Trends in Plant Science

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Opinion

Resources for Crop Production: Accessing the Unavailable

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An acute imbalance between human population and food production is projected, partially due to increasing resource scarcity; dietary shifts and the current course of technology alone will not soon solve the problem. Natural ecosystems, typically characterized by high species richness and perennial growth habit, have solved many of the resource–acquisition problems faced by crops, making nature a likely source of insights for potential application in commercial agriculture. Further research on undomesticated plants and natural ecosystems, and the adaptations that enable them to meet their needs for N, P, and water, could change the face of commercial food production, including on marginal lands.

Highlights

Natural ecosystems and undomesticated plants have solved many resource-acquisition problems – problems challenging agriculture with economic and societal constraints on fertilizer, water and fossil energy.

Symbiotic N_2 fixation input can best be enhanced by focus on host plant.

Biologically mediated extraction of phosphate from soils is widespread – geographically and phylogenetically – in nature.

Efficacy of water use can be increased by temporal regulation of transpiration, by deeper-rooted crops, and by hydraulic redistribution via roots from wetter to drier soil where it can become available to companion species.

Need for Fresh Perspectives on Food Production

Human malnutrition and starvation are major challenges for humanity. Further exacerbating the problem, the current annual rate of human population growth, 1.10% globally [1], although declining, continues to outpace developing country projected increases in crop yields – 0.83% for maize, 0.86% for wheat, and 0.63% for rice [2]. There is clear evidence that yield increases in these crop species are stagnating in some of the more productive regions of the world [3]. The situation is exacerbated by the impact of agriculture on the resources required for crop production, including the three on which we focus here – N, P, and water. Furthermore, there is real concern about the species and genetic diversity of modern cropping. The experience of the attack by Southern Corn Leaf Blight in 1970–71 [4] in the US looms as an example of the dangers of genetic uniformity within a crop species. Included in the concern of about lack of diversity is the heavy reliance on annual plants without the benefit of a substantial presence of perennial species.

Here, we offer research suggestions to invigorate agriculture and crop productivity by looking to plant adaptations and interactions among plants in nature for potential solutions in cropping systems (Figure 1, Key Figure). Natural ecosystems have withstood the test of evolutionary time and resource deprivation, resulting in plants and plant communities that are resilient when faced with low amounts of available nutrients and water. The probability is high that the world's flora of some 390 000 species includes many with functional and structural attributes that have not yet been deployed in crop production. In particular, we give attention here to the issues of diversity, N use, P acquisition, water use, and perennial growth habit.

While we recognize that undernourishment is a problem with many facets – political, economic, geographic, cultural, and agronomic [5,6] – we focus here on biological research directions that are underexploited and have the potential to increase crop yields of commercial agriculture (i.e., farming enterprises of any size that sell products off the farm) in the near future. Some of our suggested approaches have the potential to increase yields on existing commercial crop lands, but most are directed at making commercial production feasible on environmentally and

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Key Figure

Resources for plant growth can be present yet unavailable

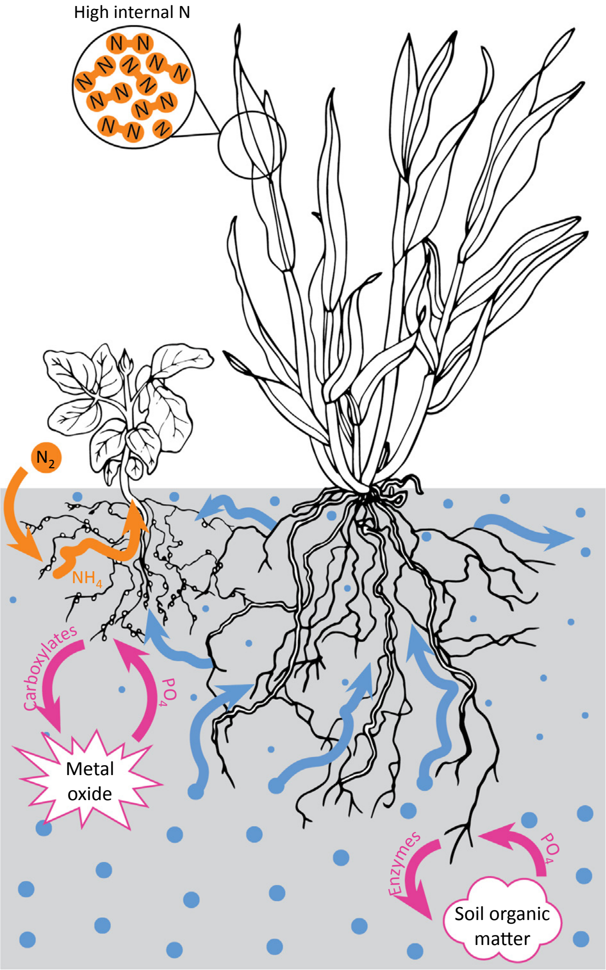

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Figure 1. Natural systems include many processes that facilitate plant acquisition of those resources – processes underutilized in commercial agriculture. Examples are depicted here for water (blue), redistributed via roots as conduits from deep to shallow soil; nitrogen (orange) transformed from N_2 to NH_3 by microbial symbionts, and retained for recycling in large-stature plants; and phosphorus (red), released from plant-unavailable forms by plant exudates.

economically marginal lands, including those currently relegated to subsistence agriculture with the potential to move to the commercial agriculture essential for future development. Several of the avenues we highlight have been well known to agronomists for decades but need renewed research attention to stimulate commercial production.

Diversity: Solution, or False Hope?

Hundreds of studies in natural and investigator-designed ecosystems have shown that functional diversity can result in enhanced use of light, water, and nutrients, and diminished pest problems [7]. However, farmers are in the business of capturing resources and managing pests as means to an end – crop production – and that is where diversity is not necessarily the best option. Although mixtures of functional groups often yield more than the average of their component species in monoculture, they rarely yield more than an equal area of the most productive species in the mixture. Not surprisingly, commercial farmers usually opt for the most productive species, and they typically grow it in monoculture. Nevertheless, in commercial agriculture, diversity of plant traits can help suppress pests, increase effectiveness of water use, enhance pollination, diminish damage due to wind, ensure full use of growing-season sunlight and precipitation, and restore soil organic matter, just as it does in natural systems.

Subsistence farmers improve resource use, augment dietary variety, and reduce risk through use of species combinations (e.g., maize–bean–squash in Mesoamerica). Furthermore, some of the benefits of diversity are routinely achieved in commercial agriculture by temporal diversity (e.g., crop rotations and relay cropping) or by spatial diversity (e.g., trap crops, companion crops, and strip crops). Diversity is also deployed commercially where species identity and relative abundance in the harvested product are not crucial – forage crops and plant mass for fuel, for example.

Mixing species in the same place at the same time, however, raises the challenges in commercial cropping to another level. One biological constraint is the design of food-producing plant assemblages of strong ecological combining ability [8]: mixtures of species having complementary stature, phenology, and resource acquisition. Some farmers grow mixtures of species (e.g., canola + pea + lentil) on a commercial scale and report ecological and economic benefits, but replicated trials with monocultures matched to site conditions are scarce. This is a research need and opportunity for teams of agronomists and ecologists.

Growing species mixtures for human food may be even more strongly constrained by a technological issue: complexity management – sowing, weed control, inputs tailored to needs of species, and harvesting. Consequently, an important research priority is machinery capable of dealing with such complexity, likely using emerging sensory technology [9,10]. The speed, precision, control over timing, economies of scale, relief from drudgery, and labor savings that accompany mechanization are key to increasing food production.

N, the Key Ingredient

Some of the best opportunities for knowledge transfer from natural systems to agriculture may lie in plant adaptations for mediating biogeochemical cycles and improving plant nutrition. An essential component of amino acids and nucleic acids, N is of key importance because of its critical role in plant growth and crop yield (Box 1). Natural grasslands, woodlands, and forests export relatively small amounts of N through leaching, denitrification, and volatilization. They retain and recycle most N, and losses are typically replenished by fixation of atmospheric N_2 by microbes, dry and wet atmospheric fallout, and soil reserves [11].

Commercial crops, in contrast, result in the removal of large amounts of N from fields as a critical component of harvested plant product. High crop yields are only possible if soil stores of N are replenished, typically by manufactured N fertilizer, applied globally at >100 Tg/year [12]. Furthermore, fertilizer N inputs and outputs tend to be geographically imbalanced. Where N is scarce or expensive (e.g., much of Africa), soil reserves of N diminish; consequently, crop yields are poor and sustained commercial production is difficult. In contrast, where N fertilizer

Box 1. Nitrogen

Crop yields closely track N inputs [40], but a broad range of problems face N application, ranging from scarcity to harmful excess. The current research portfolio on N fertilizer placement, timing, and uptake needs to be increased, and guidance may be obtained from natural ecosystems. Two properties of natural systems – retention/reuse and N_2 fixation – offer underexploited models potentially useful to agriculture.

Could Bigger Be Better?

The retain-and-recycle-N attribute of natural plant communities might be obtained in crop production through the propensity of some species to develop large plant stature and to accumulate N in high concentration (see Figure 1 in main text). High-N, large-stature plants might be crop species themselves or cover crops consisting of a single species or a diverse mixture. The tissues of these species could be managed for N conservation and reuse based on the more common use of shoots as green manures or on belowground organs (e.g., the unharvested residual from yam bean, *Pachyrhiza* spp., [41]). In rice, work is underway to increase culm size and strength to obtain yield increases [42]; large culms open the possibility of storing and recycling non-structural N (as well as phosphorus and potassium).

Tweak the Host Plants, not the Microbes

Nearly all N_2 fixation research has focused on the bacterial partner in the symbiosis. This seemed a logical option, and the bacteria lent themselves to ready selection for superior strains. Nevertheless, little has come of this research because the N_2 fixation rate by nodules containing minimally competent bacteria is largely regulated by the host plant [43]. N_2 fixation activity is closely integrated into N and water cycling within the host plant, and it is the flow of N and water under the regulation of the host plant that determines nodule N_2 fixation activity.

applications exceed plant uptake (e.g., China), off-site environmental quality and human health suffer. It is not surprising then, that N has received more attention in both agronomic and environmental research than any other mineral nutrient [11,13–15].

Biological fixation (Figure 1) would help solve many crop production challenges associated with N, yet few N_2-fixing species are part of the commercial agriculture portfolio. Only the composite category of pulses (11 genera of grain legumes grown for human consumption) makes it onto the list of major food crops [16], and except for soybean (*Glycine max* L. Merr.), grown for its seed protein and oil, and clovers (*Trifolium* spp.) and alfalfa (*Medicago sativa* L.), both grown for forage, the land area devoted to legumes is minor although growing in some regions [17].

P – Breaking it Loose from the Soil

P is the critical component of plant molecules involved in energy flow. Consequently, limited plant uptake of phosphate (the plant-available form of P) severely reduces crop yields. Ironically, many soils where yields are constrained by P do contain substantial P, but it is unavailable to most crops because it is complexed with Al, Fe, or Ca, or it is locked into organic matter. Unavailability can be corrected locally by application of manures, biosolids and P-rich composts [18], but supply and distribution limit the scope of their use. At larger landscape scales, unavailability is typically corrected with P fertilizer (coupled with lime applications on acid soils), which will become increasingly difficult as global supplies of rock phosphate tighten and costs increase [19].

Scarcity of readily available soil P is most acute and extensive in highly weathered (or old) soils of the tropics and subtropics [20], but P can also become limiting to crop yield in younger soils after long-term, repetitive harvests. Nevertheless, many plant species in natural ecosystems have evolved to live, and even thrive, on soils with low available P [21–23]. Studies from Australia, in particular, provide insights on plant success in mining P from soils having virtually no readily available P [22,24]. The roots of these plants release particular carboxylates (in many cases via specialized cluster roots) capable of replacing P that is tightly bound in soil mineral complexes, making the P available to plants (Box 2).

Box 2. Resolving the Paradox of Soil Phosphorus

The paradox of P scarcity for plant growth in many soils is its presence in the soil in unavailable forms. Plants have resolved this dilemma with a number of mechanisms, including translocation and reuse, high P-use efficiency (i.e., carbon gain per unit P), and, two that we highlight here – making metal-bound P available for uptake, and releasing phosphate from organic soil P.

A number of plants release carboxylate (of certain small organic molecules) into the rhizosphere to facilitate release of P from hydrous oxides of iron and aluminum (see Figure 1 in main text). Furthermore, some species meet their nutrient needs by carrying nutrient acquisition one step further by combining P release and uptake with fixation of atmospheric N_2. This dual-resource-acquisition phenomenon is known for several domesticated legume genera, for example, *Cajanus* (pigeon pea), *Kennedia*, *Lupinus* (lupines), and *Cicer* (chickpea) [44–46], and it is likely that among the thousands of unstudied N_2-fixing species there are many more that are effective at P acquisition. A two-pronged research agenda is called for: screen undomesticated plant species for crop candidates that mine P and fix N_2, and, in crop breeding programs, screen genotypes for host plants with these dual traits.

Many plants depend heavily on P recycled from decomposing plant material and soil organic matter [47,48] (see Figure 1 in main text). While some phosphate is leached from senescent leaves to potentially become a no-cost P source for microbes and plant roots [49], most P from soil organic matter is obtained by plants using enzymes to release the P [50,51]. Organic soil P exists in several forms: some forms are more abundant than others [52], and some are more readily accessible than others [53]. Pairing the particular chemical characteristics of soil organic P with plant-rhizosphere mechanisms that mineralize that form of P would go a long way toward enhancing P uptake and recycling in many agricultural systems.

In addition to cluster roots, natural systems have solved the dilemma of scant available P in many other ways (Figure 1). For example, a recent study of Panamanian forests found that two-thirds of 541 tree species were associated with low-P (<2 ppm dissolved phosphate) soils [23]. Nevertheless, few of those solutions that evolved in trees have worked their way into commercial crop plants. One exception is the commercial application of plant-growth promoting rhizobacteria (PGPRs), which demonstrably enhance plant growth, although scientists do not yet fully understand the processes involved [25,26]. Eventual understanding of the mechanisms that enable a rich diversity of species to perform well in low-P environments, and the ability to fine-tune PGPRs for particular species and soils, could lead to an array of underexplored options for food production.

The phosphate released from metal oxides or organic matter, as described in Box 2, may be only briefly available for plant uptake, as it can quickly revert to low-availability chemical forms or be immobilized by soil microbes. Thus, in addition to better information on P-release mechanisms, research on immediate capture of released phosphate is needed. Abundance and distribution of fine roots, and effective mycorrhizae for crop plants, are two areas that merit further investigation.

Water, the Geographic Limiter

Globally, rain-fed agriculture is constrained by climate. Food production is constrained in altitude and latitude by temperature, and, in regions where temperature permits agriculture, production is centered on climates in which annual rainfall does not greatly deviate from potential evapotranspiration. Wetter climates present a host of biological constraints (herbivores, diseases, and weeds) and soil impoverishment due to high rates of nutrient leaching, while drier areas mean abiotic constraints such as water scarcity and salinity [27].

In many regions of dry climate, water is available at depth in the soil but beyond the reach of the roots of annual crops, at least during part of the growing season. There are two ways to access that water: deep-penetrating roots by the crop itself, or potentially a companion species that

Box 3. Bioirrigation

Water moves in plant roots from high hydrostatic pressure to low hydrostatic pressure. One consequence of this physical process is the possibility of water transport through roots from regions deep in the soil where water is plentiful up to dry soil surface layers. Subsequent release of the water into the upper soil layers makes water available for uptake for both the uplifting plant and its neighbors (see Figure 1 in main text). Hydraulic redistribution has been documented for decades in tree-dominated natural ecosystems [54,55], but putting it into practice for crop production has proven difficult.

Across 26 empirical studies, hydraulic redistribution averaged 0.3 mm/day (range 0.04–1.3) and accounted for an average of about 15% of annual transpiration demand [56]. These rates are small, but sufficient to facilitate plant survival during drought; a feature that may be particularly relevant in perennial production systems [57]. Interspecific transfer of modest amounts of water via hydraulic redistribution has been documented between deep- and shallow-rooted perennial forage legumes [58] and between annual crops – deep-rooted pearl millet (*Pennisetum glaucum*) and drought-susceptible rice (cultivar NERICA-4) [59].

In addition to the small amount of water made available, interspecific competition is a barrier to use of hydraulic redistribution in cropping systems: the lifting species is almost invariably larger than the potential beneficiary. One innovative attempt to mitigate this problem involved detopping a deep-rooted forage species grown adjacent to oilseed rape (*Brassica napus*); some additional water became available to the rape and enhanced its survival [60].

There is reasonable expectation that hydraulic redistribution could prove useful in perennial-crop agriculture and agroforestry, but extending its application into annual cropping schemes is uncertain. Nevertheless, if successful, it might reduce the interannual variance in crop yields in water-marginal environments where a small amount of additional water at a crucial stage in the plant life cycle could mean the difference between no yield and some yield.

can tap into deep water and transport it for release into soil layers accessible by the crop plants (Box 3 and Figure 1).

Breeding plants that use water at a reduced rate early in the growing season are another way to address water limitations. Unless the water is subsequently lost to evaporation or weeds, early-season conservation can make more water available to sustain physiological activity, particularly seed growth, during late-season drought [28]. Early-season water conservation can be achieved through partial stomatal closure either under high atmospheric vapor pressure deficit or early in the soil drying cycle. While such stomatal response is expressed in ancestral lines of crop species, selection pressure for high yields – commonly under well-watered conditions – seems to have de-emphasized them. Recent research has now identified a few genotypes in nearly all major crops with these traits, and commercial varieties are being developed specifically for their expression [29].

Perennial Hope

Perennial plants dominate almost all natural terrestrial ecosystems, and the environmental advantages of long-lived plants – soil protection, buildup of soil organic matter, within-plant nutrient storage, and more complete exploitation of soil water and nutrients – are well documented [30]. Thus, it seems incongruous that annual plants dominate food production. How did that come to be? The leading hypothesis is that the preadaptation of annual plants to the disturbed sites deployed by humans for agriculture led to an easy path for domestication of annuals [31]. The potential advantages of perennials are counterbalanced by several potential, but not inevitable, disadvantages, including comparatively low yields, risk of pest buildups, and long lead time prior to harvest.

Although efforts have been underway for decades to perennialize major grain crops, [32], efforts to date constitute a small fraction of what has been dedicated to the development of annual crops. Therefore, it is perhaps not surprising that annual grain lines developed to take full advantage of a favorable growing season remain more productive. Nevertheless, in today's world of changing interannual environments, and a near-future world in which fertilizers and water are less readily available, it is appropriate to devote more attention to exploring and increasing the productivity of perennial species that are outside of current agricultural practices. An encouraging recent report [33] describes a perennial rice hybrid that produced yields comparable to those of locally used varieties through four cropping cycles; farmers preferred the perennial because of its lower labor requirements.

One advantage of perennials is their resilience in response to varying environments. Another advantage is that they could offer improved acquisition of available N, P, and water through the annual oscillations of growth conditions. For example:

- Gene sequencing evidence identifies certain phylogenetic lineages in which establishment of plant–microbe symbioses that fix N_2 are likely to be far more feasible than others [34]. Most of the precursor lineages are woody legumes [35].
- Ectomycorrhizae are known for effective P acquisition on the poorest soils; all ectomycorrhizal plants are perennials [36,37].
- Water and nutrient acquisition from great soil depth is more readily accomplished by the extensive, permanent root systems of perennials than by annuals.
- Perennial plants have a far greater array of chemical (both quantitative and qualitative), physical, and biological defenses (including symbiotic arthropods) against herbivores than do annual plants [38].

As soil carbon storage, erosion reduction, and fertilizer costs become increasingly important criteria in crop choice, the potential value of perennials is likely to become more widely appreciated.

Concluding Remarks

Increasing food production is challenge enough, without the added impediment of doing so in the face of potentially reduced supplies of fuels, fertilizers, and water. Clearly, we need additional efforts on all fronts.

We have identified several plant adaptations and mechanisms found in natural ecosystems related to acquisition of N, P, and water that could lend themselves to cropping systems, and surely there are many more. Some processes in nature are reasonably well understood, while others require more research before they are likely to contribute to food production (see Outstanding Questions).

Innovations with the potential to increase food production confront many barriers in addition to limited biological research; a point we illustrate with N_2-fixing crops. Given that symbiotic N_2-fixing plants typically have high protein content, and the agronomic benefits of legumes have been touted by scientists for more than a century [39], why has the diversity of commercially grown legumes not grown larger? Relatively small trading of legume products in the market place, lack of farmer awareness of agronomic benefits of including legumes in crop rotations, and limited investment in research including the lack of financial incentives for seed companies to invest in self-pollinated species (such as most legumes) are among the reasons. Parallel barriers would likely be encountered by any proposed change, whether it involved resource acquisition or crop identity.

A common thread among the resources we highlight is that they are often present yet unavailable: N_2 in the atmosphere calls for biological fixation; P chemically bound in soil calls for biologically mediated release; and water at depth calls for vertical transport. Today, much

Outstanding Questions

What are the levels of benefit as observed in natural ecosystems that can be expected from temporal partitioning in resource use among species in such practices as relay cropping and intensive crop rotations? Which benefits are unobtainable except through increasing the number of species?

Are some benefits of functional diversity obtainable from attributes of single species? Examples might include larger-stature plants that retain greater nutrient mass; litter quality that fosters heterotrophic N fixation; and rapid growth and extensive resource acquisition by perennial roots on herbaceous species.

Nutrient retention in plant tissues reduces the likelihood of loss through leaching, and recycling of previously accessed nutrients reduces the need for fertilizer. Are there crop species, or potential crop species, that accrue large amounts of essential mineral nutrients and retain a substantial portion in postharvest debris?

Which host-plant traits lend themselves most readily to modification likely to lead to enhanced N_2 fixation?

Are there opportunities to domesticate perennial plants that have high yield potential? Annual grains have high food yields, but perennials excel at resource acquisition and nutrient retention. So far, attempts to make perennials of annuals have faced significant challenges. Is it time to take the opposite approach, and emphasize the domestication of perennials?

crop production operates on the basis of adding resources, rather than accessing potential supplies that are biologically difficult to access. Resource scarcity is a matter of both amount and accessibility. Cropping systems in many parts of the world would benefit from incorporation of traits and processes that enable them to access resources that are present but just beyond reach.

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References

1. United Nations (2017) *World Population Prospects: The 2017 Revision, Key Findings and Advance Tables*. Department of Economic and Social Affairs, Population Division. Working Paper No. ESA/P/WP/248
2. Alexandratos, N. and Bruinsma, J. (2012) *World Agriculture Towards 2020/2050: the 2012 Revision*. ESA Working paper No. 12-03, Food and Agriculture Organization of the United Nations
3. Grassini, P. *et al.* (2013) Distinguishing between yield advances and yield plateaus in historical crop production trends. *Nat. Commun.* 4, 2918
4. Ullstrup, A.J. (1972) The impacts of the southern corn leaf blight epidemics of 1970–1971. *Annu. Rev. Phytopathol.* 10, 37–50
5. Muller, A. *et al.* (2017) Strategies for feeding the world more sustainably with organic agriculture. *Nat. Commun.* 8, 1290
6. Poore, J. and Nemecek, T. (2018) Reducing food's environmental impacts through producers and consumers. *Science* 360, 987–992
7. Hooper, D.U. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35
8. Harper, J.L. (1977) *Population Biology of Plants,* Academic Press
9. Shi, Y. *et al.* (2016) Unmanned aerial vehicles for high-throughput phenotyping and agronomic research. *PLoS One* 11, e0159781
10. National Academies of Sciences, Engineering, and Medicine (2018) *Science Breakthroughs to Advance Food and Agricultural Research by 2030,* National Academies Press
11. Robertson, G.P. and Vitousek, P.M. (2009) Nitrogen in agriculture: balancing the cost of an essential resource. *Annu. Rev. Environ. Resour.* 34, 97–125
12. FAO (2017) *World Fertilizer Trends and Outlook to 2020. Summary Report,* Food and Agriculture Organization of the United Nations
13. Mosier, A.R. *et al.*, eds (2004) *Agriculture and the Nitrogen Cycle: Assessing the Impacts of Fertilizer Use on Food Production and the Environment*, Island Press
14. Booth, M.S. *et al.* (2005) Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecol. Monogr.* 75, 139–157
15. Galloway, J.N. *et al.* (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320, 889–892
16. FAO (2017) *The Future of Food and Agriculture: Trends and Challenges,* Food and Agriculture Organization of the United Nations
17. Foyer, C.H. *et al.* (2016) Neglecting legumes has compromised human health and sustainable food production. *Nat. Plants* 2, 16112
18. Castán, E. *et al.* (2016) Managing the value of composts as organic amendments and fertilizers in sandy soils. *Agric. Ecosyst. Environ.* 224, 29–38
19. Cordell, D. and White, S. (2014) Life's bottleneck: sustaining the world's phosphorus for a food secure future. *Annu. Rev. Environ. Resour.* 39, 161–188
20. Walker, T.W. and Syers, J.K. (1976) Fate of phosphorus during pedogenesis. *Geoderma* 15, 1–19
21. Haridasan, M. (2008) Nutritional adaptations of native plants of the cerrado biome in acid soils. *Braz. J. Plant Physiol.* 20, 183–195
22. Lambers, H. *et al.* (2013) Phosphorus nutrition of phosphorus-sensitive Australian native plants: threats to plant communities in a global biodiversity hotspot. *Conserv. Physiol.* 1, 1–20
23. Turner, B.L. *et al.* (2018) Pervasive phosphorus limitation of tree species but not communities in tropical forests. *Nature* 555, 367–370
24. Lambers, H. *et al.* (2011) Phosphorus nutrition of Proteaceae in severely phosphorus-impoverished soils: Are there lessons to be learned for future crops? *Plant Physiol.* 156, 1058–1066
25. Pieterse, C.M. *et al.* (2016) The soil-borne supremacy. *Trends Plant Sci.* 21, 171–173
26. Verbon, E.H. and Liberman, L.M. (2018) Beneficial microbes affect endogenous mechanisms controlling root development. *Trends Plant Sci.* 21, 218–229
27. Ewel, J.J. (1999) Natural systems as models for the design of sustainable systems of land use. *Agrofor. Syst.* 45, 1–21
28. Sinclair, T.R. *et al.* (2017) Limited-transpiration response to high vapor pressure deficit in crop species. *Plant Sci.* 260, 109–118
29. Sinclair, T.R. (ed.) (2017) *Water-Conservation Traits to Increase Crop Yields in Water-Deficit Environments: Case Studies*, Springer
30. Crews, T.E. and DeHaan, L.R. (2015) The strong perennial vision: a response. *Agroecol. Sustain. Food* 39, 500–515
31. Van Tassel, D.L. *et al.* (2010) Missing domesticated plant forms: can artificial selection fill the gap? *Evol. Appl.* 3, 434–452
32. Crews, T.E. and Cattani, D.J. (2018) Strategies, advances, and challenges in breeding perennial grain crops. *Sustainability* 10, 2192
33. Huang, G. *et al.* (2018) Performance, economics and potential impact of perennial rice PR 23 relative to annual rice cultivars at multiple locations of Yunnan Province of China. *Sustainability* http://dx.doi.org/10.3390/su10041086
34. Werner, G.D.A. *et al.* (2014) A single evolutionary innovation drives the deep evolution of symbiotic N_2-fixation in angiosperms. *Nat. Commun.* 5, 4087
35. Soltis, D.E. *et al.* (1995) Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen fixation in angiosperms. *Proc. Natl. Acad. Sci.* 92, 2647–2651
36. Brundrett, M.C. (2002) Coevolution of roots and mycorrhizas of land plants. *New Phytol.* 154, 275–304
37. Corrales, A. *et al.* (2018) Ectomycorrhizal associations in the tropics – biogeography, diversity patterns and ecosystem roles. *New Phytol.* 220, 1076–1091

38. Coley, P.D. and Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27, 305–335
39. FAO (2017) *Would You Judge a Book by Its Cover? Book Cover Designs on Pulses and Legumes from the FAO Library Collections.* Food and Agriculture Organization of the United Nations
40. Sinclair, T.R. and Weiss, A. (2010) *Principles of Ecology in Plant Production,* CAB International
41. Castellanos, J.Z. *et al.* (1997) Symbiotic nitrogen fixation and yield of *Pachyrhizus erosus* (L) Urban cultivars and *Pachyrhizus ahipa* (Wedd) Parodi landraces as affected by flower pruning. *Soil Biol. Biochem.* 29, 973–981
42. Hirano, K. *et al.* (2017) Engineering the lodging resistance mechanism of post-Green Revolution rice to meet future demands. *Proc. Jpn. Acad. B* 93, 220–233
43. Sinclair, T.R. and Nogueira, M.A. (2018) Selection of host-plant genotype: the next step to increase legume N_2 fixation activity. *J. Exp. Bot.* 69, 3523–3530
44. Ae, N. *et al.* (1990) Phosphorus uptake by pigeon pea and its role in cropping systems of the Indian Subcontinent. *Science* 248, 477–480
45. Veneklaas, E.J. *et al.* (2003) Chickpea and white lupin rhizosphere carboxylates vary with soil properties and enhance phosphorus uptake. *Plant Soil* 248, 187–197
46. Ryan, M.H. *et al.* (2012) Carbon trading for phosphorus gain: the balance between rhizosphere carboxylates and arbuscular mycorrhizal symbiosis in plant phosphorus acquisition. *Plant Cell Environ.* 35, 2170–2180
47. Chapuis-Lardy, L. *et al.* (2001) Assessing organic phosphorus status of Cerrado oxisols (Brazil) using ^{31}P-NMR spectroscopy and phosphomonoesterase activity measurement. *Can. J. Soil Sci.* 81, 591–601
48. Achat, D.L. *et al.* (2013) Contributions of microbial and physical-chemical processes to phosphorus availability in Podzols and Arenosols under a temperate forest. *Geoderma* 211–212, 18–27
49. Schreeg, L.A. *et al.* (2013) Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species. *Ecology* 94, 94–105
50. McGill, W.B. and Cole, C.V. (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* 26, 267–286
51. Tarafdar, J.C. and Claasen, N. (1988) Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatases produced by plant roots and microorganisms. *Biol. Fertil. Soils* 5, 308–312
52. Condron, L.M. *et al.* (2005) The chemistry and dynamics of soil organic phosphorus. In *Phosphorus: Agriculture and the Environment* (Sims, J.T. and Sharpley, A.N., eds), pp. 87–121, ASA-CSSA-SSSA
53. Turner, B.L. (2008) Resource partitioning for soil phosphorus: a hypothesis. *J. Ecol.* 96, 698–702
54. Richards, J.H. and Caldwell, M.M. (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemesia tridentata* roots. *Oecologia* 73, 486–489
55. Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95, 565–574
56. Neumann, R.B. and Cardon, Z.G. (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytol.* 194, 337–352
57. Sinclair, T.R. (2000) Model analysis of plant traits leading to prolonged crop survival during severe drought. *Field Crops Res.* 68, 211–217
58. Pang, J. *et al.* (2013) Commensalism in an agroecosystem: hydraulic redistribution by deep-rooted legumes improves survival of a droughted shallow-rooted legume companion. *Physiol. Plant.* 149, 79–90
59. Izumi, Y. *et al.* (2018) Water supply from pearl millet by hydraulic lift can mitigate drought stress and improve productivity of rice by the close mixed planting. *Plant Prod. Sci.* 21, 8–15
60. Sekiya, N. *et al.* (2011) Applying hydraulic lift in an agroecosystem: forage plants with shoots removed supply water to neighboring vegetable crops. *Plant Soil* 341, 39–50