidstra and Bisseling 1996) and the formation of arbuscular mycorrhizas (Harrison 1997), but our understanding of these processes in a wider range of plant taxa remains incomplete. Yet that comparative ignorance does not prevent significant advances being made at the larger, ecological scales of inquiry that we consider here.

1.2 Problems Associated with Life in Soil

When photoautotrophic plants colonised land (or, more accurately, invaded the air: Niklas 1997, p. 165), they faced some novel problems. They gained access to more light with a spectral composition better suited to efficient photosynthesis, but they lost the physical support provided by water, risking gravitational compression, and free access to nutrients and water, risking dehydration (Niklas 1997, p. 252). However, soil is obviously opaque: light cannot penetrate more than a few millimetres (Tester and Morris 1987), and below-ground parts of plants therefore became dependent on the shoots for their carbon (C) supply. The invisibility of roots in soil also provides operational problems for root biologists: techniques such as computer-assisted tomography and magnetic resonance imaging (Asseng et al. 2000) or minirhizotrons (Chap. 3) must be used to visualise them with minimal disturbance.

Once plants had colonised land, the main water and nutrient reservoir became the soil. Soil provides plants with relatively predictable, long-term supplies of nutrients and water, and a secure anchorage. This is possible because of distinct physical, chemical and biological properties of soil. These same properties, however, also constrained how root systems evolved, and which continue to constrain how they function.

1.2.1 Physical Problems

The diameter of soil pores (from $<0.1 \mu\text{m}$ to $>5 \text{ mm}$, depending on soil type and texture: Brady and Weil 1999, p. 147) allows water to be retained within them by polar forces, hydrogen bonding, cohesion, adhesion and surface tension. Water moves through pores, and drains from them, at rates dependent on pore diameter: large pores are more hydraulically conductive and correspondingly less retentive than narrow pores. The water-filled pores in soil are the pathways through which water and dissolved nutrients reach plant roots. Water moves convectively through soil pores towards the roots in response to the suction generated by transpiring plants. Solutes move in that mass flow of water and they also diffuse through the water down their concentration gradients (Tinker and Nye 2000). Most land plants acquire nutrients from the soil water via their roots, which can absorb ions directly or through their associated mycorrhiza-forming fungi (Chap. 11).

The tortuosity of the soil's pore network reduces the speed at which water and solutes can move from bulk soil to root surfaces compared with their rates of movement in free solution, potentially limiting their rates of uptake by roots and microbes (Tinker and Nye 2000).

Variations in bulk density, water content and particle size distribution influence soil strength, the extent to which soil resists deformation. A root

penetrates soil by deforming it locally (Chap. 6). If a root cannot deform the soil around it, its penetration is opposed by friction and it risks being abraded, buckled and damaged. Soil strength also determines the ability of plants to anchor themselves: it declines with increasing wetness (and also in very dry soils) and this can result in the catastrophic windthrow of trees after heavy rain (Coutts 1986).

1.2.2 Chemical Reactivity

Ions dissolved in soil water exchange with those held electrostatically on the charged surfaces of soil solids including organic matter, and primary and secondary minerals (Brady and Weil 1999, p. 18). These surfaces act as reservoirs that can feed nutrients into, or remove ions from, the soil water in response to disturbances in electrochemical equilibria. Ion exchange between solid and solution phases can partly buffer the depletion of certain ions (e.g. phosphate, potassium) from the solution phase. The concentration of well-buffered solutes may be depleted in the soil around a root compared with their concentrations in bulk soil if the rate of uptake exceeds the rate of supply by diffusion and mass flow (Tinker and Nye 2000).

1.2.3 Biological Activity

Heterotrophic soil microbes decompose organic matter derived from plant, microbial and animal sources. This process liberates CO_2 into the atmosphere (a key link in the terrestrial C cycle) and releases plant-available nutrients (Chap. 13), especially nitrogen (N) and phosphorus (P). The living and dead organic fractions of soil are the major repositories of C and N in soil.

Many important ecological processes occur in soil, although they are often difficult to study. Predator–prey interactions among soil microbes and fauna such as amoebae, nematodes and earthworms and the resulting excretion of waste products drive much of the soil's biogeochemical processes. Plant–herbivore interactions occur when roots are grazed by arthropods and nematodes. Competition for limiting resources such as N can occur between and among microbes and plants and, as with most competitive interactions, it is hard to predict the eventual winner (Hodge et al. 2000). In addition, the soil harbours many potential plant pathogens (e.g. plant parasitic nematodes, fungal pathogens, soil-borne viruses).

All of this biological activity and diversity makes soil perhaps the most complex of all ecosystems. It also means that simple laboratory systems (e.g. Petri dishes, hydroponics) bear scant resemblance to a root system's normal environment. Clean, controlled laboratory conditions are needed to study particular physiological and molecular mechanisms, but they have limited

ecological relevance for which interactions among organisms and processes are of most interest.

1.2.4 Heterogeneity

Soil is not a well-mixed medium. Interactions between climate, parent rock, topography, vegetation, biological activity and the time over which these interactions occur result in soil formation and generate heterogeneity (Rowell 1994, p. 1). These interactions do not occur uniformly and so soil is a dynamic, three-dimensional mosaic whose properties vary from point to point.

Nutrients and water tend to be distributed patchily in soil, depending on the pore-size distribution and localised inputs of organic matter. Gases may also be distributed non-uniformly. In a strongly structured, biologically active soil, anaerobic microsites can persist at the centre of aggregates (Sexstone et al. 1985). Soil bulk density is also spatially variable.

A root system will never experience exactly the same solute concentrations, water potentials or penetration resistances simultaneously over its entire surface. Spatial variation in the resistance of soil to penetration can cause roots to clump in confined soil volumes. The resulting non-uniformity of root distribution can limit rates of water and nutrient capture by the vegetation (Passioura 1991). Consequently, each field site has a unique pattern of heterogeneity. Non-standard statistical techniques are often required to deal with the large spatial and temporal variability inherent to soil data (Ver Hoef and Cressie 2001).

1.3 Evolutionary Solutions

The constraints imposed by soil on photoautotrophic activity were major spurs to the evolutionary modifications to plant morphology and physiology that occurred following the colonisation of land (Raven and Edwards 2001). Nutrients and water are extracted from soil most effectively, and with greatest competitive advantage, if absorbing organs are placed in intimate contact with water-holding pores, ion-exchanging surfaces and regions of microbial activity, and if the positions and activities of those organs are not restricted in time and space. How could this be achieved? The basic 'design requirements', and their solutions, are summarised in Fig. 1.1 and described in detail below.

Figure 1.1 defines the *Bauplan* of a root system: an idealised, generalised, archetype (Niklas 2000). It is easy to argue retrospectively the general selective advantages of this *Bauplan*; after all, this *is* what evolved. Nevertheless, it is difficult to imagine any realistic alternatives to it (Harper et al. 1991).

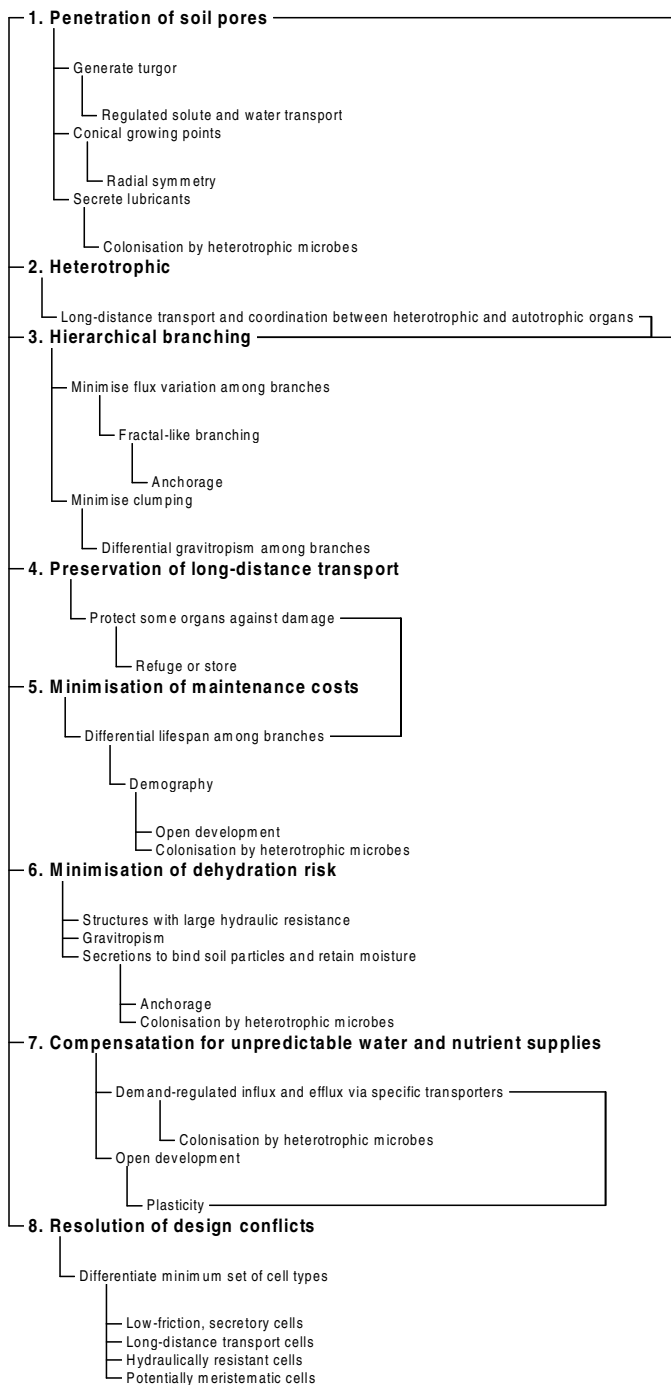


Fig. 1.1. Summary of the 'design requirements' for root systems. Primary requirements are in **bold**; also shown are some of the main secondary consequences arising from these. See Section 1.3 for details

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