

张国平 周伟军 译

植物生理生态学

Plant Physiological Ecology

[澳] Hans Lambers

[美] F. Stuart Chapin III 著

[荷] Thijs L. Pons



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Hans Lambers F. Stuart Chapin III Thijs L. Pons
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《植物生理生态学》翻译组成员名单

组长：张国平

周伟军

组员：韦康

王丹英

王美娥

张国庆

顾宏辉

程旺大

殷琛

邵国胜

王丰

汪军妹

译者序

过去的一世纪,特别是第二次世界大战以来,人类社会取得了前所未有的经济高速发展,总体上人们的生活水平得到了快速提高,不少国家与地区展现出一种全新的繁荣景象。但是,与此同时,人口、粮食、资源、环境等问题日益突出,人口不断扩大,要求生产更多粮食和其他农产品,要求提供更多的建筑材料和空间。耕地的过度扩展和集约化化学产品的大量投入(包括化肥、农药、农膜等)导致环境剧变或退化,从而影响甚至威胁人类的生活方式乃至生存。当前,高效利用自然资源、保护人类生存环境和促进可持续发展已成为时代的强音。在科学上,在以阐明植物生长发育、物质生产、资源(水、肥等)获得等基本生命活动的植物生理学和阐明群落内种间关系与互作以及物种环境适应方式的植物生态学不断发展与深入的基础上,逐步形成了由以上两门学科交叉的一门新兴学科——植物生理生态学,它以生态学和植物生理学紧密结合的形式阐明植物的基本生理生态过程及其与环境的互作。上世纪90年代后该学科又迅速汇入了分子生物学的理论与研究方法,即在宏观拓展的同时在微观上得到了深入,使植物生理生态学发展到一个新的水平。

也许是由于植物生理生态学是一门快速发展的新兴学科,迄今很少有全面介绍这一领域研究进展的专著问世。尤其在国内外,已有不少高等院校陆续为本科生和研究生开设了植物生理生态学课程,校译者也已为研究生讲授这一课程多年,但一直缺乏相应的高质量教材或参考书。两位译者几年前分别在日本和瑞典从事合作研究时接触到由 Hans Lambers 教授等人编写的植物生理生态学(Plant Physiological Ecology),阅读后可谓耳目一新,认识到该书内容新颖、系统,特别是有关植物水分和养分利用的种间及种内差异的生理生态机制、植物对逆

境的分子生理反应和生态适应性、物种间互作的分子机理与生态学意义等内容,均为当前本学科研究前沿和热点。为此,我们在承担的相应课程中引进了该书的内容,收到了很好的教学效果。同时,为了使我国有更多的人从中受益,我们萌发了将其翻译为中文的念头。

本书由三位在植物生理生态学研究领域享有盛名、分别来自澳大利亚、美国和荷兰的著名学者撰写,其中 Hans Lambers 博士目前同时兼任着澳大利亚西澳大学和荷兰乌得勒支(Utrecht)大学的教授,是国际著名刊物“植物与土壤”的主编,在植物营养生态学和遗传学上研究成果卓越,其他两位作者在研究方向上各有特色和专长。正如英国布里斯托尔(Bristol)大学 David Clarkson 教授在原书序言中写道:“本书非常适当地以植物从大气中获得碳为切入点:光合作用无疑是地球上所有生物的基础,已经有无数杰出的植物科学家尽其毕生精力在这一领域进行了研究,从而使人们对光合作用的分子生物物理和生物化学要比其他所有植物生命过程有更多的了解。同时,不同环境变量对光合作用生理学及其调节也有很多研究。但是,光合作用发生在一种植物个体无法控制的环境中,即植物必须对付不同的温度、雨量、光强、二氧化碳等条件。植物不能改变这些环境,必须通过其灵活的生理反应减轻这种环境的不良影响。本书的后面一部分,焦点落在地下部位:为了改善养分供应,植物可以改变根际环境,在征集养分中它们从微生物的活动中得到益处。本书最后,讨论了植物与微生物之间的互作,植物进化过程中的生化对策,帮助它们与其他生物的竞争与生存斗争。”由此,我们可以领悟本书的主要内容及其特色。

尽管在“译作”伊始,我们已意识到这是一项十

分耗费精力的艰难过程,但实际翻译过程中遇到的困难远远超出了我们的预期。该书涉及的专业跨度大,新僻词汇多,给我们正确的遣词和表达带来了极大的困难,不少地方使我们深感力不从心。值得庆幸的是,我们可以借助本校图书资料丰富和学科与专业人才齐全的优势,从而减少谬误。但是,由于校译者水平有限,加之时间仓促,此书中文版译文中肯定还存在不少问题甚至错误,敬请读者谅解,并衷心希望批评指正,以便在再版时更正。

参加本书翻译的人员有韦康(缩写、名词解释)、王丹英(第2章)、王美娥(第2章)、张国庆(第2章)、顾宏辉(第3、4章)、程旺大(第5章、第8章)、殷琛(第6章)、邵国胜(第7章)、王丰(第9章)、汪军妹(第10章)等,第1和11章由张国平翻译。全书由张国平和周伟军校阅。肖玉苹、黄有总、戴飞、何云、许玲等同学也参与了本书的校订和绘图工作。

本书的校译者十分感谢三位原作者特别是

Hans Lambers 教授对我们开展本项工作的大力支持,他欣然为本中文版作序,多次来函提供勘误材料,并在校译者之一张国平教授访问西澳大学和他任浙江大学访问期间解答有关问题,这些对减少校译错误无疑是很有作用的。校译者感谢斯普林格(Springer)出版社在理解中国专业图书出版特点的基础上,仅收取象征性的版权费授予了我们本书的中文版版权,这是我们的目标得以实现的关键。我们也要感谢浙江大学为本书提供了专项出版基金。浙江大学出版社的王锴博士为本书的编辑付出了大量心血,在校译过程中得到本校常杰教授、陈学新教授、傅承新教授、唐桂礼编审、杜玲玲女士等同仁的帮助,在此一并致谢。

张国平 周伟军

2005年4月12日于杭州华家池

《Plant Physiological Ecology》中文版序

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 are. 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 released 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 ecophysiologicalists. 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 ecophysiologicalists 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 ecophysiologicalists 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 make 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.



Hans Lambers

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