Update on the State of Nitrogen and Phosphorus Nutrition

Symbiotic Nitrogen Fixation and Phosphorus Acquisition. Plant Nutrition in a World of Declining Renewable Resources

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Since 1960, the world’s population has doubled to 6 billion people. During the next 40 years, the population is projected to increase and stabilize at 8 to 9 billion people (Table I). In the 1960s, agricultural specialists predicted that food production would not keep pace with the burgeoning population growth. However, unforeseen advances in plant germplasm improvement (Green Revolution), the unprecedented use of fertilizers, and expanded use of irrigation not only allowed food production to keep up with but also to outpace population (Waggoner, 1994; Dyson, 1999). Forty years ago, 25% of the world’s population went to bed hungry each day. Since that time, improvements in food production have reduced that hungry percentage to about 17% even as population doubled. Yet, today 0.8 to 1.0 billion people are chronically undernourished (consume fewer than 2,000 calories per day), 100 million preschool children have a vitamin A deficiency, and 400 million women between the ages of 15 to 49 have an iron deficiency leading to anemia (Conway and Toenniessen, 1999). Even in the developed world, micronutrient deficiency due to poor dietary intake is a major problem among the poor. Although on a global scale food production is adequate and consumer prices for food remain low, on the local scale offending discrepancies in food production and availability are causes for concern (Waggoner, 1994; Dyson, 1999).

Although we can produce enough food to feed today’s population, that achievement has come at the cost of an ever-increasing impact on Earth’s sustainability. The striking increase in the use of nitrogen (N) and phosphorus (P) fertilizers between 1960 and 2000 by intensive agricultural practices has led to degradation of air and water quality (Bumb and Baanante, 1996; Pinnstrup-Anderson et al., 1997; Tilmann et al., 2001). At the same time, the enhanced use of water for irrigation has resulted in soil salinization and depletion of both ground and surface water supplies (Rosegrant, 1997; Postel, 2001).

Can we feed the projected 8 to 9 billion people in 2040? Probably yes, but at an accelerated impact on sustainability and environmental quality (Waggoner, 1994; Trewavas, 2001). As currently practiced, agriculture will require an additional 40 and 20 Tg (10^{12} g or million metric tons) of N and P fertilizer, respectively, applied to agricultural soils to meet food production needs in 2040 (Table I; Bumb and Baanante, 1996; Frink et al., 1999). It is astounding that irrigation water equivalent to 10 times the flow of the Nile River will be required to meet these agricultural demands (Postel, 2001).

As defined by Golley et al. (1992), sustainable agriculture is that which is managed toward greater resource efficiency and conservation while maintaining an environment favorable for the evolution of all species. More simply, sustainability is meeting today’s needs without compromising the needs of the future. By either of these definitions, crop production is compromising the global future use of N, P, and water sustainability. The thesis of this essay is that neither N nor P are renewable resources and their future use in agriculture will be impacted by declining availability and increased cost. Although this author considers water to be another nonrenewable resource, it will not be addressed here and the reader is directed to Rosegrant (1997), Gleick (2001), and Postel (2001).

NITROGEN

Even though N is among the most abundant elements on Earth, it is the critical limiting element for growth of most plants due to its unavailability (Smil, 1999; Socolow, 1999; Graham and Vance, 2000). Only sunlight and water are more important. Production of high-quality, protein-rich food is extremely dependent upon availability of sufficient N. Plants acquire N from two principal sources: (a) the soil, through commercial fertilizer, manure, and/or mineralization of organic matter; and (b) the atmosphere through symbiotic N₂ fixation. All of the nutritional N required by humans is obtained either directly or indirectly from plants. However, since the 1970s, management of N inputs into agricultural systems has become a contentious issue.

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The N issue revolves around excessive use in intensive agriculture, the cost of natural gas, the depletion of fossil fuels required for N fertilizer production, and the lack of readily available N fertilizer sources for extensive agriculture. Prior to 1930, the N cycle on Earth was in dynamic equilibrium (Frink et al., 1999; Smil, 1999) with 150 Tg passing through the N₂ fixing-unfixing cycle (Waggoner, 1994; Socolow, 1999). Grain crop yields until the 1930s were about 0.5 to 1.0 metric tons Ha⁻¹, with N supplied primarily from crop rotations and manures. At this level of production, the average farmer could feed three to five people (Waggoner, 1994). These values equate to today’s subsistence farming in developing countries. Anthropogenic addition of fixed N via fertilizer into intensive agriculture became common practice after 1945, increasing from 5 Tg in 1950 to 90 Tg in 2000 (Table I). Accompanying grain yield increased to about 7 metric tons Ha⁻¹, allowing a single farmer to feed more than 100 people. Agriculture’s contribution to global N must also include the 45 to 50 Tg coming from symbiotic N₂ fixation (Smil, 1999; Socolow, 1999). Therefore, modern agriculture adds as much N to the global cycle as the pre-industrial N₂ fixing-unfixing cycle. If predictions are correct, addition of N by agriculture will surpass the pre-industrial equilibrium of 150 Tg by 2040.

Why does anthropogenic addition of N by agriculture matter? A grain yield of 5 to 9 metric tons Ha⁻¹ requires the addition of 200 to 300 kg N Ha⁻¹ (Heichel, 1987; Peoples et al., 1995). The efficiency of N recovery by grain crops ranges from 35% to 75% with an average near 50% (Smil, 1999; Socolow, 1999). For example, N recovery by maize, which has a grain N content of 1.5%, is 39% for the first 100 kg of N fertilizer and only 13% for the second 100 kg (Socolow, 1999). This large residual quantity of N remaining in soil due to inefficient recovery by crops has been implicated in a number of environmental and health problems (Galloway et al., 1995). Microbial nitrification and denitrification of soil N are major contributors to NOₓ and N₂O emissions from agricultural soils (Socolow, 1999). Due to its long residence time and absorption of IR radiation, N₂O acts as a greenhouse gas, stimulating global warming. In comparison, NOₓ depletes stratospheric ozone and is a toxic pollutant to plants. Fertilizer N not recovered by the crop can also rapidly enter surface and groundwater pools through runoff and leaching, respectively. Excess NO₃⁻ in drinking water from fertilizer N has been implicated in methemoglobinemia in infants and young children when concentrations rise above 10 mg NO₃⁻ N L⁻¹ (Galloway et al., 1995; Smil, 1999). Excess NO₃⁻ in surface runoff has been associated with eutrophication and hypoxia in aquatic ecosystems (Galloway et al., 1995). Although the question of global N deposition on land due to intensive agriculture is controversial with ranges calculated between 2 to 45 kg Ha⁻¹, current thought suggests that excess N from agriculture reduces biodiversity and ecosystem function (Galloway et al., 1995; Frink et al., 1999; Smil, 1999; Tilman et al., 2001). Successful management of N is requisite for maximizing crop quality and yield with minimal impact on the environment and natural resources.

Exacerbating the N issue in agriculture is that production of N fertilizer, predominantly through the Haber-Bosch process, requires extensive use of non-renewable fossil fuel resources (Heichel, 1987; Galloway et al., 1995). Production of 1 metric ton of N fertilizer requires 873 m³ (32,000 ft³) of natural gas or 35 million British thermal units (BTUs). In the U.S., N fertilizer production and use requires 3% to 5% of the country’s annual natural gas production. The fragile nature of the relationship between natural gas production, N fertilizer, and crop needs was exemplified by the 4-fold increase in natural gas prices during the winter of 2001. The rapidly escalating price of natural gas from $2.50 million BTU⁻¹ to $10 million BTU⁻¹ resulted in a fertilizer production cost increase from $100 to $363 metric ton⁻¹. At that price, N fertilizer compromises farm profitability. Although the price increase in natural gas seen in 2001 is probably temporary, it vividly demonstrates that N fertilizer production is susceptible to any energy shortage or crisis.

A conundrum to the N issue is contrasting availability of N fertilizer for extensive agriculture as practiced in the developing world. Due to weak infrastructure, poor transportation, and high cost, N fertilizer is frequently unavailable for subsistence farmers, leaving N from intercropping legumes and other species capable of symbiotic N₂ fixation as the only source of N. Without doubt, germplasm with enhanced N acquisition and use, improved crop management strategies to use applied N fertilizer efficiently, and renewable sources of N are imperatives for future sustainability.

### PHOSPHORUS

P is second only to N as the most limiting element for plant growth (Bieleski, 1973; Vance et al., 2000).

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**Table I. Agriculture production and resource use, the recent past to the near future**

Data derived from United Nations Food and Agriculture Organization, Waggoner (1994), Bumb and Baanante (1996), Rosegrant (1997), Dyson (1999), Smil (1999), Tilman et al. (2001), and Postel (2001). Mt, Metric tons; Tg, 10¹² g or million metric tons.

<table>
<thead>
<tr>
<th>Item</th>
<th>1960</th>
<th>2000</th>
<th>2030–2040</th>
</tr>
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<tbody>
<tr>
<td>Food production (Mt)</td>
<td>1.8 × 10⁹</td>
<td>3.5 × 10⁹</td>
<td>5.5 × 10⁹</td>
</tr>
<tr>
<td>Population (billions)</td>
<td>3</td>
<td>6</td>
<td>8 (maybe 10)</td>
</tr>
<tr>
<td>Irrigated land (% of arable)</td>
<td>10</td>
<td>18</td>
<td>20</td>
</tr>
<tr>
<td>Cultivated land (hectares)</td>
<td>1.3 × 10⁹</td>
<td>1.5 × 10⁹</td>
<td>1.8 × 10⁹</td>
</tr>
<tr>
<td>Water-stressed countries</td>
<td>20</td>
<td>28</td>
<td>52</td>
</tr>
<tr>
<td>N fertilizer use (Tg)</td>
<td>10</td>
<td>88</td>
<td>120</td>
</tr>
<tr>
<td>P fertilizer use (Tg)</td>
<td>9</td>
<td>40</td>
<td>55–60</td>
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</table>
The amount of P in plants ranges from 0.05% to 0.30% of total dry weight. The concentration gradient from the soil solution to the plant cell exceeds 2,000-fold, with an average free P of 1 nM in the soil solution (Bieleski, 1973; Ragothama, 1999). This concentration is well below the $K_m$ for plant uptake. Thus, although bound P is quite abundant in many soils, it is largely unavailable for uptake (Bieleski, 1973; Schactman et al., 1998). Crop yield on 40% of the world’s arable land is limited by P availability. P is unavailable because it rapidly forms insoluble complexes with cations and is incorporated into organic matter by microbes. The acid-weathered soils of the tropics and subtropics are particularly prone to P deficiency and aluminum (Al) toxicity (von Uexküll and Mutert, 1995). In intensive agriculture, a grain crop yield of 7 metric tons Ha$^{-1}$ requires the addition of 90 to 120 kg P Ha$^{-1}$ (Bieleski, 1973; Bumb and Baanante, 1996). However, even under adequate P fertilization, only 20% or less of that applied is removed by the 1st year’s growth. This results in P loading of prime agricultural land. Runoff from P-loaded soils is a primary factor in eutrophication and hypoxia of lakes and marine estuaries in the developed world. An even greater reason for concern is that by some estimates inexpensive rock phosphate reserves could be depleted in as little as 60 to 80 years (Council for Agricultural Science and Technology, 1988; Runge-Metzger, 1995). P fertilizer use increased 4- to 5-fold between 1960 and 2000 and is projected to increase further by 20 Tg year$^{-1}$ by 2030 (Table I).

As noted by Abelson (1999), a potential phosphate crisis looms for agriculture in the 21st century. Sustainable management of P in agriculture requires that plant biologists discover mechanisms in plants that enhance P acquisition and exploit these adaptations to make plants more efficient at acquiring P, develop P-efficient germplasm, and advance crop management schemes that increase soil P availability.

**IMPROVING N AND P SUSTAINABILITY**

Plants have adopted two broad strategies that enhance N and P acquisition and use (Table II): (a) those directed toward improved acquisition or uptake, and (b) those targeted to conserve use (Lajtha and Harrison, 1995). Strategies that lead to better uptake or acquisition include expanded root surface area through increased root growth and root hair development (Lynch and Brown, 1998; Zhang and Forde, 1998; Gilroy and Jones, 2000), organic acid synthesis and exudation (Marschner et al., 1986; Gilbert et al., 1998), enhanced expression of $\text{NO}_3^-$, $\text{NH}_4^+$, $\text{PO}_4^{3-}$ transporters (Ragothama, 1999; Gilroy and Jones, 2000), aquaporins, and mycorrhizal associations (Marschner and Dell, 1994; Harrison, 1997), and symbiotic N$_2$-fixing root nodules (Peoples et al., 1995; Vance et al., 2000). Strategies aimed at conserving N and P involve internal remobilization of N and P, decreased growth rate (Schactman et al., 1998; Ragothama, 1999), more growth per unit N or P taken up (Lynch and Brown, 1998), and modified carbon/N metabolism (Gilbert et al., 1998; Plaxton and Carswell, 1999). Because most legumes used by humans display all of these adaptive strategies, they are ideal for crop management schemes aimed at enhancing sustainability and buffering against the dependence on N and P fertilizer. Please note that although I focus on the use of legumes for farming in a world of declining renewable resources, the use of other plant families and approaches is not excluded.

In intensive agriculture, the role of legumes and biological N$_2$ fixation unfortunately has declined in recent years due to availability of inexpensive fertilizers and land application of manures (Graham and Vance, 2000; Vance et al., 2000). An important additional feature in this decline has been the potential loss of income by using legumes in rotations. However, with N and P contamination threatening large areas (North America, China, and Europe), excess grain production, the heightened awareness of organic production, relevance to human health, and the importance of biodiversity in agriculture, the time is ripe to reaffirm the importance of legumes in sustainable management of N and P (Table III). Peterson and Russell (1991) have estimated that properly managed alfalfa (*Medicago sativa*)-corn (*Zea mays*) rotations in the U.S. upper midwest (Corn Belt) could reduce fertilizer inputs by up to 25% without loss of production and give a realized net return of $70 to $90 million. Depending upon the management and cropping system, legume green manures have the potential to replace more than 100 kg N Ha$^{-1}$ for a subsequent grain crop. This equates to a savings of between $60 to $90 Ha$^{-1}$ in N fertilizer. The enhanced yield due to the rotation effect coupled to the savings in fertilizer expense offset most potential loss in income. Smil (1999) and Socolow (1999) estimate

<table>
<thead>
<tr>
<th>Strategy Adaptation</th>
<th>Table II. Plant adaptations to low N and P</th>
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<tr>
<td>Enhanced acquisition or uptake</td>
<td>Expanded root surface area (more roots and root hairs, cluster roots, and longer roots)</td>
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<tr>
<td>Enhanced expression of $\text{NO}_3^-$, $\text{PO}_4^{3-}$ transporters, aquaporins, and phosphatases</td>
<td>Increased organic acid synthesis and exudation</td>
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<td>Increased organic acid synthesis and exudation</td>
<td>Mycorrhizal symbiosis</td>
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<tr>
<td>Mycorrhizal symbiosis</td>
<td>Rhizobial symbiosis</td>
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<tr>
<td>Conservation of use</td>
<td>Internal remobilization</td>
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<tr>
<td>Internal remobilization</td>
<td>Decreased growth rate</td>
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<tr>
<td>Decreased growth rate</td>
<td>More growth per unit N or P (nutrient use efficiency)</td>
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<tr>
<td>More growth per unit N or P (nutrient use efficiency)</td>
<td>Modified carbon and nitrogen metabolism</td>
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Adapted from Lajtha and Harrison (1995).
that the use of legumes and other N₂-fixing associations accompanied by good agronomic practices (proper soil tests and fertilizer application) along with the use of germplasm having efficient N uptake could effectively save 20 Tg N year⁻¹ (comparable savings could probably accrue for P use). Not only would a savings in N fertilizer occur with expanded use of legumes in intensive agriculture, but also the potential for N leaching into groundwater and volatilization of N into the atmosphere could be reduced because legume N is less susceptible to the chemical and physical conversions that lead to such losses. An unrecognized benefit of expanded use of N₂-fixing species in agriculture is their contribution to carbon sequestration. The biological fixation of 90 Tg N year⁻¹ (50% by legumes) is equivalent to sequestering an additional 770 to 990 Tg of carbon year⁻¹.

In extensive agriculture of the developing world, von Uexküll and Mutert (1995) recommend that the first phase of reclaiming acid soils low in P and N is the use of a legume cover crop supported by liming and conservative P application. Incorporation of the legume residue results in higher soil organic matter content and increased P and N availability. Snapp (1998) identified long duration legumes having indeterminate growth and low harvest index as critical to improving P and N sustainability in small holder and subsistence agriculture in Africa. On the Indian subcontinent and in other semiarid regions having weathered soils, intercropping of pigeon pea (Cajanus cajan) with cereals is a proven management scheme for increasing available N and P. In India, more than 90% of pigeon pea production is in intercropping. Ae et al. (1990) demonstrated that this success is due, at least in part, to exudation of piscid acid from roots of pigeon pea, which enhances the availability of phosphate from iron-phosphate (Fe-PO₄). Mycorrhizal inoculation of pigeon pea further improved P uptake in this study. Thus, in addition to providing an immediate source of dietary N, incorporation of pigeon pea residues after seed harvest make P and N more available to a subsequent crop. The development of soybean (Glycine max L. Mer.) germplasms and rhizobial inoculants for low fertility, acidic soils of the Brazilian Cerrado has been an extraordinary success (Spehar, 1995), allowing Brazil to become a leading exporter of soybeans. Good progress has been made in selecting common bean (Phaseolus vulgaris), a staple for intercropping in Latin America and many other areas of the world with low P and low N soils, for both improved N₂ fixation and P acquisition (Bliss, 1993; Yan, 1998). Progress in common bean was made by selecting germplasm for increased nodule, percent N, root and root hair production, and organic acid exudation.

The well-characterized legume, white lupin (Lupinus albus), has proven an illuminating model system for understanding plant adaptations to low P and N habitats (Skene, 1998; Watt and Evans, 1999). White lupin can effectively acquire P even though it does not form a mycorrhizal symbiosis. Instead, its adaptation to P stress is a highly coordinated modification of root development and biochemistry resulting in cluster roots that exude copious amounts of organic acids and acid phosphatase (Gilbert et al., 1998; Neumann et al., 1999). Cluster root formation is accompanied by extensive root hair growth that increases root surface by greater than 100-fold. Prolific release of the acids, citrate and malate, solubilize bound inorganic P, whereas exudation of acid phosphatase is important in solubilizing organically bound P (Marschner et al., 1986). A further adaptation to low P in cluster roots is enhanced uptake of P and expression of PO₄⁻ transporters (Neumann et al., 1999; Lui et al., 2001). Because of these adaptations, P uptake is greatly enhanced in cluster root zones. Furthermore, sufficient P is released to support the growth of a companion crop. For example, wheat (Triticum aestivum) intercropped with white lupin had a 1.5-fold greater P uptake and double the dry matter of wheat grown alone (Marschner et al., 1986). An additional feature of white lupin adaptation to low P is that symbiotic N₂ fixation seems less susceptible to inhibition by low P. Nodulation is prolific in cluster root zones and N₂ fixation continues unabated for up to 5 weeks after planting in low P conditions (G. Gilbert, J. Schulze, and C.P. Vance, unpublished data).

Any mention of enhancing P and N availability and uptake must make mention of mycorrhizal-plant associations. Mycorrhizal fungi (inclusive of vesicular-arbuscular, ecto-, and ericoid-mycorrhizae) associate with 80% of the terrestrial plant species (Marschner and Dell, 1994; Smith et al., 1994). The growth of mycorrhizal fungi on and in plant roots dramatically increases the surface area of roots available for soil exploration of nutrients, particularly P, but also N (Marschner and Dell, 1994). The uptake of PO₄⁻, NO₃⁻, and NH₄⁺ by external hyphae is a primary contributor to the adaptation of land plants to nutrient-poor soils. Van der Heijden et al. (1998) demonstrated that the diversity of vesicular-arbuscular mycorrhizae in soils was a dominant factor for maintaining biodiversity and ecosystem func-

Table III. Importance of legumes in agriculture

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<th>Importance</th>
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<tr>
<td>High protein food for humans and animals</td>
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<tr>
<td>Reduce N fertilizer requirements</td>
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<tr>
<td>Provide N for rotations and intercrops</td>
</tr>
<tr>
<td>Enhance soil health</td>
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<tr>
<td>Reclamation of acid soils</td>
</tr>
<tr>
<td>Improve P cycling</td>
</tr>
<tr>
<td>Improve disease and pest control</td>
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<tr>
<td>Weed control as cover crops</td>
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<tr>
<td>Provide diversity and beauty</td>
</tr>
<tr>
<td>Phytofiltration</td>
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<td>Enhance carbon sequestration</td>
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Adapted from Peoples et al. (1995) and Graham and Vance (2000).
tioning. Increased mycorrhizal diversity was highly correlated with efficient use of soil P within a mixture of plant species. Giller and Cadisch (1995) report that legumes, except for a few species, are dependent upon mycorrhizae for efficient P uptake. They note that tree legumes inoculated with rhizobia and mycorrhizae are recommended for reclamation of nutrient-poor, heavily degraded soils. Although the role of mycorrhizae in plant P acquisition has been well documented for more than 30 years, room is available for research progress on their role in acquiring other nutrients. Moreover, the use of mycorrhizae in agricultural systems will only be fully realized as we: (a) ascertain how mycorrhizal diversity contributes to growing crops, (b) identify the biochemical and genetic mechanisms regulating nutrient exchange, and (c) determine whether there is a yield penalty for effective symbiosis.

The plant strategies identified in Table II as enhancing N and P acquisition or use are genetically controlled and subject to genetic improvement either through traditional plant breeding or through transgenic technology. Some traits like symbiotic N2 fixation and mycorrhizal symbiosis obviously will be more difficult to improve than others due to their complexity. Through genetic analysis of alfalfa, soybean, sweet clover (Medicago alba annua [Desr.]), and pea (Pisum sativum) mutants, we know that single loci control nodule formation (Vance, 1997; Saguanuma, 1999) and those same loci or closely linked ones also control aspects of mycorrhizal associations (Harrison, 1997). However, we have no functional knowledge of the gene(s) involved. Other than the progress made in improving N2 fixation in common bean, progress with other species has been very slow (Herridge and Danso, 1995). This probably stems from the fact that at least 50 genes from the plant and 50 from the bacteria are associated with effective nodule formation and function (Vance, 1997; Schultz and Kondorosi, 1998). It would not be surprising if equal numbers of genes were involved in mycorrhizal symbiosis (Harrison, 1997).

The recent sequencing of the Arabidopsis genome has given new insight into the uptake, transport, and mobilization of N and P. At least 56 genes have been identified in Arabidopsis that are involved with uptake of N, P, and water (16 PO4−, 16 NO3−, and four NH4+ transporters; 20 aquaporins). However, because Arabidopsis does not form symbioses with either rhizobia or mycorrhizae, other genetic models must be developed. Medicago truncatula and Lotus japonicus, both small-seeded, self-compatible, legumes with a small genome (450 Mb) and rapid life cycle, are among several models for genomic approaches to symbiosis (Handberg and Stougaard, 1992; Cook, 1999; Gresshoff et al., 2001). Large expressed sequence tag projects accompanied by structural genomics and mutagenesis approaches are enlightening the field of plant genetic control of the complex traits governing symbiotic N2 fixation and mycorrhizal symbiosis.

Tantalizing results showing improved N and P acquisition obtained by overexpressing single genes involved in NO3− and PO4− uptake hold promise for future application. Over the last few years, numerous genes encoding NO3− and PO4− transporters have been isolated and characterized (Schachtman et al., 1998; Ragotthama, 1999; Gilroy and Jones, 2000). High expression of these genes is frequently seen at the root tip and in young root hairs. Moreover, their expression is responsive to the nutrient supply of the rooting medium. For example, the LePT1 PO4− transporter from tomato is up-regulated by low P and the NO3− transporter genes LeNRT1-1 and LeNRT1-2 are up-regulated by NO3− addition (Gilroy and Jones, 2000). In efforts to understand molecular regulation of NO3− uptake, Huang et al. (1996) created an Arabidopsis deletion mutant for the low affinity NO3− transporter (AtNRT1). They also rescued the mutant by overexpression of AtNRT1. The deletion mutant was impaired in NO3− uptake, whereas overexpression reversed the uptake deficiency and enhanced NO3− accumulation. In a similar manner, Mitsuakawa et al. (1997) showed that overexpression of the Arabidopsis high-affinity PO4− transporter in cultured tobacco (Nicotiana tabacum) cells resulted in enhanced biomass accumulation under PO4−-limiting conditions.

When plants are subjected to low P conditions, secretion of acid phosphatase from roots is a common response (Gilbert et al., 1999; Richardson et al., 2001). It is unclear whether release of acid phosphatases into the rhizosphere improves P acquisition. However, because phytate can represent up to 30% of soil organic P, any enzymatic degradation of phytate could release substantial P for plant growth. Richardson et al. (2001) recently demonstrated that secretion of phytase from Arabidopsis roots improved growth and P nutrition. Under low P conditions, white lupin secretes an acid phosphatase capable of phytate degradation into the rhizosphere (Gilbert et al., 1999). We are currently developing alfalfa plants that overexpress acid phosphatase in efforts to improve P nutrition.

P acquisition has also been improved through approaches aimed at increasing citrate synthesis in and/or exudation from plant cells. This approach is based upon the large body of evidence showing that exudation of citrate and malate from roots effectively solubilizes unavailable P sources (Marschner et al., 1986). Rhizosphere acidification by exudates leads to desorption of PO4 from the soil matrix with a concomitant increase in availability. Koyama et al. (1999) developed carrot (Daucus carota) cell lines that overexpressed mitochondrial citrate synthase. These cell lines had improved growth on Al-PO4− medium as compared with untransformed controls. In a similar approach but using a bacterial citrate synthase
driven by the cauliflower mosaic virus $^{35}$S promoter, Lopez-Bucío et al. (2000) demonstrated that overexpression of citrate synthase resulted in increased secretion of citrate into the rhizosphere and enhanced P accumulation.

Because malate is critical for bacteroid respiration in N$_2$ fixation and root nodule amino acid synthesis (Udvardi and Day, 1997; Vance, 1997) as well as being intimately related to P uptake, we are overexpressing the enzyme malate dehydrogenase in alfalfa in efforts to enhance malate synthesis and exudation to improve P and N nutrition (D.A. Samac, M. Tesfaye, J. Schulze, M. Denton, S. Temple, D.L. Allan, and C.P. Vance, unpublished data). Initial results suggest that transgenic plants containing malate dehydrogenase driven by the cauliflower mosaic virus $^{35}$S promoter show higher organic acid formation, improved P accumulation, and N$_2$ fixation as compared with either transformed or nontransformed controls.

Evidence is accumulating that overexpression of selected individual genes involved in N and P acquisition can improve nutrient uptake. As the arsenal of plant genes involved in these processes expands, we will undoubtedly see more successful examples. Because of the urgent need for plant germplasm having improved N and P use efficiency, research programs that combine traditional plant breeding and transgenic technology will be imperative.

SYNOPSIS

The world is on the brink of a new agriculture, one that involves the marriage of plant biology and agroecology under the umbrella of biotechnology and germplasm improvement. Although N and P fertilizers will continue to play a major role in intensive agriculture, depletion of natural resources, loss of biodiversity, and long-term unsustainability necessitate alternative strategies be investigated and implemented to buffer against food insecurity and environmental degradation. Furthermore, because improved N and P use by plants has immediate and direct benefit in extensive agriculture in developing countries where access to fertilizers is limited, funding for research at international centers should be a high priority. The following recommendations deserve attention: (a) reemphasize the use of legumes and symbiotic N$_2$ fixation to improve soil N and P fertility while reducing fossil fuel consumption and providing a source of dietary N; (b) develop intercropping schemes that foster efficient N and P use; (c) continue to isolate, characterize, and develop fundamental understanding of individual genes holding promise of application to improving N and P use; (d) enhance the expression of genes and increase the synthesis of gene products, such as those involved in transport of nutrients and exudation of organic acids, through both traditional plant breeding and transgenic technology and incorporate these traits into adapted germplasm; and (e) assess the factors limiting rhizobial and mycorrhizal interactions with plants with the goal of site-(region) specific inoculation.

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LITERATURE CITED


