ELBS

Plant Root Systems

Their function and interaction with the soil

R. Scott Russell

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Plant root systems:

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R. Scott Russell
Formerly Director
Agricultural Research Council
Letcombe Laboratory

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Preface

This book is concerned with the growth and function of the root systems of plants in the soil which is their natural environment. It is a broad subject; the developmental physiology of plants and the physics, chemistry and microbiology of the soil all come within its scope. To attempt a comprehensive discussion in a single volume would be impracticable, but a narrower approach could not provide an adequate basis for considering the responses of root systems to the soil which can influence the growth and productivity of plants. This is to me the subject of central interest and fortunately it is now easier than at an earlier time to attempt a synthesis of information drawn from the plant and soil sciences. Some of the increasing opportunities and incentives – both academic and agricultural – for interdisciplinary studies are considered in the opening chapter.

The selection of topics for fuller discussion later in the book has been mainly guided by the criteria that they are germane to understanding soil/plant relationships, that they lie across conventional boundaries between the plant and soil sciences and that the inadequacy of present information is a particular encouragement to further study. Experts in individual fields will recognize that many important aspects are considered only cursorily and the reader is referred to the extensive literature for fuller information.

The book is addressed to advanced students or research workers who have been trained in one or other of the plant, or soil, sciences and are attracted to exploring relationships between plants and the soil. Although I have referred mainly to the growth of agricultural crops, much of the discussion also has application to the study of natural vegetation.

It is a pleasure to express my indebtedness to those without whose

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encouragement and aid this book would not have been written; they have no responsibility for its limitations. First in time came the late Professor F. G. Gregory and Professor Helen Porter at the Imperial College, London, who initially encouraged me to consider the physiology of the whole plant. Later there was the fortunate opportunity for association successively with Professor E. W. Russell and the late Dr R. K. Schofield on soil/plant problems in Oxford. More recently, with my colleagues at Letcombe, it became possible to develop these interests further. I am most grateful to those who have discussed and commented on parts of the book during its preparation – Drs D. A. Barber, J. R. Burford, R. Q. Cannell, D. T. Clarkson, M. C. Drew, F. B. Ellis, K. Gales, M. J. Goss, M. B. Jackson and J. M. Lynch of Letcombe and Dr M. P. Greaves of the Weed Research Organization – and especially Dr M. G. T. Shone who read the entire manuscript. Messrs M. A. Ward and K. B. Whorwood assisted in the drafting of diagrams and the checking of references. Mrs S. M. O'Driscoll gave invaluable secretarial help. My wife prepared the author index having already tolerated a shared existence with the manuscript for too long a period.

R. Scott Russell

Letcombe
1977

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One

Introduction

> Of the two environments in which plants grow, the soil is much the more complex. This is true whether air and soil are each considered from the physical, chemical or biological viewpoint. The soil not only affects the development and activities of roots directly, but also, by modifying the function of roots, it affects the growth and yield of the above-ground parts . . . to a large degree, soil is a product both of climate and vegetation.
>
> *Weaver (1926)*

It is now half a century since Weaver's classic *Root Development of Field Crops* was issued by the same publisher as this book. The opening sentence of his preface described his subject as 'greatly neglected'. The same claim could have been made more recently; plant and soil scientists have usually found little common interest in the study of the growth and function of root systems in the soil. Working often in separate faculties of universities, or departments in research institutes, their lines of enquiry steadily diverged. The situation is now changing; the results of past research have revealed new avenues of enquiry, the exploration of which requires their combined skills, and the needs of agriculture have provided new incentives to this joint endeavour. A brief review of some aspects of this changing situation can help both to identify approaches which may be most profitable in the future and to understand why information is now so limited on a number of topics discussed later in this book.

One obvious discouragement to investigating the growth and function of root systems has been their variable form and their extensive branching, which complicate experimentation especially when they are concealed by the soil. But this only partially explains why the subject did not receive more attention. A more cogent reason was that, by comparison with other subjects, the performance of root systems seemed of minor interest. Different considerations led plant physiologists and soil scientists to the same conclusion.

To physiologists, the above-ground tissues of plants presented the most intriguing and important problems, the central role of photosynthesis in plant metabolism being the most obvious reason. By comparison, until relatively recently, roots were thought to fulfil only the secondary roles of absorbing water and nutrients and anchoring plants in the soil. The detailed study of root systems was perhaps also discouraged because, when they experience a uniformly favourable environment, their size can much exceed that necessary to supply the needs of the plant. Thus, when methods for the quantitative analysis of plant growth were developed, shoot tissues alone were often considered; 'whole plant physiology' in reality often meant the physiology of the shoot system alone. The mechanisms responsible for the absorption of ions were extensively studied but physiological interest mainly centred on transport processes across membranes, as opposed to the integrated performance of the intact root system; fragments of root, slices of storage tissue or algal cells were often the preferred experimental materials. Forty years ago there was novelty in Steward's endeavours to identify the zones of the root systems of intact plants in which absorption was most rapid (e.g., Prevot and Steward, 1936) and as a later chapter will show (pages 75–82) this subject remained largely unexplored until new techniques became available.

Perhaps the nutritional relationships of plant root systems would have received greater attention from plant physiologists if the earlier soil scientists had not been so successful. Pioneers such as Boussingault, Lawes and Gilbert laid the foundations of modern fertilizer technology before the middle of the nineteenth century. They realized that the nutrient requirements of crops, could be identified largely by observing the effects of added nutrients on their growth and by measuring the quantities of inorganic substances present in them and in the soil. This approach, which involved little consideration of root structure, led to considerable increases in the productivity of crops several decades before knowledge of plant physiology had developed sufficiently for it to be helpful in this work.

The manner in which the physical structure of the soil can influence the movement of water and the ingress of air received much attention from soil scientists but the effects of other aspects of the soil environment on root growth were little considered. It was widely recognized that the penetration of roots could be restricted by the compaction of the soil and before the end of the nineteenth century Pfeffer (1893) carried out the first quantitative study on this question but it did not again receive much attention until sixty years later (see chapter 8). Meanwhile interest grew in the microbiology of the soil, especially in the fixation of nitrogen, but inorganic fertilizers were so successful in improving plant growth that the influence of the microflora of the soil on the absorption of nutrients by plants was often thought to be of minor importance. It was not surprising, therefore, that discussions of how soil conditions affect plant growth were concerned largely with chemical and physical properties which influence the supply of nutrients in the solution phase, with the movement and storage of water or with aeration.

The middle of the present century saw a change in emphasis. It arose partly from increasing knowledge of the physiology of root function and partly from new agricultural needs. Academic and practical interests stimulated each other. Research on the hormonal mechanisms which control plant growth led to the realization that the absorption of water and nutrients is only part of the function of root systems. They are also the source of compounds which are involved in regulating development throughout the entire plant; the effects on shoot growth of anaerobic soil conditions have, for example, been found to be due at least partially to the modification of the synthesis of hormones in roots or their translocation to shoots. It is now evident that the explanation of many responses of the above-ground parts of plants to environmental factors can be adequately explained only if the performance of their roots is also considered.

These developments have many implications for the conduct of research designed to enhance crop production. A major aim in such studies is often to increase the photosynthetic efficiency of plants; the importance of this question is obvious because the amount of solar energy which crops utilize is usually but a small fraction of the theoretical maximum (see, for example, Penman, 1971). The earlier idea that, from this viewpoint, it was necessary to take account only of the structure and development of the shoot system is now called in question; the possibility must also be considered that root function may have an important, though indirect, effect. Thus, the manner in which root systems respond to their environment is coming to occupy a more central place in physiological studies. The publication of two comprehensive symposium volumes while this book was in preparation (Carson, 1974; Torrey and Clarkson, 1975) reflects the recent trend. Changing agricultural needs have made it particularly timely.

In the western world, where the modern scientific study of agriculture began, there was a long-established tradition that elaborate tillage and crop rotations, supplemented appropriately by land drainage and the use of fertilizers and manure, were essential to maintain the fertility of the land. The value of this laborious work was unquestioned by the earlier generations of agricultural scientists – labour was cheap, the fertility of the farmlands in Europe had in general been increased by these methods; moreover, the disturbance of the soil was necessary for the control of weeds. Tillage was thus widely regarded as a wholly beneficial procedure and a main determinant of the yield of crops. Developments during the present century have now led increasingly to the abandonment of this belief. Sometimes there has been an urgent need to restrict the extent of tillage to avoid soil erosion and to conserve water in new agricultural lands. Sometimes innovation, stimulated by the rising cost and scarcity of labour, has led to the realization that the productivity of some soils can be fully maintained if tillage is simplified or even eliminated – a development lately much facilitated by chemical herbicides.

The study of how the soil can best be cultivated has thus become a major subject of agricultural enquiry. In many countries one of the obvious needs for expanding food production, to meet the needs of a growing population, is to find ways of utilizing land which has hitherto been unproductive; elsewhere the current economic incentives to reduce the effort and energy expended on crop production must be expected to continue. There are two obvious requirements – to identify the restraints to plant growth which soil conditions can impose and to develop the most efficient methods for circumventing them, taking account of local circumstances. The first task lies jointly with plant and soil scientists; the second depends on the application of their findings by agronomists, engineers and farmers. To emphasize these needs is not to suggest that they provide the only avenue to increased agricultural production. The importance is obvious of developing new crop varieties and improved methods for the control of pests and diseases; the avoidance of the large post-harvest losses which now occur through the spoilage or misuse of agricultural produce could also make a great contribution. None the less the considerable restraints which soil conditions now often impose on the productivity of agriculture is evident.

There are thus powerful stimuli for plant and soil scientists to work together. But the difficulties which beset such enterprise must not be disregarded. They arise in any attempt to study complex systems. In 1959 Professor Porter (1960) discussed the dilemma which must be faced in deciding how the growth of plants can be most profitably studied; her views apply equally – or more – to the study of the still more complex soil/plant system:

> The problem before the physiologists is how best to study such a complex system. How can we find out first what it will do and how it does it? There are two main avenues of attack. The behaviour of the system under a variety of environmental conditions can be observed and also recorded in a quantitative manner by measuring such things as

> area of the leaves, the rate at which they emerge, . . . and so forth. To some this seems an unsatisfactory procedure because it cannot tell us how things happen in molecular terms. The alternative is to pull the system to bits and study its components, *knowing that in so doing most of the parts will get damaged and their behaviour in isolation may be quite different from that in the intact organism.** These two lines tend to diverge from one another at present. . . . Physiologists, according to their training or temperaments or perhaps by chance, may, I think, be divided into groups. What we might call the extroverts, who follow the first method and study the plant as a whole, and the introverts, who adopt the second and plunge into the realms of enzymology and organic and physical chemistry, not to say physics, and there are as well the schizophrenics, who have a foot in both camps and try to stem the divergence of viewpoints.

Professor Porter's statement underlines the fact that, although progress in understanding any complex system depends largely on detailed studies on its individual components, the relevance of this information may be uncertain unless the system is also considered as a whole. This is the only way to show whether, during the dissection of the system, some of its parts were so distorted that their behaviour became unrepresentative, or indeed whether some important ones were entirely overlooked. The recognition of this need does not, however, answer the essential question: is it now practicable in some useful degree to stem the divergent viewpoints from which plant physiologists and soil scientists have usually approached soil/plant relationships? Will the attempt to do so usually yield only an unco-ordinated – or 'schizophrenic' – assembly of trivial observations which equally lack scientific interest and practical relevance?

It is the thesis of this book that some useful progress can now be made provided that the individual components of the system are first examined separately and that the limitations of any synthesis which can now be attained are recognized. It would, for example, seem premature, until many present uncertainties have been resolved and the main rate-limiting factors under different circumstances are more clearly defined, to propose elaborate procedures for predicting the response of crops to the varying conditions of soil, nutrition and weather which they experience in the field. But none the less this development of predictive models is an eventual aim.

These considerations have determined the structure of this book. The obvious starting point is to consider the responses of the whole plant and especially its root system when its full potential for growth can be reasonably displayed – that is to say in the absence of the stresses which soil conditions frequently impose. *Part I* is concerned with this subject. The co-ordination of growth throughout the plant is examined in the opening chapter; thereafter the form of root systems, and their absorption of nutrients and water are discussed, emphasis being given to aspects relevant to the integrated performance of the

*The present author's italics.

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