Preface

Nitrogen: Too Much and Too Little of a Good Thing

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Nitrogen, plants, and the environment, the three intertwined themes of this volume, are not only of interest in their own right but also can be viewed from an anthropocentric perspective: Humans and plants interact with environmental nitrogen (N) from opposite poles. We, as all terrestrial vertebrates, ingest a daily excess so that our average excretion of urinary N (16 g/d) is the equivalent of the protein N in 1000 soybeans (~250 g)—protein that the plant dedicated the major portion of its "lifetime N" to deposit. We hunt, gather, cultivate, and industrially fix our N, whereas plants are usually N-limited. N presents a challenge to plants as arguably the major limiting environmental mineral nutrient. However, anthropogenic excesses of N (e.g., in artificial fertilizer, combustion of bio- and fossil fuels, and in poorly treated waste), present other environmental challenges to plants and to the biosphere in general. The proper stewardship of plants can lead to amelioration of many environmental problems, including those brought on by too much, or too little, N. Stewardship, of course, begs an understanding of the bio/chemical transformations of N and of how plants acquire and use it.

On a dry weight basis N is the most abundant plant macronutrient derived from the soil. It is also one of the three plant macronutrients (NPK) in common compound fertilizers. In relative abundance N is significantly higher than phosphorus (P) in plant dry weight[1]. To be utilized N and P must be presented to the plant in proper chemical form, meaning that abundance of these elements in the environment is not necessarily equivalent to their availability to plants. The atmosphere is about 80% N_2 but, because of the stability of its triple bond, N_2 is usually not available as a biological N source. Further, N is relatively rare in the earth's crust so that natural and many agricultural systems are usually limited by N availability. This was especially true in the pre-industrial era before mass production of artificial fertilizers.

The biological route of N_2 to reactive N (Nr) is exclusively by reductive fixation to ammonia in some bacteria. (Nr is defined in Chapter 1 as all forms of inorganic N different from N_2, essentially N with a non-zero valence.) Since plants are anchored in the soil, which is usually relatively N-poor, and since their aerial portions do not fix N_2 (unlike their superb ability to fix the much less abundant CO_2), plants have evolved strategies to acquire, conserve, and recycle Nr. These strategies form part of the N cycle, whereby bacteria convert N_2 to NH_3 which, in turn, is sequestered in carbon skeletons as organic molecules, or which is used by soil bacteria as an electron source, oxidizing NH_3 to nitrite and nitrate, compounds for which plants have evolved efficient uptake and reduction mechanisms. Nitrate and nitrite, in turn, can be electron acceptors for denitrifying bacteria in anaerobic soils, leading to re-release of N_2 (Chapters 1 and 17), and obligate co-release of the pollutant, N_2O[2]. This very simplistic description does not do justice to the roles that plants play in the cycle, nor does it consider the massive anthropogenic inputs of Nr into the cycle and the causes and ramifications of those inputs. One goal of this book is an attempt to address aspects of plant roles in the (new) global N cycle (Chapter 1). Nr encompasses both plant nutrients and pollutants. Negative players among the latter can be carcinogens, greenhouse gases, and ozone depleters.

Within the "environmental" theme, our goal is the coverage of various operative environmental scales in plant N acquisition and assimilation. One 'micro-scale' deals with the many specialized interactions of plants with the bacterial world: associations of legumes with rhizobia (Chapters 2, 8, and 16) and of many trees with actinorhizal bacteria (Chapters 6 and 7), the latter of great importance in boreal forests. Even more primordial associations are those of plant roots with fungi: The mycorrhizae play a crucial role in N provisioning to plants, and N-providers are not limited to the ectomycorrhiza (ERM) (Chapter 4). The arbuscular mycorrhiza (ARM), well-recognized as aiding in P provision, also play a role in "virtual extension" of the plant root system, and N provision culminates from an interesting spatial and root-fungal delimitation of components of the arginine/urea cycle (Chapter 3). Indeed, plants do not excrete arginine-derived urea as do terrestrial mammals but employ it as a recyclable N intermediate.

"Never say never" is a proper adage applied to interactions in nature. Two-component symbioses are often our first view of an association, later revealed to contain other players. A case in point is the potential role(s) of bacteria in the ARM association, considered in Chapter 3. Bacterial endophytes may provide N directly to the plant, or improve the plant's ability to "mine" N. These questions on endophytes are addressed in Chapter 11, which also considers potential agronomic applications of the endophytic bacteria. And, the extensive leaf surface area provided by plants is an environment not ignored by microbes; Chapter 10 discusses ramifications of phylloplane colonization on plant N acquisition. One is that there is much nutrient and "waste" exchange on the leaf surface, and much of it influenced by phylloplane microorganisms.

Clearly, N is not only a nutrient, but also a component of simple, inorganic signaling compounds, such as nitric oxide (NO) and nitrate (NO_3^-). NO is but one of the possible forms between NH_3 (N valence –3) and nitrate (N valence +5). Such inter-conversions catalyzed by soil and endophytic bacteria are considered in Chapter 17, especially in light of regulatory effects on the plant. NO and nitrate also have profound effects on legume nodulation and root development. In general the polluting effects of excessive Nr need also to take into account the altered environmental levels of regulatory Nr molecules.

At higher trophic levels, plant interactions with insects and herbivores are worthy of increased study. Chapters 12 and 14 portray the evolutionary and environmental complexities of plant interactions with insects, from the "exotic" ant-plant associations to more general questions of N flux between plant and insect. Such a flux is highly regulated given the incredible panoply of plant proteins aimed at insect proteases, discussed in Chapter 13, a discussion also germane to "plant investment strategies" in N-containing insecticides.

On a global scale, massive anthropogenic inputs of Nr from burning of fossil and biofuels, human waste treatment, the Haber-Bosch process and concomitant intensive agriculture open up issues of equitable distribution of nitrogenous fertilizer—its overuse in Europe, North America, and China compared to under-use in much of the developing world[3]. Excessive inputs lead to Nr being not only a soil pollutant, but also a greenhouse gas and an ozone-depleter, in the form of N_2O[4]. Ice core analyses indicate rising atmospheric nitrate (derived from NO and N_2O) with the advent of the industrial age[5]. So, a new mandate, in addition to more equitable distribution of fertilizer, is to reduce fertilizer use overall (thus avoiding such negative outcomes as eutrophication, health problems, dead zones, reduced species diversity, etc.) To lower Nr in soil, water, and air requires improved cultural practices, increased biological N-fixation, and efficient means of industrial denitrification (anammox avoids N_2O evolution[2]). A more long-range strategy is to improve the N use efficiency of plants, topics broached in Chapter 1.

Badly degraded and eroded soils, of course, suffer from N-depletion, and Chapter 9 shows how recruitment of proper leguminous trees and rhizobial and ARM isolates can lead to dramatic recovery of three types of degraded soils (erosion ditches, mine sites, "detopped" mountains) in Brazil's Rio de Janeiro state. To be sure, soil is more than a semi-solid solution of nutrients; amendments of proteins, N-rich polypeptides secreted by plants and ARM, undoubtedly influence soil texture, tilth, humidity, and other factors. Roles of plant-secreted proteins in influencing the microbial rhizosphere are considered in Chapter 5. And, it has been reported that plants can consume intact microbes as nutrient sources[6].

Hundreds of millions of years of N-acquisition have led to evolved associations of plants with bacteria (rhizobial and actinorhizal) and fungi (ARM and ERM). Intriguing evolutionary questions on the origins and relatedness of these associations are discussed in Chapters 2, 6, and 16. Chapter 15 discusses roles of flavones and isoflavones in the complex chemical signaling between plants and their potential symbionts, chemical signals operative not only in the rhizosphere but in the establishment and development of N_2-fixing nodules.

The need is clear for integrating the complexities inherent in plant performance, environmental interactions, and N inter-conversions. A greater appreciation of these interactions will lead to better understanding of our place, and that of plants, in our shared environment. We thank the authors for their excellent contributions to an appreciation of the complex N-Plant-Environmental interactions. We thank Justin Jeffryes for reinforcing the need for this volume. And our interactions with Justin's Wiley-Blackwell colleagues, Shelby Allen and Susan Engelken, to name two, have been nothing short of pleasant, and productive, in bringing the volume to fruition.

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