

Preface

I congratulate Professor Guoping Zhang with the completion of the translation of *Plant Physiological Ecology*. All three authors of this book were delighted with Professor Zhang's plan to make an abbreviated translation, and we were also very pleased that Springer-Verlag supported his initiative. From my personal experience, I know that the book will be used widely, by students interested in agriculture, horticulture and forestry as well as by those interested in natural ecosystems. China is rapidly increasing its production of food and fibre, to satisfy the demand of its growing population. To do so, a sound understanding of plant functioning in managed systems is essential. China also harbours one of the world's 25 hotspots of biodiversity. To preserve this natural resource, a profound understanding of how this natural system functions is important. This translation should help students to better understand plant functioning in managed and natural systems.

Plant physiological ecology is a discipline of plant science that is rapidly increasing in importance in China, as it is elsewhere in the world. There has been a vast increase in publications by Chinese authors on plant physiological ecology in the international literature. I have made a couple of visits to China in recent years, and lectured at a range of institutions there. I am impressed by the interest in plant physiological ecology, and how fundamental knowledge is being used for a better understanding of practical problems. These problems often relate to agriculture or horticulture. Excellent papers on intercropping and soil sickness have been published by authors based in China. Other problems deal with the effects of increasing pressure on China's natural systems.

In the past few decades, ecophysiologicalists have accumulated a wealth of information on above-ground plant traits and processes. Therefore, we now have a very good understanding of leaf gas exchange in different environments. Early research concentrated on major differences between C_3 species vs. C_4 and CAM species. In the more recent past, sophisticated portable gas-exchange equipment and stable-isotope analyses have been used to assess leaf photosynthetic performance. This has led to the appreciation of more subtle differences amongst C_3 species, e.g., along moisture gradients, in different parts of the canopy, and as dependent on habitats that induce differences in plant nitrogen or phosphorus status. Leaf traits such as turnover, specific leaf area, and the associated anatomy have been studied in comparisons of fast- and slow-growing species and species from widely different habitats. These traits have also been correlated with gas-exchange characteristics, showing distinct trends amongst species from contrasting habitats. These general trends, e.g., rate of photosynthesis vs leaf nitrogen concentration and RGR with habitat, are now well known. However, equally well known are numerous exceptions, which have hardly been given any attention. These exceptions might tell us at least as much as the general trends. In comparison with our relatively good understanding of the structure and functioning of leaves in contrasting habitats, our understanding of roots is still very limited.

What would be equivalent root traits that would need to be studied to obtain a better understanding of below-ground plant functioning? The below-ground counterpart of photosynthetic carbon acquisition strategies are strategies of nutrient acquisition. These may involve symbiotic partners, e.g., rhizobia (to acquire N) or mycorrhizal fungi (to acquire nutrients that diffuse very slowly in soil, e.g., P). We still have to

learn a lot about the significance of different mycorrhizal systems; this knowledge is the below-ground counterpart of what we know about subtle differences in C_3 photosynthesis between species. Alternative strategies for nutrient acquisition depend on the exudation of a range of compounds that enhance the availability of nutrients in the rhizosphere. This strategy is most pronounced in species that make 'proteoid' or 'cluster' roots. The strategy to depend on root exudates appears an alternative to the mycorrhizal strategy, i.e. most species with cluster roots have no or weakly developed mycorrhizal associations. Root traits such as root turnover, specific root length and the associated anatomy are now being studied for fast- and slow-growing species. However, we are still to investigate how these traits relate to nutrient acquisition. Clearly, below-ground components of higher plants need to be studied in far greater details to obtain a better understanding of the functioning of plants in their environment.

Interactions between plants and surrounding organisms

Plants share resources and frequently compete for them. They may compete by using essentially similar, but more effective, mechanisms to acquire the resources (resource competition). Alternatively, they may compete using chemicals that interfere with the neighbour's growth or metabolism (interference competition or allelopathy). Interference competition is a fact of nature, but many of the results published in this area can be interpreted in an alternative manner. Of particular interest are the competitive (allelopathic) interactions between mycorrhizal and non-mycorrhizal species. Interactions between mycorrhizal species may be positive, but those between non-mycorrhizal and non-mycorrhizal species are frequently negative. This should warn us against a simplistic interpretation of phosphate fertiliser trials. Phosphate fertilisation may suppress the mycorrhizal symbiosis, and thus reduce the negative effects the mycorrhizal fungus has on the non-mycorrhizal species.

Chemical interactions between plants can also be positive (facilitation). For example, white lupin may mobilise sparingly available phosphate in its rhizosphere, and neighbours may benefit from this. This principle can be exploited in agriculture, e.g., in the intercropping systems in China, where these interactions may increase yields significantly.

Chemical interactions also play a role in the signalling between host plants and their microsymbionts or parasitic plants. Chemical signals are released by the host, and recognised by the microsymbiont, which then releases signals that are recognised by the higher plant. The system has been studied in the greatest detail in the legume-rhizobium system, but it is bound to be equally significant in mycorrhizal systems. In the case of parasitic plants, the signal that is released by the host may be a cue for germination or for haustorium formation. Understanding the signals between host and parasitic plants may help us control the plant parasites, which frequently become pests in Africa and Asia.

Other fascinating chemical interactions between plants and surrounding organisms include the attraction of 'bodyguards' upon attack by herbivores. Once thought to be a curiosity, it is now thought to be fairly common.

Interactions between plants and their neighbours are not invariably chemical, but may involve the phytochrome system. This phytochrome system is used to 'sense' neighbours, and avoid close contact.

Root exudation

Root exudation is significant both as a strategy to mobilise sparingly available nutrients in the rhizosphere, as discussed above, and it is also very important in the process of detoxification of aluminium and lead.

Citrate is frequently a major component of root exudates. However, its effect on phosphate mobilisation, relative to the effect of malate, strongly depends on soil pH. At high pH, malate is rather ineffective, and chickpea and white lupin release very little malate and large amounts of citrate under those conditions. At low soil pH, malate is as effective as citrate, but, containing only 4 carbon atoms as compared with the 6 carbon atoms in citrate, is more efficient. Thus, this response appears to be adaptive. Is this response unique for these two crop species, or is it fairly common? How is this soil component associated with pH 'sensed' by the roots? What is the signal-transduction pathway between sensing pH and releasing the appropriate composition of carboxylates? These are clearly challenging developments in this area that is only just opening up. There are also indications that roots sense other soil components and respond to these much in the same way as they respond to soil pH.

Citrate, malate or oxalate are major carboxylates in root exudates that are released upon exposure to aluminium in the rhizosphere by aluminium-resistant genotypes. The exact compound that is released depends on species, but the effect is similar – precipitation of aluminium by the exudate carboxylates. There is also evidence that oxalate release by lead-resistant rice genotypes confers resistance to lead in the root environments. Other heavy metals could be detoxified in a similar manner by root exudates, but as yet there is no evidence to support this contention. Exudate release might offer a strategy to engineer plants with greater resistance to heavy metals, if the exudates precipitate these metals. Alternatively, root exudation might enhance the mobility of heavy metals and allow plants to remove these from the soil more rapidly, in a process generally called phytoremediation.

Plant ecophysiology in the 21st century

More than ever, plant ecophysiology depends on the use of a wide range of 'tools'. These include molecular tools, which, for example, have been used to elucidate the role of the phytochrome system in sensing neighbours. Molecular tools will be vital in elucidating how soil pH and as yet unidentified soil components are sensed. If *Arabidopsis thaliana* shows the same response as chickpea and white lupin, carboxylate-releasing accessions of *A. thaliana* might be used to elucidate these fascinating aspects of ecophysiology.

Molecular tools will also be valuable in assessing root exudation *in situ*, using reporter genes that allow the detection of specific exudates. This will provide us with more detailed information which exudates are released in time and space.

Despite the increasing need for molecular tools, we must not forget the other end of the spectrum, that is the plant's ecology. Investigating plants and the natural habitat in which they have evolved for millions of years is vital for our understanding of adaptive traits. For exactly that reason, locations of Western Australia which have not been disturbed by recent glaciations, are of enormous significance for ecophysiologists. These are natural laboratories which offer numerous examples of close associations between plant species that occurred in the same or similar environments for millions of years, and that specific environment. Plant ecophysiologists should use these natural laboratories to learn more about interactions between plants and their natural environments. Thus, they will discover vital traits that might be used in developing crop species that are better able to cope with their managed environment.

What are the key aspects plant ecophysiologists might focus on? Global change remains a popular and relevant area. However, if we need to feed a growing world population, non-renewable resources such as phosphate deserve more attention. In the industrial world, phosphate is not considered a major issue, because of liberal use of fertiliser and import of phosphate in animal feed from developing countries. Occasionally, phosphate is a pollutant in the industrial world, because of leaching and run-off into rivers and streams. Since most of the ecophysiological research is carried out in rich, industrial countries, research on efficient acquisition and use of phosphate has not received the attention it deserves. Much is to be learned from native plants that naturally grow in phosphate-impoverished soils, and from crop species that require less input from phosphate fertilisers than most, e.g., cereals. The genus *Lupinus* offers a unique opportunity, in that few species of this genus bear 'cluster' roots which makes them superior crop plants in phosphate acquisition. A better understanding of the biology of cluster roots might help us develop other *Lupinus* species with 'cluster' roots, and ultimately crop plants of other genera with these superior traits. The remarkably high sensitivity of species that have evolved on phosphate-impoverished soils to phosphate fertilisation offers another challenge. Understanding the phenomenon of phosphate toxicity in these species might lead to a better understanding of the metabolism and sensing of phosphate in higher plants.

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