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6 Ecological Research in Agricultural Ecosystems: Contributions to Ecosystem Science and to the Management of Agronomic Resources

G. Philip Robertson and Eldor A. Paul

Summary

Ecological research in agronomic systems has a long and rich history that has contributed much to our basic understanding of all terrestrial ecosystems. Of particular note are contributions to (1) soil organic matter concepts, (2) knowledge of specific nitrogen-cycling processes such as mineralization-immobilization, denitrification, nitrogen fixation, and biphasic nitrate leaching, and (3) understanding of soil resource heterogeneity. Recent concerns about the long-term sustainability of high productivity agriculture and the high environmental cost of many such systems provides managers opportunities for better application of ecosystem concepts. These opportunities include managing the temporal linkage between nutrient release from soil organic matter and the demand for nutrients by plant uptake, managing agronomic inputs such as fertilizers and pesticides with spatial precision, and using whole watershed input-output balances to assess and manage unwanted nutrient exports. The application of modern ecosystem concepts to emerging agronomic needs is an important frontier in ecosystem science with the potential to benefit both ecosystem theory and practical issues related to farm policy and management.

Introduction

Ecological research in agricultural systems dates from the 19th century—from our earliest efforts to understand the field biology of row crops such as barley and wheat. From the outset, this research has furthered our basic understanding of ecosystems in general. Early recognition by Leibig (1847) and others that plant resource needs can easily exceed available soil resources provided early insight into plant nutrient acquisition and the maintenance of soil nutrient pools, and furnished a basis for our current

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understanding of nutrient interactions in ecosystems (e.g. Bolin and Cook 1983). These ideas continue to influence our approaches to ecosystem nutrient retention today. Early research by soil microbiologists working principally in agronomic soils laid the foundation for our understanding of the microbial basis for many ecosystem-level nutrient fluxes, especially those related to nitrogen, carbon, and sulfur. Dinitrogen fixation, mineralization-immobilization, nitrification, and denitrification are all critical nitrogen-cycling processes whose microbial ecology was first described or principally worked out in agronomic systems.

Prior to World War II, the agronomic and the ecological sciences were inextricably linked. Success in one often led to success in the other across a range of ecological hierarchies, from the physiological response of individual organisms to community and ecosystem-level dynamics. After 1945, however, with the advent of large-scale, mechanized, chemically based farming practices, ecology took a role subordinate to engineering in the design and implementation of food production systems. The availability of inexpensive fertilizer freed the agronomist from the need to understand the ecological basis for most microbial processes, and instead forced attention toward the fate and efficiency of alternative fertilizers. The availability of effective herbicides reduced the need to understand plant competition for limiting resources and the colonization and persistence of soil seed banks. The availability of pesticides obviated the need to understand the field and landscape-level population dynamics of most pest predators, instead directing attention toward the specificity of different chemicals and their application windows. Additionally, plant breeding changed harvest indices, root/shoot ratios, leaf areas and duration, and the secondary chemistry of leaf tissue, which concomitantly created an even greater need for more intensive crop management.

With the recent emergence of sustainable agriculture and environmental awareness as social and political issues in many countries, a balance is being restored, largely in response to social concerns that modern production-level agriculture carries an unnecessarily high environmental cost. Proponents of a more ecologically based agriculture cite problems associated with excess herbicide, pesticide, and fertilizer use: both the direct economic expense that makes many farms only marginally viable, as well as the indirect, externalized costs now paid by society as a whole. The long-term costs of erosion, excess water use, and salinization further subtract from the ledger.

For ecologists, reintegrating ecological concepts into high productivity farming systems presents a set of new challenges that can be considered an ecosystem frontier (sensu this volume) in its own right. As such, many of the contributions of agricultural ecosystem research to ecology are surely in the future. Nevertheless, even over the past three decades, when ecology in developed regions was as separate as possible from agronomic research, important contributions to ecosystem science have been made. Further-

more, ecosystem science has begun to significantly influence agronomic management, particularly in the areas of whole-system (both field-scale and watershed-scale) nutrient budgets and soil carbon management.

In this chapter we have attempted to outline three major contributions of research in agroecosystems to the general body of ecosystem science, as well as emerging ways in which ecosystem science is affecting the management of high productivity agricultural ecosystems.

Contributions of Agroecosystem Research to Ecosystem Science

Consider the effects of converting a prairie or native deciduous forest to row-crop agriculture, in which a mixed-species, slow-growing perennial plant community on a stable soil profile is replaced with a single fast-growing annual species on a soil profile that is inverted annually. This massive disturbance resets the successional clock on a yearly basis, introduces a major exotic plant (i.e. the crop) to the system, physically disrupts the soil food web and its structural support, and alters plant soil temporal relationships. This leads to a dramatic reorientation of many ecosystem processes and attributes. Among the most drastic are gradual but substantial changes in soil organic matter—its quantity, quality, and turnover rate—with concomitant changes in soil food web dynamics; rapid and major changes in soil structure and soil water and solute movement; major changes in certain nitrogen-cycling processes; and potentially major changes in the spatial distribution or heterogeneity of soil resources within the ecosystem. Consequently, it makes sense that advances in our general understanding of these ecosystem-level processes have been particularly accelerated in agronomic systems, and, therefore, that ecosystem research in row-crop systems has made particular contributions to ecosystem science in these areas.

Moreover, because annual crop ecosystems are highly pulsed, they are systems in which net fluxes of such nutrients as nitrogen are more readily interpreted, especially with the aid of carbon- and nitrogen-isotope technologies, largely developed in agronomic systems. Contrast this with the difficulty of understanding fluxes in perennial native ecosystems, which are dependent on the much less easily measured gross fluxes that occur without major changes in available nutrient pool sizes.

From the outset, we believe that the question "How has research in agricultural ecosystems benefited ecosystem science?" is a red herring. As many have pointed out in recent years, we should be moving beyond the applied vs. basic, disturbed vs. natural, managed vs. unmanaged paradigm of ecological research toward a perspective that is more gradient-oriented (Elliott and Cole 1989; Paul and Robertson 1989). All ecosystems today are affected by human intervention, whether intentional or not, and agricultural

systems are simply closer to the intensely and intentionally disturbed end of the spectrum than are such remote ecosystems as arctic tundra, which, up to this time, may be subject mainly to the widespread but less intense, unintentional human disturbance of the chemical and physical climate.

In its purest sense, then, agricultural ecology is not targeted toward understanding ecological processes in row-crop ecosystems, but rather toward understanding ecological processes in extractive ecosystems that are actively maintained at an early stage of secondary succession. In this light, agricultural ecology becomes no different from forest ecology, restoration ecology, or the ecology of unmanaged ecosystems—the key is an understanding of the ecology of successional systems, for which, of course, there is a rich literature. The relevant question then becomes "How has agricultural ecosystem research contributed to our understanding of ecological processes in early successional, chronically disturbed ecosystems in general?" From a management standpoint, the converse question becomes, "What ecological knowledge about early successional ecosystems can we use to actively manage these systems to minimize the environmental and economic costs of a highly productive, extractive ecosystem?"

In the following three sections, we discuss in turn the particular contributions of agronomically related research to our present understanding of soil organic matter, specific nitrogen-cycling processes, and soil resource heterogeneity in early successional ecosystems in particular.

Soil Organic Matter

Models of soil organic matter dynamics now being applied in a wide variety of ecosystems (e.g. vanVeen and Paul 1981; Jenkinson et al. 1987; Parton et al. 1987) derive largely from an understanding of soil carbon dynamics developed in agricultural soils or in comparisons of grassland to agricultural soils. Results from long-term studies of carbon loss following the conversion of temperate-region ecosystems to agriculture typically show a rapid, several-decade decline in soil organic matter levels following the onset of cultivation (see Figure 6.1; Paul et al. 1997). Typically after two to three decades in warm climates, organic matter levels reach a new equilibrium level, often 50 to 80% of original levels in the whole profile and less in the topmost horizon. But both the rate at which carbon is lost from a soil and the level to which soil carbon pools decline depend on a large number of interacting factors: (1) climate; (2) soil texture; (3) the stability of soil aggregates; (4) the quality and quantity of new plant litter inputs; (5) the nature and timing of further soil disturbance; and (6) various other site-specific factors that affect feedbacks between soil processes and plant growth. These interactions make predictions of the rate of carbon loss and the potential rate of carbon recovery difficult in the absence of quantitative models that include these feedbacks.

Efforts to predict the rate and equilibrium level of soil carbon storage following disturbance have been successful only since modelers have also

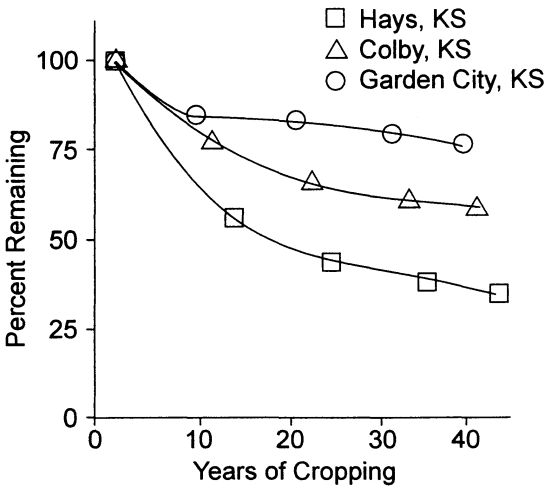

FIGURE 6.1. Soil organic matter loss following cultivation at three sites in the midwestern United States. Redrawn from Haas et al. 1957.

incorporated into their models the concept of multiple soil carbon pools, that is, pools of organic carbon that turn over at different rates. The most widely available models (e.g. Century, Rothamsted, Socrates) recognize at least three soil organic matter pools (see Figure 6.2); for example, Century (Parton et al. 1987) defines an active fraction that consists of microbial biomass and metabolites with a turnover rate on the order of months to years, a slow fraction of stabilized decomposition products with a turnover rate on the order of decades, and a passive fraction of recalcitrant, highly stabilized organic matter that turns over on the order of centuries to millennia.

Only recently have these fractions become analytically identifiable as well. A combination of acid hydrolysis and ^{14}C dating (Paul and vanVeen 1978; Paul et al. 1997) together with CO_2 release from long-term soil incubations (Figure 6.3; sensu Stanford and Smith 1972) now provide a reasonable means for quantifying passive, slow, and active soil carbon pools. The identification of these pools occurred principally through work in cultivated ecosystems or in native vs. cultivated comparisons (e.g. Shields and Paul 1973; Jenkinson 1977; Juma and Paul 1981). Similarly, the subsequent models (Hunt 1977; Jenkinson 1977; vanVeen and Frissel 1979; McGill et al. 1981; Molina et al. 1983; vanVeen et al. 1984; Parton et al. 1987; Grace et al. 1996) and thus far their most rigorous tests (e.g. Paustian et al. 1992; Figure 6.4) have been respectively developed and conducted primarily in agronomic systems. The application of these models in other systems and their utility for assessing atmosphere-soil carbon dioxide exchange is becoming especially important with respect to evaluating histori-

cal and future global change scenarios (e.g. Schlesinger 1984; Jenkinson et al. 1991; IPCC 1996).

Related to the conceptual development of soil carbon models is the associated development of soil food-web models. Although not developed initially in agronomic systems, experimentation in arable soils has provided substantial insight for identifying important members of soil food webs and their functional significance (Elliott et al. 1984; Hunt et al. 1987; Coleman and Crossley 1996). Of particular note has been the emerging recognition of the importance of protozoan and other faunal grazing for making pulses of nitrogen available to the plant community (Edwards 1983; Clarholm 1985),

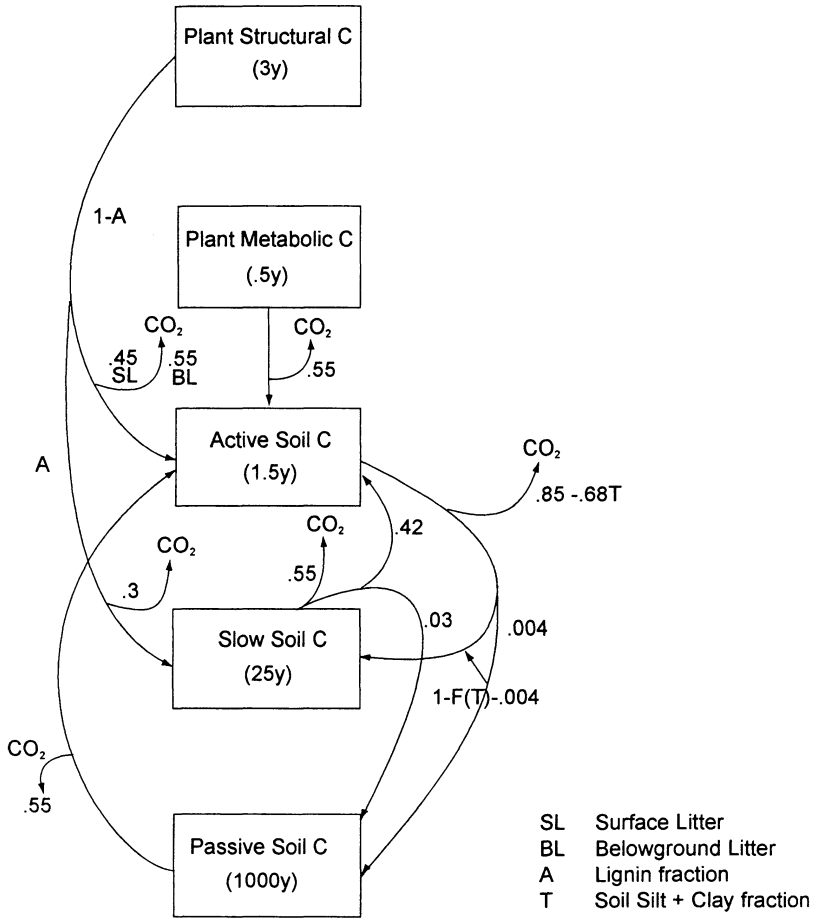

FIGURE 6.2. Structural components of the Century soil organic matter model. Values next to arrows are transfer coefficients for the carbon pools noted; values in parentheses are the approximate turnover times for the noted pool. From Paustian et al. 1992.

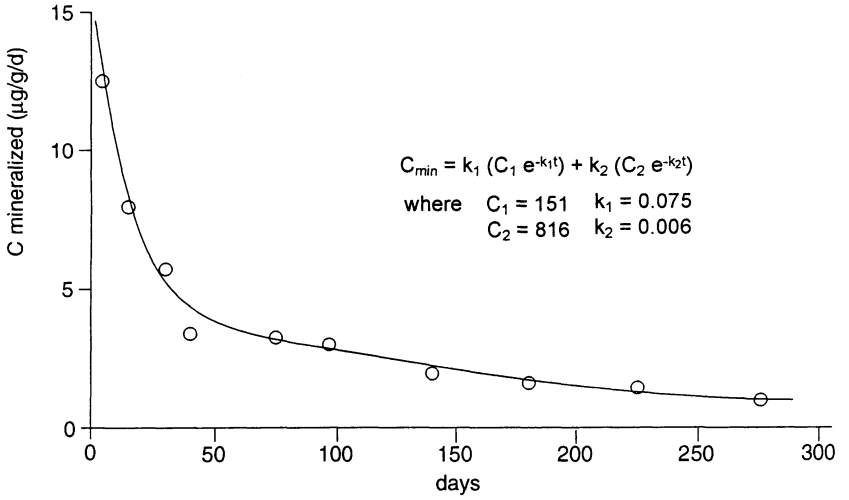

FIGURE 6.3. Long-term carbon mineralization in a cultivated soil from the KBS LTER site. The solid line is fit with the two-pool nonlinear model as noted in figure ($r^2 = 0.99$); units for the active fraction C1 and the slow fraction C2 are $g C g^{-1}$ soil; the passive fraction C3 (total soil C less C1 and C2) = $7{,}785 g C g^{-1}$ soil.

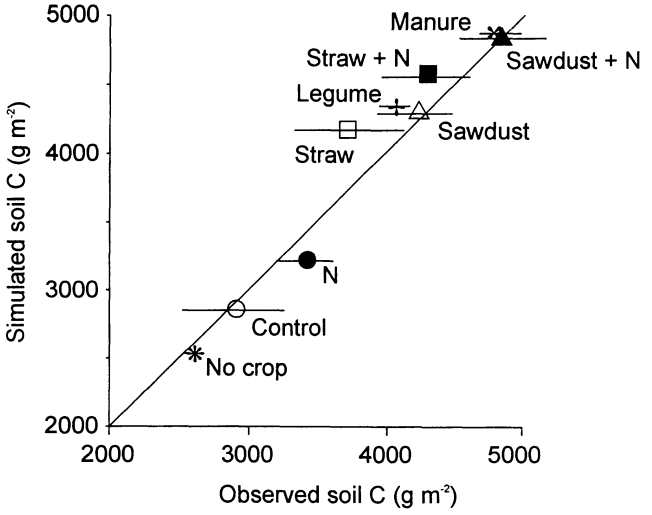

FIGURE 6.4. Actual vs. simulated soil carbon pools in a Swedish soil following thirty years of oat and barley cropping with the amendments noted. From Paustian et al. 1992.

and the potential importance of fungal- vs. bacterial-dominated food webs (Hendrix et al. 1986) with consequent potential effects on decomposition rates and nutrient availability (Beare et al. 1992). These dynamics are crucial drivers in trophic-based models of soil nitrogen cycling (Hunt et al. 1987; Moore and de Ruiter 1991). Soil biotic interactions also appear to be crucial regulators of soil aggregate structure as a consequence of their binding effects on soil mineral particles (Oades 1993); this phenomena was initially clarified in agricultural ecosystems.

Nitrogen Cycling: Process-Specific Advances

The history of terrestrial nitrogen-cycling research is no more specific to agricultural systems than it is to forest, grassland, wetland, or any other habitat. In fact, it can be argued that from a watershed standpoint, our understanding of whole-system nitrogen dynamics in agronomic systems has lacked a parallel understanding of nitrogen cycling in forest catchments, despite the early use of stable isotopes in agronomic systems (e.g. Allison 1955). For at least three—and possibly four—crucial nitrogen-cycling processes, however, the knowledge worked out in agricultural ecosystems represents a second major contribution of agroecological research to ecosystem science. These processes include denitrification, dinitrogen fixation, and nitrate leaching via preferential flow, in addition to nitrogen-mineralization-immobilization. Denitrification, the biological reduction of soil nitrate to the dinitrogen gases nitrous oxide (N_2O) and nitrogen (N_2), is carried out by microorganisms that have been isolated from a wide variety of environmental habitats, including every terrestrial ecosystem examined thus far. Because most denitrifiers are facultative anaerobes that use nitrate as a terminal electron acceptor only when oxygen is limiting, however, the presence of denitrifiers—even if they can be shown to be metabolically active—does not necessarily imply active denitrification. Particularly in upland soils, the persistence of denitrifiers might be attributed to a short-lived competitive advantage present only during transient rainfall events when the soil is saturated and nitrate is freely available.

The new availability of ^{15}N in the 1950s and its application in agronomic studies provided evidence that denitrification in upland soils *might* be biogeochemically important. Only a portion of the ^{15}N applied as fertilizer in various cropping systems could be recovered in plant, soil, and leachate pools several months later; the remainder, sometimes totaling 50% of the ^{15}N applied, was ascribed to some combination of experimental error plus denitrification (Hauck 1981; Firestone 1982). Careful mass-balance studies without ^{15}N showed potential losses of a similar magnitude (e.g. Rolston et al. 1979) but with equal uncertainty. Not until a selective metabolic inhibitor of nitrous oxide reductase was discovered in the mid-1970s (Yoshinari et al. 1977) and tested largely in agronomic soils (Duxbury 1986) did it become possible to evaluate denitrification fluxes directly. These evalua-

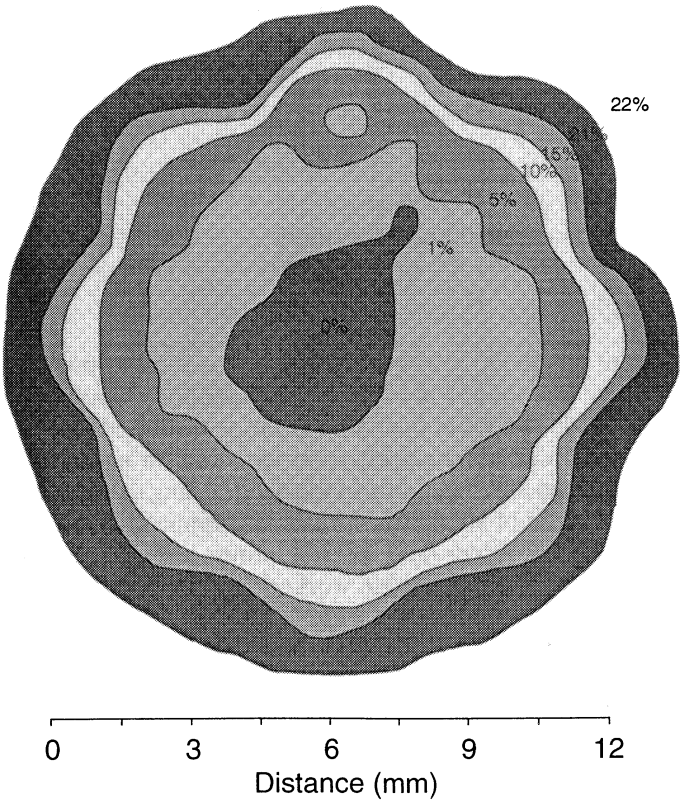

FIGURE 6.5. Oxygen profile in a 1.2 cm diameter aggregate from a Mollisol soil from Iowa; note the anaerobic center. Redrawn from Sexstone et al. 1985.

tions showed that denitrification can indeed account for 20 to 50% of the nitrogen lost from many cropping systems (Firestone 1982; Tiedje 1988).

Field-level denitrification research in row-crop ecosystems paved the way for similar research in other upland communities. Of particular importance has been research providing a conceptual basis for denitrifier habitat. As noted before, early recognition that denitrification is an anaerobic nitrate-requiring process kept many microbiologists from considering well-drained ecosystems as serious candidates for denitrification until the development of oxygen (O_2) models (e.g. Arah and Smith 1989) that showed the theoretical potential for persistent anaerobiosis in such soil microsites as aggregate centers and micropores. Confirmation of the anaerobic potential of soil aggregates came with the development of O_2 microelectrodes (Revsbech et al. 1981), applied to soil microsites in 1985 (Sexstone et al. 1985; Figure 6.5).

Why are aggregates anoxic? In part, anoxia is the result of limitations on gas diffusion across the water film that surrounds most aggregates; O_2 diffuses through water more slowly (more than an order of magnitude slower) than through air. Diffusion itself, however, is only a problem when it does not occur as quickly as O_2 consumption within the aggregate—which explains why most denitrification in soil may be associated with such small organic matter particles as relatively fresh plant litter (Parkin 1987) and invertebrate feces (Elliott et al. 1990).

With the conceptual groundwork for denitrification in well-aerated soils laid out by workers in agronomic systems, it has been a relatively short jump to apply these concepts to entire landscapes comprised of many different types of ecosystems. Tiedje (1988) presented a landscape-level conceptual framework for denitrification that identifies controls on denitrification at several different scales (Figure 6.6). In this context, it has not been surprising to find nitrogen gas fluxes from well-drained forested sites that appear to equal or exceed nitrogen lost from other pathways at these sites (e.g. Virginia et al. 1982; Mellilo et al. 1983; Robertson and Tiedje 1985, 1988; Robertson et al. 1987; Groffman and Tiedje 1989).

At a regional scale, denitrification in upland soils largely exceeds denitrification in other habitats and can play a large role in the overall nitrogen economy of the region. In their subcontinent nitrogen budget for

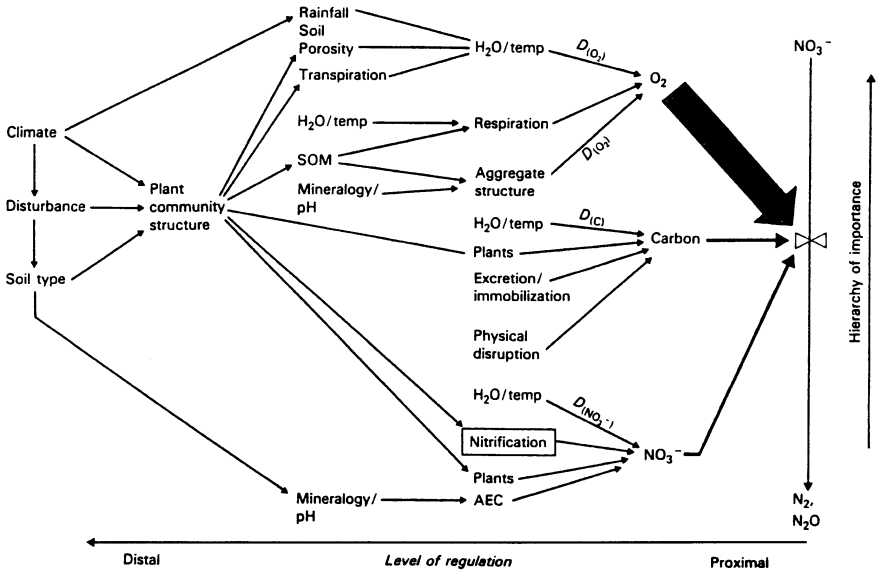

FIGURE 6.6. Proximal vs. distal controls on denitrification. From Robertson (1988) after Groffman et al. (1988).

West Africa, for example, Robertson and Rosswall (1986) estimated denitrification losses of nitrogen at $1.1\,Tg\,N\,y^{-1}$, roughly equivalent to hydrologic exports of nitrogen from the region. Jordan and Weller (1996) estimated that only 5% ($0.7\,Tg\,N\,y^{-1}$) of total anthropic nitrogen inputs to the United States ($15.3\,Tg\,N\,y^{-1}$) are lost as river discharge—with the remaining 14 Tg N plus nonanthropogenic sources either stored in aggrading ecosystems, sediments, and groundwater, or (more probably) lost through denitrification and perhaps fire.

For at least three other important biogeochemical processes our ecological understanding has also been developed largely in agricultural ecosystems: biological nitrogen fixation, nitrogen mineralization-immobilization, and biphasic solute loss. The history of dinitrogen-fixation research dates from the 19th century (Havelka et al. 1982), with much of the terrestrial research focused on the ecology and biogeochemical impact of the legume-Rhizobia symbiosis, discovered in 1886 (Hellriegel 1886, in Havelka et al. 1982)—a dominant feature of many agronomic management practices especially prior to the widespread availability of nitrogen fertilizers (e.g. Pieters 1927). Similarly, much of what we know about mineralization-immobilization transformations in soils originated from work in agronomic systems, especially dating from isotope work beginning in the 1950s (Jansson and Persson 1982). For example, the capacity for litter of different carbon/nitrogen ratios to differentially immobilize and release nitrogen and thereby affect soil nitrogen availability now dominates our understanding of decomposition in terrestrial ecosystems (e.g. Melillo et al. 1982), and has played an important role in ecosystem concepts ranging from system-level stoichiometry (Reiners 1986) to nutrient-use efficiency (Vitousek 1982).

Moreover, biphasic solute flow was first identified and explored principally in agronomic soils, although in contrast to N_2 fixation and mineralization-immobilization, its biogeochemical importance has only recently been recognized. Biphasic water flow refers to the tendency of water flowing through soil to move preferentially through macropores and soil channels rather than through the soil matrix (Thomas and Phillips 1979; Bouma 1981; Beven and Germann 1982; White 1985; Sollins 1989). Water in aggregates and in fine pores remains relatively static, and solute exchange between immobile and mobile phases can be very slow.

Much of the motivation for research on biphasic flow has stemmed from interest in zero-till conservation tillage techniques that aim to conserve a soil structure more conducive to carbon and water retention. Reducing erosion is typically promoted as the principal agronomic benefit of conservation tillage, now employed on a majority of cropland in the United States, but effects on solute and, consequently, on nutrient retention (e.g. Wild 1972) and on loss of nitrogen to groundwater is also important. In nonagronomic systems the importance of biphasic flow and its sensitivity to disturbance is only now being enumerated (Sollins 1989); it is becoming

apparent, however, that any disturbance that has the potential to affect aggregate structure, macroporosity, or the formation of soil channels also has the potential to affect solution nutrient losses via effects on soil water flow paths. Processes that affect aggregate structure and soil porosity include invertebrate (especially earthworm) activity, root turnover, fungal mycelia growth, and such larger-scale processes as root-throws, burrowing mammals, and harvest or site preparation activities.

Soil Resource Heterogeneity

A third area in which ecosystem-level research in agronomic systems has led research in other systems is that of soil resource heterogeneity. Ecologists have been in the forefront of efforts to understand plant resource variability since ecology first became a discipline. Recognizing plant distribution patterns and identifying their cause and consequence is a hallmark of plant community ecology; decades of work in successional systems has placed significant emphasis on the need to understand differences in soil resources among different communities and especially within seres. Historically, however, relatively little effort has been directed toward understanding within-community patterns of resource availability. Traditionally, such patterns have been ignored in favor of understanding mechanisms underlying between-community or between-ecosystem differences; within-system variability has been seen largely as a statistical hurdle to be overcome by adjusting a sample size upward just enough to statistically differentiate any between-system differences that may exist. Recently, however, led by advances developed in agronomic systems, new insights about in situ spatial variability are emerging for a broad variety of both terrestrial and marine ecosystems.

Although elucidating the variability of belowground resources has been the explicit subject of a number of studies dating from the 1950s (e.g. Downes and Beckwith 1951; Snaydon 1962; Pigott and Taylor 1964; Zedler and Zedler 1969; Allen and MacMahon 1985), only recently have the geostatistical tools that allow this variability to be closely examined become available (Robertson 1987; Rossi et al. 1992; Robertson and Gross 1994). Workers in agronomic ecosystems—as early adopters of these tools—led the way among life scientists. As a field, geostatistics was developed by mathematical geologists in the 1970s to describe mineral distributions for the mining industry (e.g. David 1977; Journel and Huijbregts 1978; Krige 1981). During the 1980s, geostatistical approaches were adopted by soil scientists seeking to understand soil morphological processes within agricultural landscapes, and in particular, patterns of such soil physical and chemical properties as stone content, infiltration capacity, and conductivity (e.g. Webster and Cuanalo 1975; Burgess and Webster 1980; Vieira et al. 1983; Trangmar et al. 1985; Webster 1985; Webster and Oliver 1990). Later in the decade, soil biologists began describing patterns of biological activity

across individual cropping systems (e.g. Folorunso and Rolston 1985; Parkin et al. 1987; Trangmar et al. 1987; Aiken et al. 1991; Ambus and Christensen 1995), and by the early 1990s, terrestrial ecologists had incorporated the technique and had begun applying geostatistics to questions of resource heterogeneity in noncropped communities (e.g. Robertson et al. 1988, 1993; Jackson and Caldwell 1993; Gross et al. 1995; Fetcher et al. 1996; Schlesinger et al. 1996).

Geostatistics offer substantial power for identifying the scale of environmental variation in landscapes and for describing patterns of variability at different scales. The degree of structured variability that has been uncovered for important ecological processes has been surprising to many, and in a variety of ways agronomic systems are well suited for addressing questions about the ecological significance of the variability identified. Robertson et al. (1997), for example, planted a single genotype of soybeans across a 48-hectare (ha) row-crop ecosystem that—despite decades of tillage and cropping—varied internally by up to an order of magnitude for many important system-level attributes such as soil organic matter and nitrogen availability (e.g. Figure 6.7). Although the variability for most attributes examined was strongly structured, in some cases at multiple scales (e.g. Figure 6.8), there was very little correspondence between specific groups of attributes and soybean productivity; at most less than 50% of

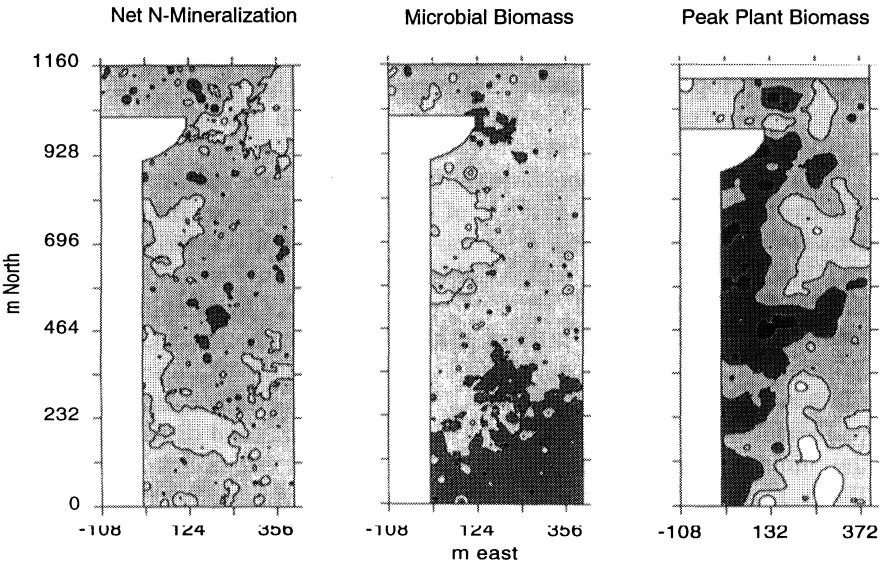

FIGURE 6.7. Spatial variability across a 48-hectare agricultural site in southwestern Michigan; patterns correspond to even increments in levels for a given property: a) net N mineralization (0.30–0.70 mg N g^{-1} d^{-1}); b) microbial biomass (39–95 mg C g^{-1}); and c) peak plant (soybean) biomass (170–347 g m^2) (From Robertson et al. 1997).

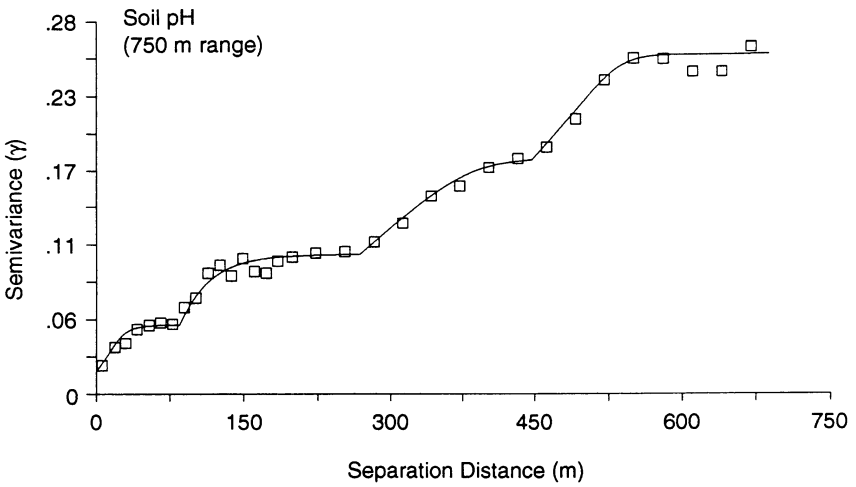

FIGURE 6.8. Nested spatial autocorrelation (semivariance) of soil pH within a 48-hectare row-crop ecosystem in southwestern Michigan. From Robertson et al. 1997.

the variation in plant productivity could be explained by variation in soil chemical and physical properties. Such findings challenge our understanding of controls on productivity at scales between the individual plant and the landscape, and underscore the value of agronomic systems for addressing questions of broad relevance to many ecosystems.

Applications of Ecosystem Science to Management Issues: Success in the Making

Inasmuch as several important advances in ecosystem science have been made in whole or in part in agronomic settings, it is not difficult to identify the application of these particular concepts as important contributions of ecosystem science to agronomic management. On the other hand, credit may be premature: in some cases, the effective application of ecosystem-level concepts predates their scientific understanding by centuries. Take, for example, organic matter management. The inclusion of legumes in long-term rotation strategies and the application of animal wastes to farm fields was part of the agronomic toolbox long before the development of active fraction concepts, in fact, long before nitrogen was even recognized as an essential nutrient (e.g. Oakley 1925; Francis and Clegg 1990). The effect of rotations on soil color, that is, on soil organic matter levels, was recognized and used to manage fallows even during the Roman Empire. It is therefore unfair to say that our new understanding of organic matter dynamics has contributed much to the design of modern cropping systems. In fact, the

application of this knowledge is only now occurring, as it becomes clear to agronomists that a means is needed to more efficiently manage the within-year nutrient-release curve in annual cropping systems, as well as a means to rebuild soil organic matter where it has been lost without resorting to long fallow periods.

High productivity cropping systems in which managed productivity may be twice the productivity of the native ecosystem that was displaced (Robertson 1997) can place tremendous demands on the nutrient-supplying capacity of a soil. During a maize crop's rapid vegetative growth phase, a period of about three to four weeks when plants are past the seedling stage and growing exponentially, a single crop can withdraw on the order of $4\,kg\,N\,ha^{-1}\,d^{-1}$. This contrasts with mineralization rates under both native vegetation and disturbed systems that typically sum to some fraction of this (Keeney 1980; Robertson 1982; Paul 1989). This underscores the importance of providing either fertilizer or a source of readily mineralized organic matter to the cropping system at this growth stage. In the absence of abundant fertilizer, biologically derived nitrogen must be provided by aligning soil nitrogen-mineralization rates with plant nitrogen demand, and this is a major goal of efforts to reduce the present reliance on synthetic nitrogen in high productivity row-crop ecosystems (Figure 6.9; Hendrix et al. 1992; Robertson 1997). It is probable that emerging knowledge about the decomposition dynamics of crop residues (in particular, knowledge about controls on active fraction formation and turnover) will play a large role in allowing us to approach this nitrogen-management goal, and this topic is a major issue in soil fertility research today.

In contrast to efforts aimed at providing sufficient nitrogen for rapidly growing crop plants is the converse problem of restricting excess agricultural nutrients in surface and groundwater supplies and in the atmosphere. One of the greatest challenges facing the confined-animal industry today is the emerging environmental problem of excess nitrogen and phosphorus loading that stems from land application of animal waste. Environmental concerns in Europe and in some U.S. states have already led to specific restrictions on the amount and timing of manure applications to cropping systems, and these restrictions are apt to become even more common as poultry, swine, and dairy operations continue to become increasingly concentrated in large confined-animal operations. In Europe, several countries have adopted watershed input-output balances as the basis for assessment and regulation of agricultural production systems; further understanding of the basis for soil organic matter acretion and mineralization-immobilization relationships will aid efforts to optimize nutrient retention in these systems. It will be important to maintain a concomitant watershed-level focus in this effort, because many processes that can attenuate nutrient loss operate at different scales and along different portions of hydrologic flow paths (e.g. Lowrance et al. chapter 5; Peterjohn and Correll 1984; Robertson and Rosswall 1986; Barry et al. 1993).

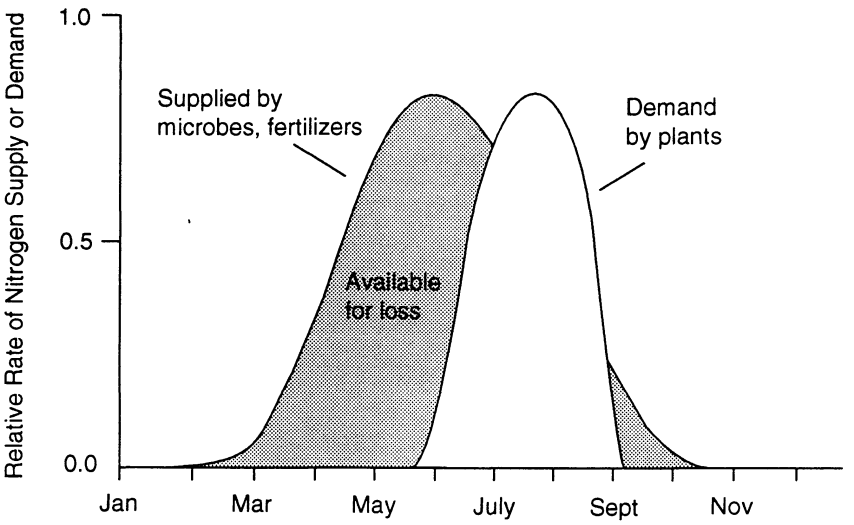

FIGURE 6.9. Temporal asynchrony between nutrient supply rate (from mineralization) and plant nutrient demand in a hypothetical row-crop ecosystem. From Robertson 1997.

Emerging knowledge about the relationship between plant productivity and the spatial distribution of soil resources will further aid efforts to increase ecosystem-level nutrient-use efficiency. New technologies that allow fertilizers to be applied differentially across individual fields—so-called site-specific farming practices (Robert et al. 1993)—have been touted for their potential ability to match resource inputs with resource needs. Without further information about the scale of soil biological activity in arable soils, however, and without matching application technology to this scale, it is improbable that the potential of the technology will ever extend beyond maps of such larger-scale soil properties as drainage class and topographic relief (Groffman 1997). Thus, knowledge of "biological precision" will be an important consideration in efforts to develop effective site-specific farming practices, and may well decide its theoretical effectiveness and, therefore, its economic viability.

The application of other ecosystem concepts should also provide the substantive insight needed to effectively manage the agricultural land base. For many concepts, the derivation of knowledge is coming full circle. Regional multi-watershed nutrient budgets were first developed for agricultural purposes (e.g. Lipman and Corybeare 1936; Ayers and Branson 1973; Miller and Smith 1976; Keeney 1979), and the whole-crop lysimeters first deployed in the Coshocton, Ohio watershed in the 1930s were arguably among the very first watershed-level biogeochemical experiments. Since then, however, most watershed-level experimentation has focused on forested regions, led by studies at the Coweeta Experimental Forest in

North Carolina (Swank and Crossley 1988), the Hubbard Brook Experimental Forest in New Hampshire (Likens and Bormann 1996), and the H.J. Andrews Experimental Forest in Oregon (Sollins et al. 1980). Only with the renewed interest in coastal eutrophication and groundwater quality (e.g. Turner and Rabalais 1991; Cole et al. 1993; Nixon 1995; Howarth et al. 1996) have landscape-level nutrient-cycling issues become refocused again at a farm-management level (e.g. Barry et al. 1993). Whole-ecosystem experimentation at the level of individual fields and even within fields, with subsequent extrapolation to farms and then to agricultural watersheds, holds much promise for helping to guide the development of a more productive, environmentally safe agriculture, in the same way that such research in forested watersheds (e.g. Likens and Bormann 1996) is helping to guide the effective management of forest resources.

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References

Aiken, R.M., M.D. Jawson, K. Grahammer, and A.D. Polymenopoulos. 1991. Positional, spatially correlated, and random components of variability in carbon dioxide efflux. *Journal of Environmental Quality* 20:301–308.

Allen, M.F., and J.A. MacMahon. 1985. Impact of disturbance on cold desert fungi: comparative microscale dispersion patterns. *Pedebiologia* 28:215–224.

Allison, F.E. 1955. The enigma of soil nitrogen balance sheets. *Advances in Agronomy* 7:213–250.

Ambus, P., and S. Christensen. 1995. Spatial and seasonal nitrous oxide and methane fluxes in Danish forest-, grassland-, and agroecosystems. *Journal of Environmental Quality* 24:993–1001.

Arah, J.R.M., and K.A. Smith. 1989. Modeling denitrification in aggregated soils: relative importance of moisture tension, soil structure, and oxidizable organic matter. in J.A. Hansen, and K. Henriksen, eds. *Nitrogen in Organic Wastes Applied to Soils*. Academic Press, London, U.K.

Ayers, R.S., and R.L. Branson. 1973. *Nitrates in the Upper Santa Ana river basin in relation to groundwater pollution.* California Agricultural Experiment Station Bulletin Number 861. University of California, Riverside.

Barry, D.A., J.D. Goorahoo, and M.J. Goss. 1993. Estimation of nitrate concentrations in groundwater using a whole farm nitrogen budget. *Journal of Environmental Quality* 22:767–775.

Beare, M.H., R.W. Parmelee, P.F. Hendrix, D.C. Coleman, and D.A.J. Crossley. 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecological Monographs* 62:569–591.

Beven, K., and P.F. Germann. 1982. Macropores and water flow in soil. *Water Resources Research* 18:1311–1325.

Bolin, B., and R.B. Cook, eds. 1983. *The major biogeochemical cycles and their interactions.* John Wiley & Sons, Chichester, England.

Bouma, J. 1981. Soil morphology and preferential flow along macropores. *Agricultural Water Management* 3:235–250.

Burgess, T.M., and R. Webster. 1980. Optimal interpolation and isarithmic mapping of soil properties. II. Block kriging. *Journal of Soil Science* 31:315–331.

Clarholm, M. 1985. Possible roles for roots, bacteria, protozoa and fungi in supplying plants. Pages 355–365 in A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher, eds. *Ecological Interations in soil: plants, microbes, and animals.* Blackwell, Oxford, England.

Cole, J.J., B.L. Peoerls, N.F. Caraco, and M.L. Pace. 1993. Nitrogen loading of rivers as a human-driven process. Pages 141–157 in M.J. McDonnell and S.T.A. Pickett, eds. *Humans as components of ecosystems: the ecology of subtle human effects and populated areas.* Springer-Verlag, New York.

Coleman, D.C., and D.A.J. Crossley. 1996. *Fundamentals of Soil Ecology.* Academic Press, San Diego, CA.

David, M. 1977. *Geostatistical ore reserve estimation.* Elsevier Scientific Publishing Co., Amsterdam.

Downes, R.G., and R.S. Beckwith. 1951. Studies in the variation of soil reaction. I. Field variations at Barooga, NSW. *Australian Journal of Agricultural Research* 2:60–72.

Duxbury, J.M. 1986. Advantages of the acetylene method of measuring denitrification. Pages 73–92 in R.D. Hauck and R.W. Weaver, eds. *Field measurement of dinitrogen fixation and denitrification.* Soil Science Society of America, Madison, WI.

Edwards, C.A. 1983. Earthwork ecology in cultivated soils. Pages 123–137 in J.E. Satchell, ed. *Earthwork ecology.* Chapman & Hall, New York.

Elliott, E.T., and C.V. Cole. 1989. A perspective on agroecosystem science. *Ecology* 70:1597–1602.

Elliott, E.T., D.C. Coleman, R.E. Ingham, and J.A. Trofymow. 1984. Carbon and energy flow through microflora and microfauna in the soil subsystems of terrestrial ecosystems. Pages 425–434 in M.J. Klug and C.A. Reddy, eds. *Current perspectives in microbial ecology.* American Society Microbiology, Washington, DC.

Elliott, P.W., D. Knight, and J.M. Anderson. 1990. Denitrification in earthworm casts and soil from pastures under different fertilizer and drainage regimes. *Soil Biology and Biochemistry* 22:601–606.

Fetcher, N., B.L. Haines, R.A. Cordero, D.J. Lodge, L.R. Walker, D.S. Fernandez, and W.T. Lawrence. 1996. Response of tropical plants to nutrients and light on a lanslide in Puerto Rico. *Journal of Ecology* 84:331–341.

Firestone, M.K. 1982. Biological denitrification. Pages 289–326 in F.J. Stevenson, ed. *Nitrogen in agricultural soils.* American Society of Agronomy, Madison, WI.

Folorunso, O.A., and D.E. Rolston. 1985. Spatial variability of field-measured denitrification gas fluxes. *Soil Science Society of America Journal* 48:1214–1219.

Francis, C.A., and M.D. Clegg. 1990. Crop rotations in sustainable agricultural systems. Pages 107–122 in C.A. Edwards, R. Lal, P. Madden, R.H. Miller, and G. House, eds. *Sustainable agricultural systems.* Soil and Water Conservation Society, Ankeny, IA.

Grace, P.R., K. Bryceson, K. Hennessy, and M. Truscott. 1996. Climate change and soil carbon resources. Pages 19–23 in *Land use in a changing climate, Maurice Wyndham series.* University of New England Press, Armidale, Australia.

Groffman, P.M. 1997. Ecological constraints on the ability of precision agriculture to improve the environmental performance of agricultural production systems. Pages 52–64 in *Precision agriculture: spatial and temporal variability of environmental quality.* John Wiley and Sons, Chichester, U.K.

Groffman, P.M., and J.M. Tiedje. 1989. Denitrification in north temperate forest soils: spatial and temporal patterns at the landscape and seasonal scales. *Soil Biology and Biochemistry* 21:613–626.

Groffman, P.M., and J.M. Tiedje. 1989. Denitrification in north temperate forest soils: relationships between denitrification and environmental factors at the landscape scale. *Soil Biology and Biochemistry* 21:621–626.

Groffman, P.M., J.M. Tiedje, G.P. Robertson, and S. Christensen. 1988. Denitrification at different temporal and geographical scales: proximal and distal controls. Pages 174–192 in J.R. Wilson, ed. *Advances in nitrogen cycling in agricultural ecosystems.* CAB International, Wallingford, U.K.

Gross, K.L., K.S. Pregitzer, and A.J. Burton. 1995. Spatial variation in nitrogen availability in three successional plant communities. *Journal of Ecology* 83:357–367.

Haas, H.J., C.E. Evans, and E.F. Miles. 1957. Nitrogen and carbon changes in Great Plains soils as influenced by cropping and soil treatments. *USDA Technical Bulletin 1164*, Washington, DC.

Hauck, R.D. 1981. Nitrogen fertilizer effects in nitrogen cycle processes. Pages 551–562 in F.E. Clark and T. Rosswall, eds. *Terrestrial nitrogen cycles.* Swedish Natural Science Research Council, Stockholm.

Havelka, U.D., M.G. Boyle, and R.W.F. Hardy. 1982. Biological nitrogen fixation. Pages 365–422 in F.J. Stevenson, ed. *Nitrogen in agricultural soils.* American Society of Agronomy, Madison, WI.

Hendrix, P.F., D.C. Coleman, and D.A. Crossley, Jr. 1992. Using knowledge of soil nutrient cycling processes to design sustainable agriculture. *Journal of Sustainable Agriculture* 2:63–82.

Hendrix, P.F., R.W. Parmelee, D.A. Crossley, Jr., D.C. Coleman, E.P. Odum, and P.M. Groffman. 1986. Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* 36:374–380.

Howarth, R.W., G. Billen, D. Swaney, A. Townsend, N. Jaworski, K. Lajtha, J.A. Downing et al. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic ocean. *Biogeochemistry* 35:75–139.

Hunt, H.W. 1977. A simulation model for decomposition in grasslands. *Ecology* 58:469–484.

Hunt, H.W., D.C. Coleman, E.R. Ingham, R.E. Ingham, E.T. Elliott, J.C. Moore, S.L. Rose, C.P.P. Reid, and C.R. Morley. 1987. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* 3:57–68.

IPCC. 1996. *Climate change: the intergovernmental panel on climate change (IPCC) scientific assessment.* University Press, Cambridge, UK.

Jackson, R., and M. Caldwell. 1993. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74:612–614.

Jansson, S.L., and J. Persson. 1982. Mineralization and immobilization of soil nitrogen. Pages 229–252 in J.L. Smith and E.A. Paul, eds. *Process controls*

and nitrogen transformations in terrestrial ecosystems. American Society of Agronomy, Madison, WI.

Jenkinson, D.S. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from ^{14}C labelled ryegrass decomposing under field conditions. *Journal of Soil Science* 28:424–434.

Jenkinson, D.S., D.E. Adams, and A. Wild. 1991. Model estimates of CO_2 emissions from soil in response to global warming. *Nature* 351:304–306.

Jenkinson, D.S., P.B.S. Hart, J.H. Rayner, and L.C. Parry. 1987. Modeling the turnover of organic matter in long-term experiments at Rothamsted. *INTECOL Bulletin* 15:1–8.

Jordan, T.E., and D.E. Weller. 1996. Human contributions to terrestrial nitrogen flux. *Bioscience* 46:655–664.

Journel, A.G., and C.J. Huijbregts. 1978. *Mining geostatistics.* Academic Press, New York.

Juma, N.G., and E.A. Paul. 1981. Use of tracers and computer simulation techniques to assess mineralization and immobilization of soil nitrogen. Pages 145–154 in M.J. Frissel and H.A. Van Veen, eds. *Simulation of nitrogen behavior in soil-plant* systems. PUDOC, The Netherlands.

Keeney, D.R. 1979. A mass balance of nitrogen in Wisconsin. *Wisconsin Academy of Sciences, Arts and Letters* 67:95–102.

Keeney, D.R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. *Forest Science* 26:159–171.

Krige, D.G. 1981. Lognormal-de Wijsan geostatistics for ore evaluation. *South African Institute of Mining and Metallurgy Monograph Series Geostatistics* 1:1–51.

Liebig, J. 1847. *Chemistry in its application to agricultural and physiology*, 4th ed. Taylor and Walton, London.

Lipman, J.G., and A.B. Corybeare. 1936. Preliminary note on the inventory and balance sheet of plant nutrients in the United States. *New Jersey Agricultural Experiment Station Bulletin* 607, Rutgers, New Jersey.

Likens, G.E., and F.H. Bormann. 1996. *Biogeochemistry of a forested ecosystem. 2nd ed.* Springer-Verlag, New York.

McGill, W.B., H.B. Hunt, R.G. Woodmansee, and J.O. Reuss. 1981. PHOENIX, a model of the dynamics of carbon and nitrogen in grassland soils. *Ecological Bulletin* (Stockholm) 33:49–115.

Melillo, J.M., J.D. Aber, and J.M. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.

Melillo, J.M., J.D. Aber, P.A. Steudler, and J.P. Schimel. 1983. Denitrification potentials in a successional sequence of northern hardwood forest stands. *Ecological Bulletin* (Stockholm) 35:217–228.

Miller, R.J., and R.B. Smith. 1976. Nitrogen balance in the southern San Joaquin Valley. *Journal of Environment Quality* 5:274–278.

Molina, J.A.E., C.E. Clapp, M.J. Shaffer, F.W. Chichester, and W.E. Larson. 1983. NCSOIL, a model of nitrogen and carbon transformations in soil. Description, calibration and behavior. *Soil Science Society of America Journal* 47:85–91.

Moore, J.C., and P.C. deRuiter. 1991. Temporal and spatial heterogeneity of tro-phic interactions within below-ground food webs. *Agriculture, Ecosystems and Environment* 34:371–397.

Nixon, S.W. 1995. Coastal marine eutrophication: a definition, social causes, and future consequences. *Ophelia* 41:199–219.

Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma* 56:377–400.

Oakley, R.A. 1925. The economics of increased legume production. *Journal of the American Society of Agronomy* 17:373–389.

Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. *Soil Science Society of America Journal* 51:1194–1199.

Parkin, T.B., J.L. Starr, and J.J. Meisinger. 1987. Influence of sample size on measurement of soil denitrification. *Soil Science Society of America Journal* 51: 1492–1501.

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51:1173–1179.

Paul, E.A. 1989. Soils as components and controllers of ecosystem processes. Pages 353–374 in P.J. Grubb and J.B. Whittaker, eds. *Toward a more exact ecology, the 30th symposium of the British Ecological Society, London 1988.* Blackwell Scientific Publications, Boston, MA.

Paul, E.A., K.A. Paustian, E.T. Elliott, and C.V. Cole, eds. 1997. *Soil organic matter in agricultural ecosystems: long term experiments in North America.* CRC Publishers, Boca Raton, FL.

Paul, E.A., and G.P. Robertson. 1989. Ecology and the agricultural sciences: a false dichotomy. *Ecology* 70:1594–1597.

Paul, E.A., and J. vanVeen. 1978. The use of tracers to determine the dynamic nature of organic matter. *Transactions of the 11th International Congress of Soil Science* 3:61–102.

Paul, E.A., H.P. Collins, D. Harris, U. Schulthess, and G.P. Robertson. 1998. The influence of biological management inputs on carbon mineralization in ecosystems. *Applied Soil Ecology.* In press.

Paustian, K., W.J. Parton, and J. Persson. 1992. Modeling soil organic matter in organic-amended and nitrogen-fertilized long-term plots. *Soil Science Society of America Journal* 56:476–488.

Peterjohn, W.T., and D.L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology* 65:1466–1475.

Pieters, A.J. 1927. *Green manuring.* John Wiley & Sons, New York.

Pigott, C.D., and K. Taylor. 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. *Journal of Ecology* 52:175–185.

Reiners, W.A. 1986. Complementary models for ecosystems. *American Naturalist* 127:59–73.

Revsbech, N.P., B.B. Jorgensen, and O. Brix. 1981. Primary production of microalgae in sediments measured by oxygen microprofile, $H^{14}CO_3^-$ carbon isotope labeled bicarbonate ion fixation, and oxygen exchange methods. *Limnology and Oceanography* 26:717–730.

Robert, P.C., R.H. Rust, and W.E. Larson, eds. 1993. *Soil specific crop management.* American Society of Agronomy, Madison, WI.

Robertson, G.P. 1982. Nitrification in forested ecosystems. *Philosophical Transactions of the Royal Society London* 296:445–457.

Robertson, G.P. 1987. Geostatistics in ecology: interpolating with known variance. *Ecology* 68:744–748.

Robertson, G.P. 1997. Nitrogen use efficiency in row-crop agriculture: crop nitrogen use and soil nitrogen loss. Pages 347–365 in L. Jackson, ed. *Agricultural ecology.* Academic Press, New York.

Robertson, G.P., J.R. Crum, and B.G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. *Oecologia* 96:451–456.

Robertson, G.P., and K.L. Gross. 1994. Assessing the heterogeneity of below-ground resources: quantifying pattern and scale. Pages 237–253 in M.M. Caldwell and R.W. Pearcy, eds. *Plant exploitation of environmental heterogeneity.* Academic Press, New York.

Robertson, G.P., M.A. Huston, F.C. Evans, and J.M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69:1517–1524.

Robertson, G.P., K.M. Klingensmith, M.J. Klug, E.A. Paul, J.C. Crum, and B.G. Ellis. 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecological Applications* 7:158–170.

Robertson, G.P., and T. Rosswall. 1986. Nitrogen in West Africa: the regional cycle. *Ecological Monographs* 56:43–72.

Robertson, G.P., and J.M. Tiedje. 1985. Denitrification and nitrous oxide production in successional and old growth Michigan forests. *Soil Science Society of America Journal* 48:383–389.

Robertson, G.P., and J.M. Tiedje. 1988. Denitrification in a humid tropical rainforest. *Nature* 336:756–759.

Robertson, G.P., P.M. Vitousek, P.A. Matson, and J.M. Tiedje. 1987. Denitrification in a clearcut loblolly pine plantation in the Southeastern U.S.: differences related to harvest intensity, site preparation, and cultivation practice. *Plant and Soil* 97:119–129.

Rolston, D.E., M. Fried, and D.A. Goldhamer. 1979. Denitrification measured directly from nitrogen and nitrous oxide gas fluxes. *Soil Science Society of America Journal* 40:259–266.

Rossi, R.E., D.J. Mulla, A.G. Journel, and E.H. Franz. 1992. Geostatistical tools for modeling and interpreting geological spatial dependence. *Ecological Monographs* 62:277–314.

Schlesinger, W.H. 1984. Soil organic matter: a source of atmospheric CO_2. Pages 111–127 in G.M. Woodwell, ed. *The role of terrestrial vegetation in the global carbon cycle.* John Wiley & Sons New York.

Schlesinger, W.H., J.A. Raikes, A.E. Hartley, and A.F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77:364–374.

Sexstone, A.J., N.P. Revsbech, T.P. Parkin, and J.M. Tiedje. 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. *Soil Science Society of America Journal* 49:645–651.

Shields, J.A., and E.A. Paul. 1973. Decomposition of ^{14}C-labelled plant material under field conditions. *Journal of Soil Science* 53:297–306.

Snaydon, R.W. 1962. Micro-distribution of *Trifolium repens* L. and its relation to soil factors. *Journal of Ecology* 50:133–143.

Sollins, P. 1989. Factors affecting nutrient cycling in tropical soils. Pages 85–95 in J. Proctor, ed. *Mineral nutrients in tropical forest and savanna ecosystems.* Blackwell Scientific Publications, Oxford, England.

Sollins, P., C.C. Grier, F.M. McCorison, K. Cromack, R. Fogel, and R.L. Fredricksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in Western Oregon. *Ecological Monographs* 50:261–285.

Stanford, G., and S.J. Smith. 1972. Nitrogen mineralization potentials of soils. *Soil Science Society of America Journal* 36:465–472.

Swank, W.T., and D.A.J. Crossley. 1988. *Forest hydrology and ecology at Coweeta.* Springer-Verlag, New York.

Thomas, G.W., and R.E. Phillips. 1979. Consequences of water movement in macropores. *Journal of Environmental Quality* 8:149–152.

Tiedje, J.M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. Pages 179–244 in A.J.B. Zehnder, ed. *Biology of anaerobic microorganisms.* John Wiley & Sons, New York.

Trangmar, B., R. Yost, and G. Uehara. 1985. Application of geostatistics to spatial studies of soil properties. Pages 45–94 in N.C. Brady, ed. *Advances in agronomy.* Academic Press, New York.

Trangmar, B.B., R.S. Yost, M.K. Wade, G. Uehara, and M. Sudjadi. 1987. Spatial variation of soil properties and rice yield on recently cleared land. *Soil Science Society of America Journal* 51:668–674.

Turner, R.E., and N.N. Rabalais. 1991. Changes in Mississippi River water quality this century. *Bioscience* 41:140–147.

vanVeen, J.A., and M.J. Frissel. 1979. Mathematical modelling of nitrogen transformation in soil. Pages 133–157 in J.F.K. Gasser, ed. *Modelling nitrogen from farm wastes.* Applied Sciences Ltd., London.

vanVeen, J.A., J.N. Ladd, and M.J. Frissel. 1984. Modelling C and N turnover through the microbial biomass in soil. *Plant and Soil* 76:257–274.

vanVeen, J.A., and E.A. Paul. 1981. Organic carbon dynamics in grassland soils. I. Background information and computer simulation. *Canadian Journal of Soil Science* 61:185–201.

Vieira, S.R., J.I. Hatfield, D.R. Nielson, and J.W. Biggar. 1983. Geostatistical theory and application to variability of some agronomical properties. *Hilgardia* 51:1–75.

Virginia, R.A., W.M. Jarrell, and E. Franco-Vizcaino. 1982. Direct measurement of denitrification in a *Prosopis* (Mesquite) dominated Sonoran desert ecosystem. *Oecologia* (Berlin) 53:120–122.

Vitousek, P.M. 1982. Nutrient cycling and nitrogen use efficiency. *American Naturalist* 119:553–572.

Webster, R. 1985. Quantitative spatial analysis of soil in the field. Pages 1–70 in B.A. Stewart, ed. *Advances in soil science.* Springer-Verlag, New York.

Webster, R., and H.E. Cuanalo. 1975. Soil transect correlograms of north Oxfordshire and their interpretations. *Journal of Soil Science* 26:176–194.

Webster, R., and M. Oliver. 1990. *Statistical methods in soil and land resource survey.* Oxford University Press, Oxford, England.

White, R.E. 1985. The influence of macropores on the transport of dissolved and suspended matter through soil. *Advances in Soil Science* 3:95–120.

Wild, A. 1972. Nitrate leaching under bare fallow at a site in northern Nigeria. *Journal of Soil Science* 23:315–324.

Yoshinari, T., R. Hynes, and R. Knowles. 1977. Acetylene inhibition of nitrous oxide reduction and measurement of denitrification and nitrogen fixation in soil. *Soil Biology and Biochemistry* 9:177–183.

Zedler, J., and P. Zedler. 1969. Association of species and their relationship to microtopography within old fields. *Ecology* 50:432–442.