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Edited by P. J. Gregory, J. V. Lake and D. A. Rose
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ROOT DEVELOPMENT AND FUNCTION

Root development and function

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PREFACE

In planning this volume, we have tried to give equal weight to root development and root function and to treat both in relation to the whole range of physical environmental factors. These clearly include temperature, gravity, light and the mechanical impedance of the soil. But the boundary with the chemical environment is not sharp and our list thus includes water, which interacts with the ionic strength of the major nutrients in the soil solution. We include also soil aeration, which bears on both the access of oxygen and the escape of gases generated in the roots or soil. All these factors vary with depth in the soil and with time, adding greatly to the complexity of the subject.

The physical environment affects also the organisms associated with roots, but as will be seen, experimental evidence on the size of any such effects on mycorrhizae or nitrogen-fixing bacteria is scant.

Where possible, the approach is quantitative, including comparisons between species or between cultivars within a species, partly as a safeguard against generalizing about the probable underlying mechanisms and partly to inform those engaged in plant breeding or genetic manipulation.

After a prologue, on interactions between factors in the physical environment, we consider the effects of these factors on root development and root function, each at four levels of organization - cells, tissues, single plants and plant communities. A concluding synthesis identifies opportunities for closing important gaps in our knowledge of the subject.

This volume is based on the review papers presented at the Annual Meeting of the Environmental Physiology Group of the Society for Experimental Biology and held jointly with the Association of Applied Biologists and the British Ecological Society, at the University College of North Wales, Bangor, from the 26th to the 28th March, 1985. We thank the Group and the two societies for their generous financial support.

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P.J. Gregory,
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PROLOGUE: INTERACTIONS IN THE PHYSICAL ENVIRONMENT OF PLANT ROOTS

J.V. Lake

INTRODUCTION

Plant roots modify and interact with each of the physical factors in their environment, but only with gravity is the interaction always negligibly small. Usually roots grow in soil, but occasionally, in experiments or in a natural environment, they will be in air or water. I shall treat each physical factor in turn and indicate its interactions with others and with the plant roots. Many of the factors affect also the growth and function of the plant shoot and this in turn can have second-order effects on the soil, but I shall not attempt to specify them all.

TEMPERATURE

Close to the soil surface, temperature gradients are steep and the amplitude of the diurnal variation is greatest. A gradient of >6 K cm^{-1} in the 2 to 4 cm soil layer and an amplitude of 56 K at 0.4 cm depth were measured by Sinclair in 1922 in the Arizona desert (Sutton, 1953) and have been exceeded in various reports since, although not often convincingly. By contrast, at a depth of 50 cm, i.e. within the rooting range of many plant species, the temperature remains essentially constant by day, although still varying with season. Thus steep and rapidly changing positive or negative temperature gradients can exist along the length of a root, no doubt affecting both structure and function, but most experiments have avoided these complications.

By virtue of their water content, roots will be relatively good conductors of heat compared with the surrounding soil if it is dry, but their heat capacity will be relatively small, so root and soil temperatures are unlikely to differ greatly. A larger interaction of roots with their thermal environment results from the effects of root activity in changing the structure and water content of the surrounding soil.

In the chapters that follow, distinctions will be noted between

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the effects of temperature on development, growth and function. For example, the shape of the temperature response curve for the cell cycle, or for the induction of lateral primordia, may be quite different from that for cell expansion or root extension. Some of these measured effects (e.g. in relation to so-called thermal time) are reproducible and predictable, but have not yet been subject to biochemical interpretation.

GRAVITY

In our context, the strength and local direction of the gravitational field are almost uniform over the earth's surface. Gravity is only one amongst many factors determining the direction of root growth, but in an otherwise isotropically uniform environment the angle of a particular root to the vertical will depend on its order in the system of branching and on the strength of the gravitropic response of the species or cultivar. Research on the gravitropic response has been especially rewarding in providing increased understanding of growth regulation at the cellular level in roots, although the fundamental nature of the cell-signalling process that elicits the response itself remains unknown.

Environmental factors are rarely independent in their effects on root growth or function. In some species, the strength of the geotropic response depends on the duration, flux density and spectral composition of any light reaching the root apex. The response is minimal in darkness, but brief illumination to allow visual examination of the roots may suffice to elicit gravitropic curvature (Lake & Slack, 1961). The details of this interaction and its spectral dependence are obscure.

LIGHT

In a sandy soil, light may be transmitted through the mineral particles, usually with change in its spectral composition (Mandoli *et al*, 1982), and in all soils light may be transmitted through a film of water or through cracks. The roots themselves may act as light pipes (Mandoli & Briggs, 1984), altering in the process the spectral composition of the light so transmitted, and thus again interacting with their soil environment.

In some plant species, light has no effect on root growth. In others, light of appropriate spectral composition reaching the root apex by whatever means will slow root extension and elicit a gravitropic response (Lake & Slack, *loc. cit.*). Clearly, a competitive advantage may be conferred by the resulting ability of the root system to respond to environmental stimuli other than gravity in the soil and so to extend into zones favourable for growth and function and yet avoid surface layers where the environment may be favourable only transiently.

Light affects root growth indirectly also through regulating plant dry matter production and its partitioning between shoot and root.

MECHANICAL IMPEDANCE

A root extending through soil may force the particles aside, overcoming the mechanical impedance, or may be diverted to travel around the particles if the impedance is too great and if space allows. Similarly, a root may displace or be diverted around an aggregate of small particles. The mechanical impedance will vary between horizons in a soil profile and sometimes within a horizon if the passage of tillage implements or wheels has caused compaction. It will vary also depending on root diameter.

The passage of roots through the soil can alter the subsequent mechanical impedance, first through the effect of root exudates in providing lubrication for the passage of the root tip, second through the subsequent drying by absorption of water for transpiration and third through the creation of channels that can persist and so alter the effective mechanical impedance encountered by succeeding roots.

The conditions in the soil, e.g. dryness and compaction, that tend to increase mechanical impedance also affect access to the roots of air, water and mineral nutrients, so that carefully controlled experiments are necessary to estimate the actual effects of impedance. Although it is then found to slow extension, the evidence for any effect on development at the level of cell differentiation seems equivocal (Barlow, Chapter 1). Yet some effect might be expected because a principal factor contributing to positional recognition for a differentiating cell is thought to be the pattern of mechanical constraint by neighbouring cells (Barlow, 1984).

WATER

Apart from gravity, all the physical factors in the soil are modified by water. Hydraulic conductivity and diffusivity markedly affect the rate of absorption of water and both are complex functions of water content. Different components of the soil water potential near the root surface affect different processes in root growth and function. Steep gradients of both content and potential are common in soils and are a prime cause of gradients in both physical and chemical environmental factors along the length of the root.

Roots interact with soil water by exudation and absorption, but also by shrinking or swelling and so varying the area of their contact with the soil. This process may account for otherwise puzzling experimental observations on root function. Since water is transported to roots down a gradient of soil water potential, instrumentation that would enable potential gradients to be measured close to roots without significantly altering the flow or affecting the environment would advance the pace of research on plant water relations.

As soil dries, the ionic strength of nutrients in the soil solution may increase to a point where the osmotic potential in the soil becomes a significant component of the total water potential, although affecting water uptake only to the extent that the relevant membranes in the root tissue are semi-permeable to the ions concerned. On the other hand, the transport of mineral nutrients to roots in the soil solution may become impaired in drying soil, through a decrease in the diffusion coefficient, causing a deficiency close to the absorbing roots.

SOIL AERATION

The resistance to gas exchange between roots and the atmosphere depends not only on the volume of air-filled pores in the intervening soil layer, but also on the geometry of the pore space. Clearly, both depend on structure and water content. Pore geometry depends also on the ability of the soil to develop fissures through the effects of wetting, drying or frost and on the persistence of these fissures and of channels left (e.g. by the passage of earthworms or plant roots).

Clearly even in compact and flooded soil the partial pressure of oxygen and other gases will be in equilibrium with the atmosphere if the soil is sterile. Gradients of oxygen partial pressure are caused by the respiratory activity of roots and soil organisms; aeration is then a prime example of interaction between roots and soil.

Although the soil itself can be characterised by its diffusive resistance to oxygen transport, the oxygen partial pressure at the root surface depends also on the rate of root respiration; this is why waterlogging in winter may not be disastrous. Under conditions where root respiration is oxygen-limited the oxygen partial pressure at the root surface is presumably close to zero and the oxygen flux density to a sensor at zero potential can be used as a measure of aeration (Blackwell & Wells, 1983).

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With sparse rooting, the oxygen supply may originate from zones in the soil unoccupied by respiring organisms, rather than by a direct pathway from the air above the soil.

A decrease in oxygen partial pressure may increase the production of ethylene by soil micro-organisms and plant roots and the diffusion of ethylene away from the production sites depends on the air-filled pore volume and geometry. An increase in the ethylene concentration in plant roots caused by poor aeration can in turn result in the formation of aerenchyma - gas filled spaces within the cortex that facilitate acropetal diffusion of oxygen within the tissue; aeration is then, to some extent, restored.

In some species, poor aeration moderates or reverses root gravitropism, probably through an effect of ethylene. Such a response may be beneficial in bringing roots closer to the usually better-aerated surface soil (Jackson & Drew, 1984).

CONCLUSION

The above examples illustrate that interactions, which are not additive, characterize the relationships of soil physical factors with one another and with plant roots. These interactions should be kept in mind in the following chapters, where attention is turned to the plants themselves at various levels of organization and where inevitably the environmental factors tend to be treated one by one.

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