

NUTRIENTS IN AGROECOSYSTEMS: RETHINKING THE MANAGEMENT PARADIGM

L. E. Drinkwater¹ and S. S. Snapp²

¹Department of Horticulture, Cornell University, Ithaca, New York 14853

²Department of Crop and Soil Science and W. K. Kellogg Biological Station,
Michigan State University, East Lansing, Michigan 48824

- I. Introduction
- II. Nutrient Management in Agriculture
- III. Internal Biogeochemical Processes in Agroecosystems
- IV. Toward an Ecosystem-Based Approach to Improving Nutrient Use Efficiency
 - A. Using Plant Diversity to Restore Ecosystem Functions
 - B. Restoration of Ecosystem Function Through Plant–Microbial Interactions
 - C. Microbially Mediated Processes
- V. Plant Adaptation to Ecosystem-Based Nutrient Management
- VI. Conclusions
- Acknowledgments
- References

Agricultural intensification has greatly increased the productive capacity of agroecosystems, but has had unintended environmental consequences including degradation of soil and water resources, and alteration of biogeochemical cycles. Current nutrient management strategies aim to deliver soluble inorganic nutrients directly to crops and have uncoupled carbon, nitrogen, and phosphorus cycles in space and time. As a result, agricultural ecosystems are maintained in a state of nutrient saturation and are inherently leaky because chronic surplus additions of nitrogen and phosphorus are required to meet yield goals. Significant reductions of nutrient surpluses can only be achieved by managing a variety of intrinsic ecosystem processes at multiple scales to recouple elemental cycles. Rather than focusing solely on soluble, inorganic plant-available pools, an ecosystem-based approach would seek to optimize organic and mineral reservoirs with longer mean residence times that can be accessed through microbially and plant-mediated processes. Strategic use of varied nutrient sources, including inorganic fertilizers, combined with increases in plant diversity aimed at expanding the functional roles of plants in agroecosystems will help restore desired agroecosystem functions.

To develop crops that can thrive in this environment, selection of cultivars and their associated microorganisms that are able to access a range of nutrient pools will be critical. Integrated management of biogeochemical processes that regulate the cycling of nutrients and carbon combined with increased reservoirs more readily retained in the soil will greatly reduce the need for surplus nutrient additions in agriculture.

© 2007, Elsevier Inc.

I. INTRODUCTION

The unintended consequences of modern agriculture extend well beyond agricultural landscapes themselves (Altieri, 1989; Hambridge, 1938; Matson *et al.*, 1997; Pimentel *et al.*, 1991). Biogeochemical cycles have been profoundly altered at multiple scales (Carpenter *et al.*, 1998; Vitousek *et al.*, 1997) and the rate of soil loss still exceeds soil formation (Pimentel *et al.*, 1991). Nitrogen (N) and phosphorus (P) are the two most important nutrients limiting biological production (Chapin *et al.*, 1986; Tyrrell, 1999) and are the most extensively applied nutrients in managed terrestrial systems, mainly as soluble inorganic fertilizers (F_i). Agriculture accounts for 60% of the biologically active N from anthropogenic sources (Vitousek *et al.*, 1997). Available P in the biosphere has also increased in the last 50 years, largely as a result of P applications to agricultural lands. P flux to coastal oceans has nearly tripled, from 8×10^6 Mg year⁻¹ to the current rate of 22×10^6 Mg year⁻¹ (Howarth *et al.*, 1995). Nutrient enrichment has complex, often detrimental effects in natural ecosystems (Carpenter and Cottingham, 1997; Galloway, 2000; Vitousek *et al.*, 1997). Global N and P fluxes are projected to increase substantially as developing countries increase F_i production capacity (Galloway, 2000; Tilman, 1999). A new approach to nutrient supply in intensively managed ecosystems is required to reverse this process of global eutrophication.

In this chapter, we briefly consider the origin and consequences of the current soil fertility management paradigm. We then present an ecosystem-based conceptual framework that can serve as a basis for nutrient management in agriculture and assess the potential contributions from a wide range of ecosystem processes. Our aim is to critically evaluate the potential for intrinsic ecosystem processes to improve nutrient use efficiency and nutrient balance at the ecosystem scale while maintaining productivity.

II. NUTRIENT MANAGEMENT IN AGRICULTURE

Since the late 1800s, research efforts to improve soil fertility have been based on the premise that agricultural production must continue to increase in order to keep pace with population growth (Bear, 1926; Crookes, 1899). Initially, F_i were viewed as supplemental nutrient sources. During the first half of the twentieth century, agriculturalists emphasized the importance of long-term experimentation, temporal plant diversity, maintenance of soil organic matter (SOM) and the need to understand and manage soil biological processes (Andrews, 1947; Hopkins, 1945; Waksman, 1936).

A divergent view, that manufactured F_i could support high yields without additions of organic amendments and diverse rotations, gained support through the 1940s and 1950s to become the dominant paradigm (Hopkins, 1945; Tisdale *et al.*, 1993). This transition represented a fundamental paradigm shift. The focus of soil fertility management became the relatively small, ephemeral, soluble inorganic N and P pools rather than nutrient reservoirs with longer mean residence times (MRTs). As purchased F_i became more widespread, agronomists sought to minimize fertilizer costs while maximizing yields and profitability through the development of soil tests for plant-available nutrients combined with fertilizer trials conducted for a single growing season (Schreiner and Anderson, 1938). Dependable soil tests for available P were developed in the late 1940s and have been in common use since the 1960s (Bray and Kurtz, 1945; Olsen *et al.*, 1954). Predicting plant-available soil N has proven to be more challenging, and efforts to develop a soil test for N continue. Currently, the pre-sidedress nitrate test is the most widely recommended soil N test used to assess plant-available N just before the exponential growth phase of the crop (Magdoff *et al.*, 1984).

The impacts of nutrient losses from agricultural lands on aquatic ecosystems became apparent in the 1970s prompting a debate about how to best achieve yields without harming the environment (Carpenter *et al.*, 1998). As a result, the aim of soil fertility management has broadened to encompass both economic and environmental goals and fertilizer recommendations have undergone substantial refinement and become quite complex (Fig. 1). Meanwhile, the “ecological” agriculture paradigm also emerged in the 1980s advocating the application of ecological principles to develop food production systems based on internal, biologically driven processes in an effort to reduce external inputs while achieving adequate yields (Lowrance *et al.*, 1984). The application of ecology in agricultural pest and weed control has become embedded in US agricultural policy, resulting in management options that blend biologically and chemically based strategies (Ehler and Bottrell, 2000; Liebman and Gallandt, 1997). In contrast, an integrated

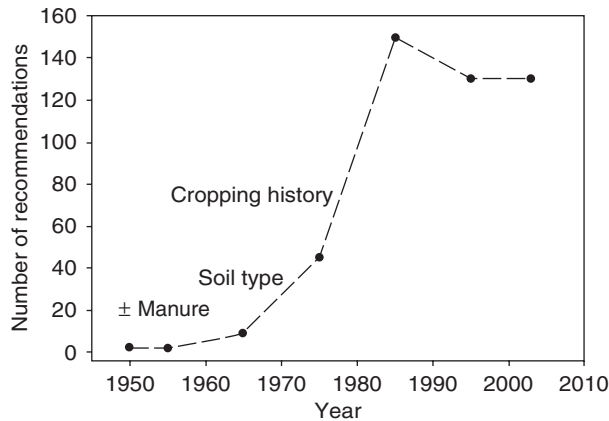


Figure 1 Refinement of N fertilizer recommendations for New York during the past 50 years by 5-year increments. Initially, recommended amounts of N fertilizer were based simply on whether animal manure would be applied. By the 1980s fertilizer recommendation tables included history of animal manure application, cropping history, and soil type resulting in >100 different fertilizer rates (i.e., in 1985, there were 5 soil types \times 10 cropping histories \times 3 manure rates). Data from Cornell Cooperative Extension, 1950–2003.

nutrient management strategy based on ecological concepts has yet to be broadly applied.

Instead, the current paradigm guiding nutrient management amounts to a technologically advanced version of the approach developed before the ecosystem concept became a guiding paradigm in ecology. The problem of improved F_i use efficiency has been viewed mainly as a consequence of temporal asynchrony and spatial separation between applied nutrients and the crop (Stevenson and Baldwin, 1969; Welch *et al.*, 1971). As a result, nutrient management research continues to emphasize improved delivery of F_i to the root zone during the period of crop uptake through modifications such as banding, fertigation, and split fertilizer applications (Bolland and Gilkes, 1998; Cassman *et al.*, 2002). Fertilizer use efficiency is evaluated using metrics that reflect crop uptake of fertilizer added in the current growing season (Cassman *et al.*, 2002). To increase crop access to N fertilizer, a variety of additives have been developed that inhibit nitrification and denitrification (Wolt, 2004). This approach has been extremely successful in terms of maximizing yields; however, attempts to reduce nutrient losses have met with limited success (Cassman *et al.*, 2002). Despite more than 30 years of concentrated effort, mass balances indicate annual N and P inputs consistently exceed harvested exports by 40 to $\geq 60\%$ resulting in substantial losses of these nutrients to the environment (Bolland and Gilkes, 1998; David and Gentry, 2000; Galloway and Cowling, 2002; Van der Molen *et al.*, 1998).

III. INTERNAL BIOGEOCHEMICAL PROCESSES IN AGROECOSYSTEMS

The reliance on F_i combined with use of chemical weed controls has led to a series of management changes that have restructured agroecosystems and uncoupled N, P, and carbon (C) cycles. Simplified rotations became possible when these technologies made it unnecessary to grow cover crops and forages in sequences that alternated with cash crops (Auclair, 1976). These crops have little or no cash value per se but help to maintain internal cycling capacity through a variety of mechanisms. Specifically, the preferential removal of winter annuals from large expanses of agricultural lands has increased the prevalence of bare fallows. This reduction in the time frame of living plant cover and C fixation combined with tillage increases soil erosion and depletion of SOM stocks (Aref and Wander, 1997; Campbell and Zentner, 1993) and increases the susceptibility of these ecosystems to nutrient saturation and nutrient losses (Fenn *et al.*, 1998; McCracken *et al.*, 1994; Tonitto *et al.*, 2006).

In these simplified rotations where bare fallow is maintained for 4–8 months, microbial assimilation is the only other major route for biologically mediated retention of added F_i . The arrangement of roots, soil aggregates, and pores creates tremendous microscale spatial heterogeneity. As a result, environmental conditions favoring either aerobic or anaerobic processes and N- or C-limiting conditions frequently co-occur within the soil matrix (van Elsas and van Overbeek, 1996). While C limitation rarely occurs in the rhizosphere (Cheng *et al.*, 1996), decomposers in bulk soil are usually C limited (Koch *et al.*, 2001) and less numerous (Rouatt *et al.*, 1960). Under the prevailing conditions in agricultural soils, microbial assimilation of N and P occurs primarily in the rhizosphere, exactly the same location as plant uptake, while processes contributing to nutrient losses predominate in bulk soil (Smith and Tiedje, 1979). Under conditions of surplus N additions, increased denitrification can also occur in the rhizosphere (Smith and Tiedje, 1979).

The reduction of plant-driven sinks in space and time combined with the emphasis on supplying soluble, inorganic nutrients creates a “fertilizer treadmill” that promotes the requirement for chronic surplus additions of F_i . In essence, it is the management framework that resulted from the transition to F_i that has created agricultural systems which inadvertently maximize nutrient saturation in space and time. The concept of ecosystem-scale N saturation was originally applied to forests receiving anthropogenic N deposition when the N additions exceed the capacity of the ecosystem to cycle or store N internally (Aber *et al.*, 1989; Agren and Bosatta, 1988; Fenn *et al.*, 1998). For the purposes of our discussion of agroecosystems, we expand the concept to apply to both N and P *when availability exceeds the*

capacity of the ecosystem to cycle or store the nutrients in internal reservoirs that can be accessed by plants or microorganisms.

It is not surprising that the degree of nutrient saturation is greatest in intensive annual crop production systems. In these systems, NO_3^- leaching is strongly correlated to N additions (Fig. 2A) indicating that other potential sinks have reached steady state conditions. Mesocosm studies following the fate of ^{15}N from organic versus inorganic sources support the idea that microbial assimilation of F_i in bulk soil is C limited (Azam *et al.*, 1985; Hodge *et al.*, 1999). The fate of soluble P is also influenced by C abundance (Kouno *et al.*, 2002) because geochemical processes leading to the adsorption and precipitation of P into occluded pools are reduced when C is available to drive microbial assimilation of P.

Agronomic ^{15}N studies indicate that strategies targeting improved crop uptake of F_i do increase the proportion of F_i assimilated by the cash crop while permitting farmers to reduce application rates (Mackown and Sutton, 1997; Tran *et al.*, 1997). However, examination of the fate of ^{15}N fertilizer in these improved management regimes raises questions about whether this strategy will lead to production systems that approach a balanced steady state. For example, in a recent study, split applications of ^{15}N fertilizer to wheat achieved comparable yields with less applied N and reduced N fertilizer losses (Matson *et al.*, 1998). However, since the proportion of fertilizer exported in the wheat increased while proportional N losses remained the same, the amount of fertilizer remaining in the soil and returned as wheat stubble/roots decreased with reduced N additions (Fig. 2B). Reductions in the quantity of fertilizer N entering the internal N cycle would lead to declines in organic soil N reservoirs and could ultimately reduce yields since the wheat crop obtained about the same amount of N from the soil in both treatments.

IV. TOWARD AN ECOSYSTEM-BASED APPROACH TO IMPROVING NUTRIENT USE EFFICIENCY

Restoration of ecosystem function and the recoupling of C, N, and P can best be accomplished by managing ecosystem processes at a variety of temporal and spatial scales to reduce the need for chronic additions of surplus nutrients. Landscape level strategies that integrate wetlands and other types of riparian buffers into agricultural landscapes are very effective in protecting sensitive natural ecosystems and are a key strategy in ecosystem-scale nutrient management (Lowrance, 1992; Mitsch *et al.*, 2001). Incorporation

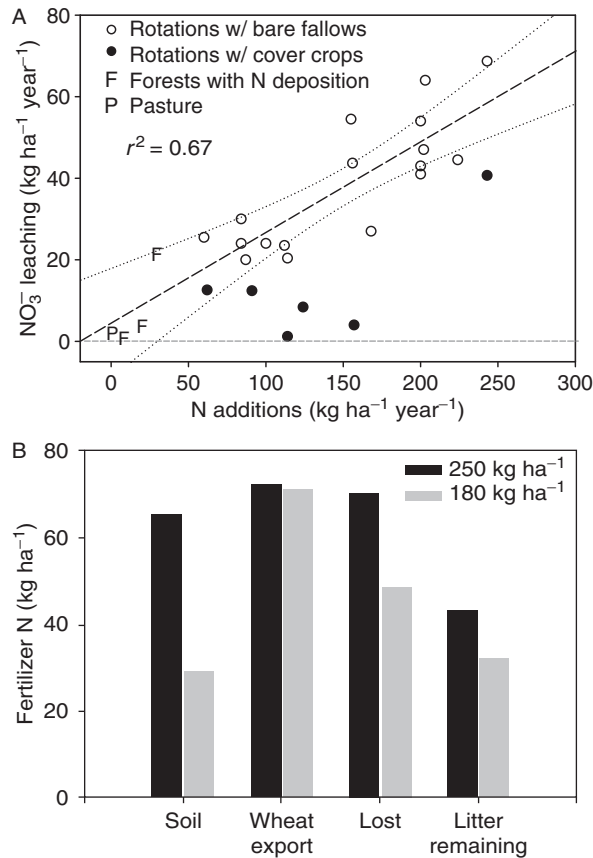
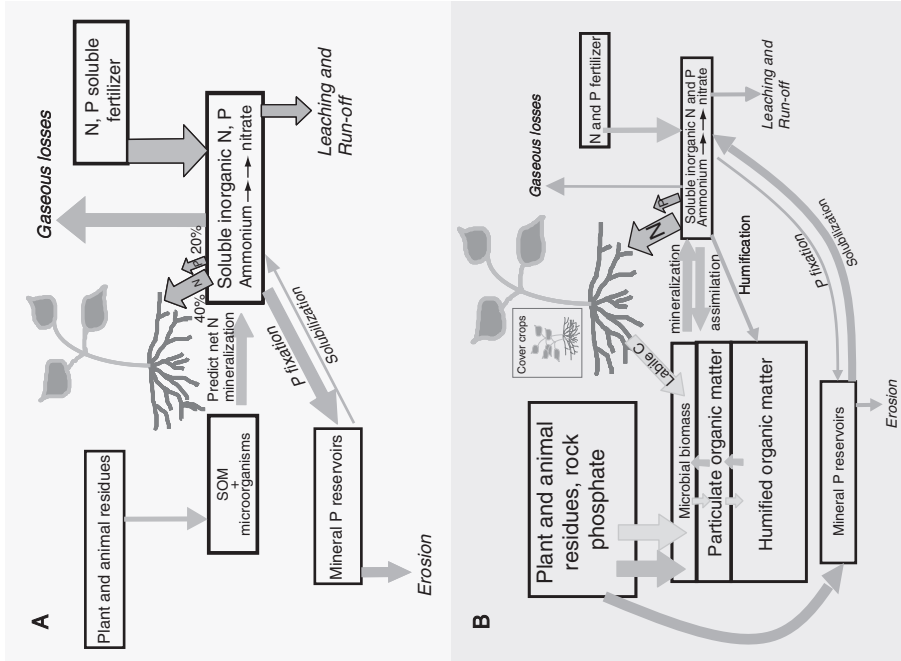


Figure 2 Fate of N relative to N additions across a range of ecosystems. (A) NO₃⁻ leaching losses relative to N additions in annual cropping systems, forests, and a pasture (Brandi-Dohrn *et al.*, 1997; Fenn *et al.*, 1998; Jemison and Fox, 1994; Kanwar *et al.*, 1997; McCracken *et al.*, 1994; Randall and Iragavarapu, 1995; Randall *et al.*, 1997; Staver and Brinsfield, 1998; Steinheimer *et al.*, 1998). Linear regression and 95% confidence intervals for annual rotations without cover crops is shown. The graph includes leaching studies that met the following criteria: (1) studies conducted in North America in annual rotations that included corn, (2) at least 2 years of data from treatments that had been in place for at least 1 year before data collection began, (3) year-round collection of leachate from below the root zone, and (4) medium soil textures (clay loam or silt loam to silty-clay loam). (B) Fate of fertilizer-derived N applied to wheat as a single application of 250 kg ha⁻¹ compared to split applications totaling 180 kg ha⁻¹. Modified after Matson *et al.* (1998) with additional data provided by the authors to L.E.D.

of strategically located plant communities that can act as nutrient sinks in managed landscapes can effectively capture particulate and soluble nutrients before they reach adjacent waterways or aquatic ecosystems (Mitsch *et al.*, 2001).

Conceptual framework for an ecological approach to nutrient management	
Current model	Ecosystem model
<p>Nutrient supply</p> <ul style="list-style-type: none"> Primarily soluble, inorganic fertilizers (F_i) Provide an optimum delivery system for F_i Use soil tests to predict plant available P and net N mineralization, then match F_i applications accordingly 	<ul style="list-style-type: none"> Strategic use of a variety of nutrient sources Maintain reservoirs with longer MRTs that can be accessed by plants and microbes Promote exchanges of C, N, and P between primary producers and decomposers
<p>Soil pools actively managed</p> <ul style="list-style-type: none"> Inorganic N, extractable P 	<ul style="list-style-type: none"> All N and P pools, organic and inorganic
<p>Plant-mediated processes</p> <ul style="list-style-type: none"> Manage crop to create a strong sink for F_i Remove all growth limiting factors 	<ul style="list-style-type: none"> Maximize C fixation, N and P assimilation in time and space through increased plant diversity
<p>Microbial and abiotic transformations</p> <ul style="list-style-type: none"> Chemical additives to inhibit nitrification and denitrification Reduce surface area of fertilizer patches Optimize pH to reduce P fixation 	<ul style="list-style-type: none"> Reduce the size of soluble, inorganic nutrient pools Promote microbial uptake and humification Promote plant-mediated microbial transformations that supply nutrients



To complement these strategies, nutrient use efficiency within agroecosystems themselves must also be improved. Our conceptual framework for an ecosystem-based approach is outlined in Fig. 3. A key feature of this conceptual model is the overarching goal of developing cropping systems that approach steady states where yields and soil reservoirs are maintained with nutrient inputs that are approximately equal to harvested exports (Fig. 3). This will require management of a wider array of ecosystem processes that govern internal cycling capacity such as decomposition, microbial assimilation, biologically mediated weathering, microbially mediated N and P transformations, and soil aggregate formation. Recoupling C, N, and P cycles will reduce the need for chronic additions of surplus nutrients by increasing the sink strength of retention pathways. As a first step, the full range of organic and inorganic nutrient reservoirs must be considered, with the goal of enhancing those with longer MRTs that can be accessed by microorganisms and plants (Fig. 3). Diversification of N and P inputs is an important means of building these pools, through greater use of recycled organic residues, biological N fixation (BNF), and mineral forms of P such as apatite. Soluble F_i should be managed to enhance assimilation of N and P in biologically regulated sinks through both plant-driven and microbially driven processes.

This framework expands the focus of nutrient management to include a variety of sinks in addition to crop uptake and to explicitly target internal as well as external sources. Enhancing biologically mediated N and P reservoirs will have long-term and cascading impacts on the internal cycling capacity agroecosystems. For example, organic P reservoirs are challenging to measure and not generally considered to be significant in supplying P to crops. As a result, organic P is not measured during routine estimates of soil P availability, although total organic P is sometimes calculated as the difference between total soil P and extractable P. However, if we manipulate the relative abundance of C and P in the soil, the small organic pools with a rapid turnover rate will

Figure 3 Conceptual model for the current nutrient management strategy (blue background) compared to our proposed ecosystem-based framework (green background). Arrow colors indicate dominant elemental fluxes as follows: N (blue), P (green), N and P (blue-green), and C (gray). (A) Under current practices, N and P are added primarily as soluble, plant-available forms. The majority of these inputs are lost either through leaching (mainly N, some P), gaseous losses (N), P fixation into occluded pools, and erosion (N and P). Soluble pools are relatively large while microbial biomass and SOM pools are reduced. (B) Shifting the focus to management of pools with longer MRTs including the range of SOM pools and sparingly soluble P would reduce standing pools of soluble inorganic N and P, increase microbially mediated assimilation and mineralization and reduce nutrient losses. Nutrient sources are diversified (BNF, organic residues, sparingly soluble rock PO_4^- and reduced amounts of soluble F_i). In both cases, labile C is exchanged to access soil reservoirs, however, this mechanism is actively promoted in our ecologically driven framework. (See Color Insert.)

compete with geochemical pathways of P adsorption and absorption that lead to P occlusion. As a result, more P would remain in organic reservoirs which can be accessed by plants either directly or through collaboration with microbes.

The few published studies that have examined agroecosystem-scale functions in diversified cropping systems designed to promote linkages between C, N, and P cycles are promising. In these systems, productivity was maintained while nutrient balances were improved and internal nutrient reserves increased (Blake *et al.*, 2000; Clark *et al.*, 1998; Drinkwater *et al.*, 1998; Gregorich *et al.*, 2001). A greater proportion of total N inputs was accounted for, either as harvested exports or as N stored in the soil, in diversified rotations using low C:N residues as N sources compared to simplified rotations managed with F_1 (Clark *et al.*, 1998; Drinkwater *et al.*, 1998). Long-term studies also indicate that P use by plants was much more efficient if P was applied in balance with C availability (Blake *et al.*, 2000) or when diversified rotations were used to increase the proportion of fertilizer P in biologically mediated pools (Bunemann *et al.*, 2004b). When nutrient sources are manipulated, a smaller proportion of the nutrients added as organic residues or apatite is taken up by the crop, however, a greater proportion is retained in various soil pools and is available to the crop in subsequent years (Azam *et al.*, 1985; Bundy *et al.*, 2001; Hodge *et al.*, 1999; Ladd and Amato, 1986). These studies suggest that a nutrient management strategy based on a broader range of ecosystem processes is worth further investigation. They also demonstrate that nutrient mass balance and storage in various soil reservoirs must be considered in conjunction with the current approach of estimating only the proportion of F_1 harvested as crop yield to accurately judge the efficacy of added nutrients.

While this kind of information is limited, there are numerous examples of research that targets a single process either in natural or managed ecosystems that could contribute to an integrated strategy for nutrient management. Our discussion will focus on three areas with the greatest potential for contributing to this approach: (1) increased plant biodiversity, (2) plant-microbial interactions, and (3) microbially mediated processes.

A. USING PLANT DIVERSITY TO RESTORE ECOSYSTEM FUNCTIONS

Efficient use of plant diversity to restore ecosystem functions will entail a more sophisticated approach than simply reinstating traditional rotations. Plants and their associated microbes regulate myriad processes which ultimately control ecosystem fluxes of C, N, and P (Eviner and Chapin, 2001; Fierer *et al.*, 2001; Hooper and Vitousek, 1997; Wedin and Tilman, 1990). Intentional management of plant diversity based on the capacity of a species to contribute to ecosystem processes will help restore desired agroecosystem

functions and can increase yields in systems where fertilizers are currently under applied (Drinkwater, 1999; Snapp and Silim, 2002; Vance *et al.*, 2003). Indeed, the potential for a single plant species to significantly influence ecosystem function is large in agroecosystems since single species effects tend to be more pronounced in ecosystems with limited biodiversity (Chapin *et al.*, 2000; Hector *et al.*, 1999), particularly when a missing functional group is added (Naeem and Li, 1997). Plant species diversity can be increased either by introducing additional cash crops or noncash crops, such as cover crops or intercrops, selected to serve specific ecosystem functions (noncash crops will hereafter be referred to as accessory crops).

The most commonly identified functional roles used in classifying accessory crops are those relating to phenology (summer/winter annuals, perennial), productive potential, plant architecture, and the nature of symbiont requirements (N-fixing, non-N-fixing). Plant species characteristics, such as litter biochemistry, root exudate composition, fine root turnover, and the characteristics of the rhizosphere environment, also influence a variety of processes that control C, N, and P cycling. Significant plant species effects have been documented for decomposition dynamics and net mineralization of N and P (Fierer *et al.*, 2001; Wedin and Tilman, 1990), aggregate formation (Angers and Mehuys, 1989; Haynes and Beare, 1997), ability to access nutrients such as Ca, Mg, and P from mineral sources (Johnson *et al.*, 1997; Kamh *et al.*, 1999; Marschner and Dell, 1994), and microbial community composition (Burke *et al.*, 2002; Kennedy, 1999; Kent and Triplett, 2002) and function (Cheng *et al.*, 2003).

Replacing bare fallows with appropriate cover crops should be a top priority of nutrient management programs. A meta-analysis of the literature showed that cover cropping reduced NO_3^- leaching by an average of 70% without incurring any sacrifice in yield compared to conventional rotations where gaps between crops were maintained as bare fallows (Tonitto *et al.*, 2006). While the potential for reducing NO_3^- leaching has been determined under a variety of environments, other impacts have received limited attention. Bunemann *et al.* (2004a) showed that including crotalaria (*Crotalaria grahamiana*) in rotation with maize shifts 50% more P fertilizer into the microbial biomass compared to continuous maize. Some recent work has screened cover crop species based on root architecture and root growth rates to identify species with the greatest potential for scavenging NO_3^- that had leached below the cash crop root zone (Thorup-Kristensen, 2001). Depending on the biochemical composition, the additional litter from these plants remains in the ecosystem and enhances internal N and P supply through additions to labile SOM pools, such as particulate organic matter, which are decomposed during subsequent growing seasons (Ladd and Amato, 1986; Puget and Drinkwater, 2001) while also contributing to humified pools with much longer turnover times. Altering the timing of labile C inputs from root

exudation may have cascading effects on the microorganisms that regulate internal cycling processes and increase the conversion of C to microbial biomass (Anderson and Domsch, 1990; Jans-Hammermeister *et al.*, 1998).

Selecting plant species for their ability to contribute to P availability is an exciting possibility that is being studied in tropical systems where P is often the major limiting nutrient. In pot experiments aimed at screening a large number of legume species for P cycling attributes lupin (*Lupinus albus*) and pigeonpea (*Cajanus cajan*) were the most effective legumes at (1) excreting organic acids and (2) enhancing P bioavailability for subsequent maize crops (Kamh *et al.*, 1999). Long-term studies comparing grass versus legume-grass pasture systems also show larger reservoirs of labile organic P (Oberson *et al.*, 2001).

To assess the full value of accessory crops, contributions to other ecosystem functions, such as enhanced disease suppression (Abawi and Widmer, 2000), reduced weed competition and herbicide requirements (Gallandt *et al.*, 1999), and pesticide reductions due to beneficial arthropod communities (Lewis *et al.*, 1997), need to be considered.

B. RESTORATION OF ECOSYSTEM FUNCTION THROUGH PLANT–MICROBIAL INTERACTIONS

Agriculture has a long history of research aimed at understanding how to improve the effectiveness of root symbionts such as rhizobia and mycorrhizae (Kiers *et al.*, 2002). Plant–mycorrhizal associations are the major mechanism for P uptake in over 80% of plant species. In low-fertility soils they also enhance uptake of NO_3^- and NH_4^+ (Marschner and Dell, 1994). Ectomycorrhizal symbiosis in perennial horticultural systems and rhizobia–legume symbioses are routinely promoted (Graham and Eissenstat, 1994; Peoples *et al.*, 1995) yet in general, agricultural production practices appear to have inadvertently reduced diversity, function, and efficiency in these symbioses, shifting a mutualistic, association to a parasitic relationship in some instances (Daniell *et al.*, 1998; Denison *et al.*, 2003; Johnson *et al.*, 1997). A promising approach based on understanding how natural selection regulates changes in mutualistic interactions has been proposed (Denison *et al.*, 2003; Johnson *et al.*, 1997; Kiers *et al.*, 2002). Knowledge of basic evolutionary processes could be used to develop agricultural management practices that favor the most effective symbionts.

Management of the exchange of C from primary producers to decomposers in return for nutrients has not been attempted in agroecosystems, despite the opportunity afforded by the rhizosphere as the site of this mutual codependency between decomposers and plants (Naeem *et al.*, 2000; Wall and Moore, 1999). Plants can stimulate decomposition of organic substrates

by supplying labile C to decomposers in the rhizosphere (Cheng *et al.*, 2003; Clarholm, 1985; Hamilton and Frank, 2001). The identity of the SOM pools accessed through this mechanism remains unknown, however, decomposition of chemically recalcitrant substrates is accelerated in the rhizosphere (Siciliano *et al.*, 2003). The rate of decomposition and N mineralization varies with plant species (Cheng *et al.*, 2003), rhizosphere community composition (Chen and Ferris, 1999; Clarholm, 1985; Ferris *et al.*, 1998), and nutrient availability (Liljeroth *et al.*, 1994; Tate *et al.*, 1991). Net mineralization does not simply depend on a surplus of nutrients relative to C during decomposition but is enhanced by the involvement of secondary consumers feeding on the primary decomposers due to differences in the stoichiometry between the two trophic levels (Chen and Ferris, 1999; Clarholm, 1985; Ferris *et al.*, 1998). This trophic cascade provides a mechanism for the primary producers to influence nutrient mineralization analogous to the so-called “microbial loop” in aquatic ecosystems where primary producers often increase excretion of soluble C under nutrient-limiting conditions (Berman and Dubinsky, 1999; Elser and Urabe, 1999). Under these conditions, food web structure is a significant regulator of nutrient availability and can determine whether the primary producers are N or P limited (Elser and Urabe, 1999). There is growing evidence that plants can influence the rate of net N mineralization through this mechanism, based on their need for nutrients by modifying the amount of soluble C excreted into the rhizosphere (Hamilton and Frank, 2001).

Greater reliance on plant-mediated mineralization for nutrient acquisition in agroecosystems would reduce the potential for nutrient losses due to the tight coupling between net mineralization of N and P and plant uptake in the rhizosphere. Inorganic nutrient pools can be extremely small while high rates of net primary productivity (NPP) are maintained if N mineralization and plant assimilation are spatially and temporally connected in this manner (cf. Jackson *et al.*, 1988). To effectively manage this process, many questions remain to be answered. In particular, understanding which SOM pools are being accessed by plant-mediated decomposition will be key as will the development of strategies to manage agroecosystems to increase these reservoirs while minimizing net mineralization in the absence of plants. Other aspects such as food web structure could also be influenced by management to optimize this process.

C. MICROBIALLY MEDIATED PROCESSES

Microorganisms represent a substantial portion of the standing biomass in terrestrial ecosystems and contribute to the regulation of C sequestration, N availability and losses, and P dynamics. The amount of N and P in soil

prokaryotes is nearly equal to the amount in terrestrial plants (Whitman *et al.*, 1998). For cultivated systems, the N and P in soil prokaryotes in the top meter of soil is estimated to average 630 and 60 kg ha⁻¹, respectively (Whitman *et al.*, 1998). Microbial biomass P turnover is rapid, approximately twice as fast as C (Kouno *et al.*, 2002), suggesting the potential for microbial P pools to support plant P requirements may have been markedly underestimated. The size and physiological state of the standing microbial biomass are influenced by management practices, including rotational diversity (Anderson and Domsch, 1990), tillage (Holland and Coleman, 1987), and the quality and quantity of C inputs to the soil (Fliessbach and Mader, 2000; Lundquist *et al.*, 1999; Wander and Traina, 1996). We see exciting possibilities for influencing microbially mediated processes. Increased knowledge of the environmental physiology of soil microbes would greatly enhance our understanding of the relationship between management and microbial community function and support intentional manipulation of microbial functional groups in favor of desired outcomes.

During decomposition, microbial community composition and metabolic status determine the balance between C respired and C assimilated into biomass. Management strategies such as reduced tillage foster increased abundance of fungal decomposers and can lead to increased C retention (Holland and Coleman, 1987). Heterotrophs in soils with greater plant species diversity or greater abundance of C relative to N appear to convert a greater proportion of metabolized C to biomass (Aoyama *et al.*, 2000; Fliessbach *et al.*, 2000).

The new molecular tools that make it possible to characterize abundance and activity of microbial functional groups open up new possibilities for intentional management of the microbial community to enhance N retention. Cavigelli and Robertson (2000, 2001) discovered that denitrifiers from an agricultural soil were more sensitive to O₂ levels and produced a greater proportion of N₂O compared to denitrifiers from an early successional plant community. Denitrifier community composition influenced both the rate of denitrification and the proportion of N₂O to N₂ produced. A second anaerobic NO₃⁻ pathway, dissimilatory nitrate reduction to ammonium (DNRA), occurs in a variety of unmanaged terrestrial ecosystems (Silver *et al.*, 2001) and could also be manipulated to enhance N conservation. Previously this process was thought to be limited to extremely anaerobic, C-rich environments such as sewage sludge and submerged sediments (Maier *et al.*, 2000). Silver *et al.* (2001) reported average rates of DNRA were threefold greater than denitrification in humid tropical forest soils and concluded that the resulting reduction in NO₃ availability to denitrifiers and leaching may contribute to N conservation in these ecosystems. The presence of microbes capable of DNRA in agricultural systems has yet to be determined, but there is no reason to expect this process to be excluded from managed ecosystems. Agricultural soils with management-induced increases in labile C pools have a greater NH₄⁺:NO₃⁻ ratio compared to soils where C is

less abundant (Drinkwater *et al.*, 1995) suggesting DNRA may be an important N-conserving process in agroecosystems that could be enhanced through management of appropriate soil organic C pools.

Microorganisms access P through several mechanisms that ultimately lead to increased P availability for primary producers (Illmer *et al.*, 1995; Oberson *et al.*, 2001). Direct excretion of phosphatase enzymes is an important mechanism for releasing P from recalcitrant organic forms such as phytic acid. Sparingly soluble P is made available through organic acid excretion, such as occurs in the soil fungus *Penicillium radicum*, isolated from a low-P rhizosphere of unfertilized wheat (Whitelaw *et al.*, 1999). In this system, PO_4^- solubilization from insoluble or sparingly soluble complexes with metals was related to titratable acidity and gluconic acid concentration. Organic acid excretion not only alters pH, but also may chelate Al^{3+} or other cations directly, further enhancing the solubilization of PO_4^- (Erich *et al.*, 2002; Laboski and Lamb, 2003). An incubation study investigating the microbial community structure in legume-maize cropping system found that fungal and gram-negative bacteria abundance tracked was correlated with the organic P pool, and that the major driver determining the size of the labile organic P pool was crop rotation and the presence of plant residues with high soluble C content (Bunemann *et al.*, 2004a).

V. PLANT ADAPTATION TO ECOSYSTEM-BASED NUTRIENT MANAGEMENT

In the last half-century, plant breeding has occurred almost entirely under management regimes that include fumigated soils with luxurious additions of nutrients and sufficient water (Boyer, 1982) and has produced modern hybrids well adapted to a microbially deficient soil environment with abundant resources. This strategy of reducing environmental variation by providing ample resources reduces gene by environment interaction and enhances the power of selection for specific traits (Banziger and Lafitte, 1997). However, it has potentially selected against traits that allow plants to maintain high NPP and yields under nonsaturating nutrient conditions (Jackson and Koch, 1997) and has contributed to the need for surplus nutrient additions.

The impact of conventional plant selection practices on belowground characteristics has rarely been investigated, although interest in this area is growing. In lettuce, comparison of wild genotypes and modern cultivars demonstrated a marked decrease in root system nutrient-scavenging ability due to altered root architecture and reduced plasticity (Jackson, 1995). Cultivar effects on root-associated microorganisms have been found more often than not, and there is now considerable evidence that rhizosphere community

composition varies at the cultivar level in agroecosystems (Briones *et al.*, 2002; Dalmastri *et al.*, 1999; Germida and Siciliano, 2001; Siciliano *et al.*, 1998). Modern wheat varieties have rhizosphere communities distinct from preindustrial varieties (Germida and Siciliano, 2001). In most cases, the functional significance of these differences in plant-associated microbial communities is not known. A notable exception is the case of traditional versus modern rice cultivars where plant-induced species differences in rhizoplane NH_4^+ -oxidizing bacteria appear to account for the greater nitrification rates in the rhizosphere of the modern variety (Briones *et al.*, 2002, 2003). Clearly, plant selection for high yields has had unintended cascading effects on the associated microorganisms and biogeochemical functions.

These examples demonstrate that plants do not exist as single organisms, but are more accurately viewed as a consortium consisting of a primary producer and many species of associated microbes. We see many opportunities for plant breeding to enhance plant-microbial-nutrient interactions in ways that contribute to restored ecosystem functions through some of the mechanisms we have highlighted in this chapter. Crop-breeding programs should select for well-adapted consortia that can achieve necessary yields by accessing nutrient reservoirs less susceptible to loss. Criteria for selection of cash crops should be expanded to include contributions to ecosystem function. For example, crop species with unique ecosystem functions such as N-fixers should be selected under conditions that will enhance these abilities while optimizing yields. On the other hand, accessory crops can be selected to enhance their capability to provide ecosystem services while filling specific niches in space and time that are compatible with cash crop production.

There are a few examples of breeding programs intentionally aimed at improving yields under conditions where nutrients are not saturating. A marked increase in N derived from BNF and yield adaptation to low-input, N-limited cropping systems was recently achieved in the Brazilian soybean-breeding program (Alves *et al.*, 2003). More modest success was achieved by the seminal collaboration of a breeder, microbiologist, and plant physiologist to improve BNF in alfalfa (Barnes *et al.*, 1984; Jessen *et al.*, 1988). Research to improve yield potential of cereal grains in low-nutrient environments has been sporadic, with mixed results until a recent concerted effort showed that it is possible to improve yields of wheat and corn in low-input environments (Banziger and Cooper, 2001).

VI. CONCLUSIONS

While the concept of sustainability as a goal has become widely accepted, the dominant agricultural paradigm still considers high yields and reduced environmental impacts to be in conflict with one another (Keller and Brummer, 2002).

The requirement for nutrient saturation in agriculture will not be easy to overcome given the economic constraints imposed on production-oriented farming systems. Nutrient surpluses in agroecosystems, and hence environmental losses, can be reduced through intentional management of intrinsic ecosystem processes. Our approach shifts the emphasis of nutrient management away from soluble, inorganic plant-available pools to organic and mineral reservoirs that can be accessed through microbially and plant-mediated processes. The goal of nutrient management under this framework would be to balance nutrient budgets as much as possible while maintaining these reservoirs. Management practices that increase the sink capacity of the ecosystem in ways that contribute to reduced needs for surplus additions should be emphasized in conjunction with breeding for cultivars and their associated microorganisms that do not require surplus additions of soluble nutrients. Understanding how plants alter microbial community structure and function to facilitate access to organic and mineral reservoirs (i.e., decomposition and assimilation of N and P from recalcitrant organic polymers, P mobilization from mineral reservoirs) will be an important consideration for cash crops. On the other hand, for accessory crops, understanding assimilatory processes that compete with P geochemical sinks and N loss pathways will be particularly important.

The critical question remains, what productivity levels can be supported by this approach? We do not believe that this question can be fully answered based on available research. Levels of NPP comparable to those achieved in high-yielding agricultural systems occur in unmanaged ecosystems (Zak *et al.*, 1994) and monocultures composed of weedy species (Abul Fatih *et al.*, 1979). Perhaps a more appropriate question is: What proportion of annual NPP would need to be allocated to provide internal ecosystem services while still meeting the goals for harvested exports? This will depend on ecosystem state factors such as climate, topography, and parent soil material, as well as socioeconomic constraints. Many climates with sufficient water and a long growing season support very high annual NPP. These conditions increase the potential for a portion of the NPP to be devoted to the provision of ecosystem functions. In contrast, areas with severe water, light, or temperature limitations, such as the arid tropics or cold temperate zones, will likely require strategic inputs of inorganic nutrients. It follows that an additional requirement for the success of this approach will be to match production systems with the strengths and limitations of the environment.

ACKNOWLEDGMENTS

We thank Mark David, Valerie Eviner, Jørgen Olesen, and David Wolfe for helpful comments on an earlier draft. We also thank the many agricultural professionals, including farmers, who have shared their real world perspective

with us over the years. This work was supported by NSF-BE/CBC #0216316 to L.E.D. and others.

REFERENCES

- Abawi, G. S., and Widmer, T. L. (2000). Impact of soil health management practices on soilborne pathogens, nematodes and root diseases of vegetable crops. *Appl. Soil Ecol.* **15**, 37–47.
- Aber, J. D., Nadelhoffer, K. J., Steudler, P., and Melillo, J. M. (1989). Nitrogen saturation in northern forest ecosystems. *Bioscience* **39**, 378–386.
- Abul Fatih, H. A., Bazzaz, F. A., and Hunt, R. (1979). The biology of *Ambrosia trifida* L. III. Growth and biomass allocation. *New Phytol.* **83**, 829–838.
- Agren, G. I., and Bosatta, E. (1988). Nitrogen saturation of terrestrial ecosystems. *Environ. Pollut.* **54**, 185–198.
- Altieri, M. A. (1989). Agroecology: A new research and development paradigm for world agriculture. *Agric. Ecosystems Environ.* **27**, 37–46.
- Alves, B. J. R., Boddey, R. M., and Urquiaga, S. (2003). The success of BNF in soybean in Brazil. *Plant Soil* **252**, 1–9.
- Anderson, T. H., and Domsch, K. H. (1990). Application of eco-physiological quotients (qCO_2 and qD) on microbial biomasses from soils of different cropping histories. *Soil Biol. Biochem.* **22**, 251–255.
- Andrews, W. B. (1947). “The Response of Crops and Soils to Fertilizers and Manures.” W.B. Andrews, State College, Mississippi.
- Angers, D. A., and Mehuys, G. R. (1989). Effects of cropping on carbohydrate content and water-stable aggregation of a clay soil. *Can. J. Soil Sci.* **69**, 373–380.
- Aoyama, M., Angers, D. A., N'Dayegamiye, A., and Bissonnette, N. (2000). Metabolism of ^{13}C -labeled glucose in aggregates from soils with manure application. *Soil Biol. Biochem.* **32**, 295–300.
- Aref, S., and Wander, M. M. (1997). Long-term trends of corn yield and soil organic matter in different crop sequences and soil fertility treatments on the morrow plots. *Adv. Agron.* **62**, 153–197.
- Auclair, A. N. (1976). Ecological factors in the development of intensive management ecosystems in the midwestern USA. *Ecology* **57**, 431–444.
- Azam, F., Malik, K. A., and Sajjad, M. I. (1985). Transformations in soil and availability to plants of ^{15}N applied as inorganic fertilizer and legume residues. *Plant Soil* **86**, 3–13.
- Banziger, M., and Cooper, M. (2001). Breeding for low input conditions and consequences for participatory plant breeding: Examples from tropical maize and wheat. *Euphytica* **122**, 503–519.
- Banziger, M., and Lafitte, H. R. (1997). Efficiency of secondary traits for improving maize for low-nitrogen target environments. *Crop Sci.* **37**, 1110–1117.
- Barnes, D. K., Heichel, G. H., Vance, C. P., and Ellis, W. R. (1984). A multiple-trait breeding program for improving the symbiosis for N_2 fixation between *Medicago sativa* and *Rhizobium meliloti*. *Plant Soil* **82**, 303–314.
- Bear, F. E. (1926). The coming need for higher yields. In “Soil Fertility Conferences in the Northern States” (N. F. Association, Ed.), pp. 5–10. National Fertilizer Association, Washington, DC.
- Berman, F. I., and Dubinsky, Z. (1999). Balanced growth and aquatic plants: Myth or reality? Phytoplankton use the imbalance between carbon assimilation and biomass production to their strategic advantage. *Bioscience* **49**, 29–37.

- Blake, L., Mercik, S., Koerschens, M., Moskal, S., Poulton, P. R., Goulding, K. W. T., Weigel, A., and Powlson, D. S. (2000). Phosphorus content in soil, uptake by plants and balance in three European long-term field experiments. *Nutr. Cycl. Agroecosyst.* **56**, 263–275.
- Bolland, M. D. A., and Gilkes, R. J. (1998). The chemistry and agronomic effectiveness of phosphate fertilizers. In “Nutrient Use in Crop Production” (Z. Rengel, Ed.), pp. 139–163. The Haworth Press Inc., New York.
- Boyer, J. S. (1982). Plant productivity and environment. *Science* **218**, 443–448.
- Brandi-Dohrn, F. M., Dick, R. P., Hess, M., Kauffman, S. M., Hemphill, D. D., Jr., and Selker, J. S. (1997). Nitrate leaching under a cereal rye cover crop. *J. Environ. Qual.* **26**, 181–188.
- Bray, R. H., and Kurtz, L. T. (1945). Determination of total, organic and available forms of phosphorus in soils. *Soil Sci.* **59**, 39–45.
- Briones, A. M., Jr., Okabe, S., Umemiya, Y., Ramsing, N. B., Reichardt, W., and Okuyama, H. (2002). Influence of different cultivars on populations of ammonia-oxidizing bacteria in the root environment of rice. *Appl. Environ. Microbiol.* **68**, 3067–3075.
- Briones, A. M., Jr., Okabe, S., Umemiya, Y., Ramsing, N. B., Reichardt, W., and Okuyama, H. (2003). Ammonia-oxidizing bacteria on root biofilms and their possible contribution to N use efficiency of different rice cultivars. *Plant Soil* **250**, 335–348.
- Bundy, L. G., Andraski, T. W., and Powell, J. M. (2001). Management practices effects on phosphorus losses in runoff in corn production systems. *J. Environ. Qual.* **30**, 1822–1828.
- Bunemann, E., Bassio, D. A., Smithson, P. C., Frossard, E., and Oberson, A. (2004a). Microbial community composition and substrate use in a highly weathered soil as affected by crop rotation and P fertilization. *Soil Biol. Biochem.* **36**, 889–901.
- Bunemann, E. K., Steinebrunner, F., Smithson, P. C., Frossard, E., and Oberson, A. (2004b). Phosphorus dynamics in a highly weathered soil as revealed by isotopic labeling techniques. *Soil Sci. Soc. Am. J.* **68**, 1645–1655.
- Burke, D. J., Hamerlynck, E. P., and Hahn, D. (2002). Interactions among plant species and microorganisms in salt marsh sediments. *Appl. Environ. Microbiol.* **68**, 1157–1164.
- Campbell, C.-A., and Zentner, R.-P. (1993). Soil organic matter as influenced by crop rotations and fertilization. *Soil Sci. Soc. Am. J.* **57**, 1034–1040.
- Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N., and Smith, V. H. (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* **8**, 559–568.
- Carpenter, S. R., and Cottingham, K. L. (1997). Resilience and restoration of lakes. *Conserv. Ecol.* [online] 1–2.
- Cassman, K. G., Dobermann, A., and Walters, D. T. (2002). Agroecosystems, nitrogen-use efficiency, and nitrogen management. *Ambio* **31**, 132–140.
- Cavigelli, M. A., and Robertson, G. P. (2000). The functional significance of denitrifier community composition in a terrestrial ecosystem. *Ecology* **81**, 1402–1414.
- Cavigelli, M. A., and Robertson, G. P. (2001). Role of denitrifier diversity in rates of nitrous oxide consumption in a terrestrial ecosystem. *Soil Biol. Biochem.* **33**, 297–310.
- Chapin, F. S., III, Vitousek, P. M., and Van Cleve, K. (1986). The nature of nutrient limitation in plant communities. *Am. Nat.* **127**, 48–58.
- Chapin, F. S., III, Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Diaz, S. (2000). Consequences of changing biodiversity. *Nature* **405**, 234–242.
- Chen, J., and Ferris, H. (1999). The effects of nematode grazing on nitrogen mineralization during fungal decomposition of organic matter. *Soil Biol. Biochem.* **31**, 1265–1279.
- Cheng, W., Johnson, D. W., and Fu, S. (2003). Rhizosphere effects on decomposition: Controls of plant species, phenology, and fertilization. *Soil Sci. Soc. Am. J.* **67**, 1418–1427.
- Cheng, W., Zhang, Q., Coleman, D. C., Carroll, C. R., and Hoffman, C. A. (1996). Is available carbon limiting microbial respiration in the rhizosphere? *Soil Biol. Biochem.* **28**, 1283–1288.

- Clarholm, M. (1985). Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* **17**, 181–187.
- Clark, M. S., Horwath, W. R., Shennan, C., and Scow, K. M. (1998). Changes in soil chemical properties resulting from organic and low-input farming practices. *Agron. J.* **90**, 662–671.
- Cornell Cooperative Extension. (1950–2003). “Cornell Recommends for Field Crops.” New York State College of Agriculture and Life Sciences, Ithaca, NY.
- Crookes, W., Sir (1899). “The Wheat Problem; Based on Remarks Made in the Presidential Address to the British Association at Bristol in 1898.” G.P. Putnam’s Sons, New York.
- Dalmastri, C., Chiarini, L., Cantale, C., Bevivino, A., and Tabacchioni, S. (1999). Soil type and maize cultivar affect the genetic diversity of maize root-associated *Burkholderia cepacia* populations. *Microb. Ecol.* **38**, 273–284.
- Daniell, T. J., Husband, R., Fitter, A. H., and Young, J. P. W. (1998). Where have all the fungi gone? II. The diversity of Arbuscular mycorrhizal fungi is low in agricultural ecosystems. *J. Exp. Bot.* **49**, 40.
- David, M. B., and Gentry, L. E. (2000). Anthropogenic inputs of nitrogen and phosphorus and riverine export for Illinois. *USA. J. Environ. Qual.* **29**, 494–508.
- Denison, R.-F., Kiers, E.-T., and West, S.-A. (2003). Darwinian agriculture: When can humans find solutions beyond the reach of natural selection? *Q. Rev. Biol.* **78**, 145–168.
- Drinkwater, L. E. (1999). Using plant species composition to restore soil quality and ecosystem function. In “Designing and Testing Crop Rotations for Organic Farming” (J. E. Olesen, R. Eltun, M. J. Gooding, E. S. Jensen, and U. Kopke, Eds.), pp. 37–46. Danish Research Centre for Organic Farming, Tjele, Denmark.
- Drinkwater, L. E., Letourneau, D. K., Workneh, F., Van Bruggen, A. H. C., and Shennan, C. (1995). Fundamental differences between conventional and organic tomato agroecosystems in California. *Ecol. Appl.* **5**, 1098–1112.
- Drinkwater, L. E., Wagoner, P., and Sarrantonio, M. (1998). Legume-based cropping systems have reduced carbon and nitrogen losses. *Nature* **396**, 262–265.
- Ehler, L. E., and Bottrell, D. G. (2000). The illusion of integrated pest management. *Issues Sci. Technol.* [online] Spring.
- Elser, J. J., and Urabe, J. (1999). The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology* **80**, 735–751.
- Erich, M. S., Fitzgerald, C. B., and Porter, G. A. (2002). The effect of organic amendments on phosphorus chemistry in a potato cropping system. *Agric. Ecosyst. Environ.* **88**, 79–88.
- Eviner, V. T., and Chapin, F. S. (2001). Plant species provide vital ecosystem functions for sustainable agriculture, rangeland management and restoration. *Calif. Agric.* **55**, 54–59.
- Fenn, M. E., Poth, M. A., Aber, J. D., Baron, J. S., Bormann, B. T., Johnson, D. W., Lemly, A. D., McNulty, S. G., Ryan, D. F., and Stottleyer, R. (1998). Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. *Ecol. Appl.* **8**, 706–733.
- Ferris, H., Venette, R. C., Van Der Meulen, H. R., and Lau, S. S. (1998). Nitrogen mineralization by bacteria-feeding nematodes: Verification and measurement. *Plant Soil* **203**, 159–171.
- Fierer, N., Schimel, J. P., Cates, R. G., and Zou, J. (2001). Influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. *Soil Biol. Biochem.* **33**, 1827–1839.
- Fliessbach, A., and Mader, P. (2000). Microbial biomass and size-density fractions differ between soils of organic and conventional agricultural systems. *Soil Biol. Biochem.* **32**, 757–768.
- Fliessbach, A., Mader, P., and Niggli, U. (2000). Mineralization and microbial assimilation of ¹⁴C-labeled straw in soils of organic and conventional agricultural systems. *Soil Biol. Biochem.* **32**, 1131–1139.

- Gallandt, E. R., Liebman, M., and Huggins, D. R. (1999). Improving soil quality: Implications for weed management. *J. Crop Prod.* **2**, 95–121.
- Galloway, J. N. (2000). Nitrogen mobilization in Asia. *Nutr. Cycl. Agroecosyst.* **57**, 1–12.
- Galloway, J. N., and Cowling, E. B. (2002). Reactive nitrogen and the world: 200 years of change. *Ambio* **31**, 64–71.
- Germida, J. J., and Siciliano, S. D. (2001). Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. *Biol. Fertil. Soils* **33**, 410–415.
- Graham, J. H., and Eissenstat, D. M. (1994). Host genotype and the formation and function of VA mycorrhizae. *Plant Soil* **159**, 179–185.
- Gregorich, E. G., Drury, C. F., and Baldock, J. A. (2001). Changes in soil carbon under long-term maize in monoculture and legume-based rotation. *Can. J. Soil Sci.* **81**, 21–31.
- Hambridge, G. (1938). Soils and men—a summary. In “Soils and Men, Yearbook of Agriculture,” pp. 1–44. United States Government Printing Office, Washington, DC.
- Hamilton, E. W., III, and Frank, D. A. (2001). Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* **82**, 2397–2402.
- Haynes, R. J., and Beare, M. H. (1997). Influence of six crop species on aggregate stability and some labile organic matter fractions. *Soil Biol. Biochem.* **29**, 1647–1653.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Hogberg, P., *et al.* (1999). Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127.
- Hodge, A., Robinson, D., Griffiths, B. S., and Fitter, A. H. (1999). Nitrogen capture by plants grown in N-rich organic patches of contrasting size and strength. *J. Exp. Bot.* **50**, 1243–1252.
- Holland, E. A., and Coleman, D. C. (1987). Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* **62**, 425–433.
- Hooper, D. U., and Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302–1305.
- Hopkins, D. P. (1945). “Chemicals, Humus, and the Soil: A Simple Presentation of Contemporary Knowledge and Opinions About Fertilizers, Manures and Soil Fertility.” Faber and Faber Ltd., London, United Kingdom.
- Howarth, R. W., Jensen, H., Marino, R., and Postma, H. (1995). Transport to and processing of phosphorus in near-shore and oceanic waters. In “Phosphorus in the Global Environment” (H. Tiessen, Ed.), pp. 323–345. Wiley & Sons, Chichester, New York.
- Illmer, P., Barbato, A., and Schinner, F. (1995). Solubilization of hardly-soluble $AlPO_4$ with P-solubilizing microorganisms. *Soil Biol. Biochem.* **27**, 265–270.
- Jackson, L. E. (1995). Root architecture in cultivated and wild lettuce (*Lactuca* spp.). *Plant Cell Environ.* **18**, 885–894.
- Jackson, L. E., and Koch, G. W. (1997). The ecophysiology of crops and their wild relatives. In “Ecology in Agriculture” (L. E. Jackson, Ed.), pp. 3–37. Academic Press Inc., San Diego, CA.
- Jackson, L. E., Strauss, R. B., Firestone, M. K., and Bartolome, J. W. (1988). Plant and soil nitrogen dynamics in California annual grassland. *Plant Soil* **110**, 9–17.
- Jans-Hammermeister, D. C., McGill, W. B., and Izaurralde, R. C. (1998). Management of soil C by manipulation of microbial metabolism: Daily vs. pulsed C additions. In “Soil Processes and the Carbon Cycle” (R. Lal, J. M. Kimble, R. F. Follett, and B. A. Stewart, Eds.), pp. 321–333. CRC Press, Boca Raton, FL.
- Jemison, J. M., Jr., and Fox, R. H. (1994). Nitrate leaching from nitrogen-fertilized and manured corn measured with zero-tension pan lysimeters. *J. Environ. Qual.* **23**, 337–343.
- Jessen, D. L., Barnes, D. K., and Vance, C. P. (1988). Bidirectional selection in alfalfa for activity of nodule nitrogen and carbon-assimilating enzymes. *Crop Sci.* **28**, 18–22.

- Johnson, N. C., Graham, J. H., and Smith, F. A. (1997). Functioning and mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* **135**, 575–585.
- Kamh, M., Horst, W. J., Amer, F., Mostafa, H., and Maier, P. (1999). Mobilization of soil and fertilizer phosphate by cover crops. *Plant Soil* **211**, 19–27.
- Kanwar, R. S., Colvin, T. S., and Karlen, D. L. (1997). Ridge, moldboard, chisel, and no-till effects on tile water quality beneath two cropping systems. *J. Prod. Agric.* **10**, 227–234.
- Keller, D. R., and Brummer, E. C. (2002). Putting food production in context: Toward a postmechanistic agricultural ethic. *Bioscience* **52**, 264–271.
- Kennedy, A. C. (1999). Bacterial diversity in agroecosystems. *Agric. Ecosyst. Environ.* **74**, 65–76.
- Kent, A. D., and Triplett, E. W. (2002). Microbial communities and their interactions in soil and rhizosphere ecosystems. *Annu. Rev. Microbiol.* **56**, 211–236.
- Kiers, E. T., West, S. A., and Denison, R. F. (2002). Mediating mutualisms: Farm management practices and evolutionary changes in symbiont co-operation. *J. Appl. Ecol.* **39**, 745–754.
- Koch, B., Worm, J., Jensen, L. E., Højberg, O., and Nybroe, O. (2001). Carbon limitation induces σ^S -dependent gene expression in *Pseudomonas fluorescens* in soil. *Appl. Environ. Microbiol.* **67**, 3363–3370.
- Kouno, K., Wu, J., and Brookes, P. C. (2002). Turnover of biomass C and P in soil following incorporation of glucose or ryegrass. *Soil Biol. Biochem.* **34**, 617–622.
- Laboski, C. A. M., and Lamb, J. A. (2003). Changes in soil test phosphorus concentration after application of manure or fertilizer. *Soil Sci. Soc. Am. J.* **67**, 544–554.
- Ladd, J. N., and Amato, M. (1986). The fate of nitrogen from legume and fertilizer sources in soils successively cropped with wheat under field conditions. *Soil Biol. Biochem.* **18**, 417–425.
- Lewis, W. J., Van Lenteren, J. C., Phatak, S. C., and Tumlinson, J. H., III (1997). A total system approach to sustainable pest management. *Proc. Natl. Acad. Sci. USA* **94**, 12243–12248.
- Liebman, M., and Gallandt, E.-R. (1997). Many little hammers: Ecological management of crop-weed interactions. In “Ecology in Agriculture” (L. E. Jackson, Ed.), pp. 291–343. Academic Press, San Diego, CA.
- Liljeroth, E., Kuikman, P., and Van Veen, J. A. (1994). Carbon translocation to the rhizosphere of maize and wheat and influence on the turnover of native soil organic matter at different soil nitrogen levels. *Plant Soil* **161**, 233–240.
- Lowrance, R. (1992). Groundwater nitrate and denitrification in a coastal plain riparian forest. *J. Environ. Qual.* **21**, 401–405.
- Lowrance, R., Stinner, B. R., and House, G. J. (1984). “Agricultural Ecosystems: Unifying Concepts.” John Wiley & Sons, New York.
- Lundquist, E. J., Jackson, L. E., Scow, K. M., and Hsu, C. (1999). Changes in microbial biomass and community composition, and soil carbon and nitrogen pools after incorporation of rye into three California agricultural soils. *Soil Biol. Biochem.* **31**, 221–236.
- Mackown, C.-T., and Sutton, T.-G. (1997). Recovery of fertilizer nitrogen applied to burley tobacco. *Agron. J.* **89**, 183–189.
- Magdoff, F. R., Ross, D. J., and Amadon, J. (1984). A soil test for nitrogen availability to corn (*Zea mays*). *Soil Sci. Soc. Am. J.* **48**, 1301–1304.
- Maier, R. M., Pepper, I. L., and Gerba, G. P. (2000). “Environmental Microbiology.” Academic Press, San Diego, CA.
- Marschner, H., and Dell, B. (1994). Nutrient uptake in mycorrhizal symbiosis. *Plant Soil* **159**, 89–102.
- Matson, P. A., Naylor, R., and Ortiz, M. I. (1998). Integration of environmental, agronomic, and economic aspects of fertilizer management. *Science* **280**, 112–115.
- Matson, P. A., Parton, W. J., Power, A. G., and Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science* **277**, 504–509.

- McCracken, D. V., Smith, M. S., Grove, J. H., MacKown, C. T., and Blevins, R. L. (1994). Nitrate leaching as influenced by cover cropping and nitrogen source. *Soil Sci. Soc. Am. J.* **58**, 1476–1483.
- Mitsch, W. J., Day, J. W., Jr., Gilliam, J. W., Groffman, P. M., Hey, D. L., Randall, G. W., and Wang, N. (2001). Reducing nitrogen loading to the Gulf of Mexico from the Mississippi River Basin: Strategies to counter a persistent ecological problem. *Bioscience* **51**, 373–388.
- Naeem, S., Hahn, D. R., and Schuurman, G. (2000). Producer-decomposer co-dependency influences biodiversity effects. *Nature* **403**, 762–764.
- Naeem, S., and Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509.
- Oberson, A., Friesen, D. K., Rao, I. M., Buhler, S., and Frossard, E. (2001). Phosphorus transformations in an oxisol under contrasting land-use systems: The role of the soil microbial biomass. *Plant Soil* **237**, 197–210.
- Olsen, S. R., Cole, C. V., Watanabe, F. S., and Dean, L. A. (1954). Estimate of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circ. 939 USDA, Washington, DC.
- Peoples, M. B., Ladha, J. K., and Herridge, D. F. (1995). Enhancing legume N₂ fixation through plant and soil management. *Plant Soil* **174**, 83–101.
- Pimentel, D., McLaughlin, L., Zepp, A., Lakitan, B., Kraus, T., Kleinman, P., Vancini, F., Roach, W. J., Graap, E., Keeton, W. S., and Selig, G. (1991). Environmental and economic effects of reducing pesticide use: A substantial reduction in pesticides might increase food costs only slightly. *Bioscience* **41**, 402–409.
- Puget, P., and Drinkwater, L. E. (2001). Short-term dynamics of root- and shoot-derived carbon from a leguminous green manure. *Soil Sci. Soc. Am. J.* **65**, 771–779.
- Randall, G. W., Huggins, D. R., Russelle, M. P., Fuchs, D. J., Nelson, W. W., and Anderson, J. L. (1997). Nitrate losses through subsurface tile drainage in conservation reserve program, alfalfa, and row crop systems. *J. Environ. Qual.* **26**, 1240–1247.
- Randall, G. W., and Iragavarapu, T. K. (1995). Impact of long-term tillage systems for continuous corn on nitrate leaching to tile drainage. *J. Environ. Qual.* **24**, 360–366.
- Rouatt, J. W., Katznelson, H., and Payne, T. M. B. (1960). Statistical evaluation of rhizosphere effect. *Soil Sci. Soc. Am. Proc.* **24**, 271–273.
- Schreiner, O., and Anderson, M. S. (1938). Determining the fertilizer requirements of soils. In “Soils and Men, Yearbook of Agriculture,” pp. 469–486. United States Department of Agriculture, Washington, DC.
- Siciliano, S. D., Germida, J. J., Banks, K., and Greer, C. W. (2003). Changes in microbial community composition and function during a polyaromatic hydrocarbon phytoremediation field trial. *Appl. Environ. Microbiol.* **69**, 483–489.
- Siciliano, S. D., Theoret, C. M., de Freitas, J. R., Hucl, P. J., and Germida, J. J. (1998). Differences in the microbial communities associated with the roots of different cultivars of canola and wheat. *Can. J. Microbiol.* **44**, 844–851.
- Silver, W. L., Herman, D. J., and Firestone, M. K. (2001). Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. *Ecology* **82**, 2410–2416.
- Smith, M. S., and Tiedje, J. M. (1979). The effect of roots on soil denitrification. *Soil Sci. Soc. Am. J.* **43**, 951–955.
- Snapp, S. S., and Silim, S. N. (2002). Farmer preferences and legume intensification for low nutrient environments. *Plant Soil* **245**, 181–192.
- Staver, K. W., and Brinsfield, R. B. (1998). Using cereal grain winter cover crops to reduce groundwater nitrate contamination in the mid-Atlantic coastal plain. *J. Soil Water Conserv.* **53**, 230–240.
- Steinheimer, T.-R., Scoggin, K.-D., and Kramer, L.-A. (1998). Agricultural chemical movement through a field-size watershed in Iowa: Surface hydrology and nitrate losses in discharge. *Environ. Sci. Technol.* **32**(8), 1048–1052.

- Stevenson, C. K., and Baldwin, C. S. (1969). Effect of time and method of nitrogen application and source of nitrogen on the yield and nitrogen content of corn (*Zea mays*). *Agron. J.* **61**, 381–384.
- Tate, R. L., III, Parmelee, R. W., Ehrenfeld, J. G., and O'Reilly, L. (1991). Nitrogen mineralization: Root and microbial interactions in pitch pine microcosms. *Soil Sci. Soc. Am. J.* **55**, 1004–1008.
- Thorup-Kristensen, K. (2001). Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? *Plant and Soil* **230**, 185–195.
- Tilman, D. (1999). Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. *Proc. Natl. Acad. Sci. USA* **96**, 5995–6000.
- Tisdale, S. L., Nelson, W. L., and Beaton, J. D. (1993). "Soil Fertility and Fertilizers," 5th ed. Collier Macmillan Publishers, New York.
- Tonitto, C., David, M. B., and Drinkwater, L. E. (2006). Response of crop yields and soil N to diversified rotations: A meta-analysis. *Agric. Ecosyst. Environ.* **112**, 58–72.
- Tran, T. S., Giroux, M., and Cescas, M. P. (1997). Effect of N rate and application methods on ¹⁵N-labelled fertilizer use by corn. *Can. J. Soil Sci.* **77**, 9–19.
- Tyrrell, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature* **400**, 525–531.
- Van der Molen, D. T., Breeuwsma, A., and Boers, P. C. M. (1998). Agricultural nutrient losses to surface water in the Netherlands: Impact, strategies, and perspectives. *J. Environ. Qual.* **27**, 4–11.
- van Elsas, J. D., and van Overbeek, L. S. (1996). Bacterial responses to soil stimuli. In "Starvation in Bacteria" (S. Kjelleberg, Ed.), pp. 55–79. Plenum Press, New York.
- Vance, C. P., Uhde, S. C., and Allan, D. L. (2003). Phosphorus acquisition and use: Critical adaptations by plants for securing a nonrenewable resource. *New Phytol.* **157**, 423–447.
- Vitousek, P. M., Aber, J. D., Howarth, R. H., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H., and Tilman, D. G. (1997). Human alteration of the global nitrogen cycle: Source and consequences. *Ecol. Appl.* **7**, 737–750.
- Waksman, S. A. (1936). "Humus: Origin, Chemical Composition, and Importance in Nature." The Williams & Wilkins Company, Baltimore, MD.
- Wall, D. H., and Moore, J. C. (1999). Interactions underground: Soil biodiversity, mutualism, and ecosystem processes. *Bioscience* **49**, 109–117.
- Wander, M. M., and Traina, S. J. (1996). Organic matter fractions from organically and conventionally managed soils: II. Characterization of composition. *Soil Sci. Soc. Am. J.* **60**, 1087–1094.
- Wedin, D. A., and Tilman, D. (1990). Species effects on nitrogen cycling: A test with perennial grasses. *Oecologia* **84**, 433–441.
- Welch, L. F., Mulvaney, D. L., Oldham, M. G., Boone, L. V., and Pendleton, J. W. (1971). Corn yields with fall spring and sidedress nitrogen. *Agron. J.* **63**, 119–123.
- Whitelaw, M. A., Harden, T. J., and Helyar, K. R. (1999). Phosphate solubilisation in solution culture by the soil fungus *Penicillium radicum*. *Soil Biol. Biochem.* **31**, 655–665.
- Whitman, W. B., Coleman, D. C., and Wiebe, W. J. (1998). Prokaryotes: The unseen majority. *Proc. Natl. Acad. Sci. USA* **95**, 6578–6583.
- Wolt, J. D. (2004). A meta-evaluation of nitrapyrin agronomic and environmental effectiveness with emphasis on corn production in the Midwestern USA. *Nutr. Cycl. Agroecosyst.* **69**, 23–41.
- Zak, D. R., Tilman, D., Parmenter, R. R., Rice, C. W., Fisher, F. M., Vose, J., Milchunas, D., and Martin, C. W. (1994). Plant production and soil microorganisms in late-successional ecosystems: A continental-scale study. *Ecology* **75**, 2333–2347.