

DESIGNING AGRICULTURAL ECOSYSTEMS FOR THE HUMID TROPICS

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INTRODUCTION

Warmth, moisture, and constancy are the environmental factors responsible for the potentially high productivity of the humid tropical lowlands. Ironically, they are also the biome's greatest ecological constraints to agriculture.

Chemical weathering increases with temperature and is three to six times faster in the tropics than in the temperate zone (125, 250). This frequently leads to the development of deeply weathered soil with scant opportunity for the addition of fresh supplies of nutrients from the bedrock. High temperatures also mean potentially lower net photosynthesis; respiration approximately doubles with a temperature increase of 10° (114, 122, 178), and the oxygen inhibition of photosynthesis in C₃ plants increases with temperature (34, 166).

Potential evapotranspiration at 28° is about 1.6 m yr⁻¹ (106, 241), yet annual rainfall in the humid tropics commonly exceeds 3 m. The excess runs off across the surface or infiltrates the soil and, if the site is not fully vegetated, may carry nitrate and cations with it. Moreover, fungi, bacteria, and epiphylls, many of which are crop pests, thrive in warm, humid climates.

The lack of a harsh season comparable to temperate-zone winter or the annual drought of the seasonally dry tropics means that life, including agricultural pests, can flourish year-round. A seasonal shutdown of growth—which also depresses pest populations—is an important agricultural subsidy, one that is missing in the less seasonal tropics (36, 117, 242).

Many of the constraints imposed by the humid tropical environment can be overcome by supplying fertilizers and pest controls (207), but these amenities require locally scarce and expensive fossil fuels. Given the reality of current

rates of human population growth and colonization of the humid tropical lowlands (156), there seem to be only two options. One is for tropical countries to exchange locally abundant natural resources such as wood either for food or for the fossil fuels needed to overcome local constraints to agricultural production. The other is to develop agricultural ecosystems that are sustainable where temperatures are high and moisture is abundant all year. One way to develop such sustainable agroecosystems may be to imitate the structure and function of natural communities.

Natural plant communities have several traits that one would like to incorporate into agricultural ecosystems: sustainability, thorough use of available resources, and resistance to invasion. If, in addition, a community is successional, then gross photosynthesis normally exceeds total respiration, resulting in high net primary productivity (172, 185). Thus, successional ecosystems can be particularly appropriate templates for the design of agricultural ecosystems.

During the fallow period, which is an integral part of the shifting agriculture cycle throughout the tropics, a site is occupied by successional vegetation, which is very productive except on inherently poor soils or badly degraded sites (66). That high net productivity, coupled with the site recuperation that occurs between successive cropping periods, makes the fallow an important key to understanding existing land management and abuse. Understanding the fallow can also offer insights useful in agroecosystem design.

THE ROLE OF FALLOW

The fallow is the key to the success of many agricultural systems based on short-lived plants. In the temperate zone the fallow is seasonally imposed and, as such, its roles in maintaining agricultural productivity are usually overlooked. In the humid tropics, however, the success of shifting agriculture depends upon a culturally imposed fallow that commonly lasts several years. When land lies fallow, the successional vegetation that grows on it may be unused; it may attract game and serve as a productive hunting ground (56, 140); it may be a casually managed plant community from which long-lived crops are occasionally harvested; or it may be a diverse, intensively managed orchard that produces food, cash crops, and wood (167). It is useful to examine how a fallow, or period of occupancy by successional vegetation, restores site productivity. By incorporating some of these productivity-restoring mechanisms into the design of agricultural systems, the need for fertilizers and pesticides in tropical agriculture may be reduced.

A fallow helps to sustain agriculture in two ways. One of these is the restoration of soil fertility that occurs as nutrients are replenished and tilth is

restored. The other is the decline in agricultural-pest populations—weeds, pathogens, and herbivorous insects and nematodes—that accompanies the regrowth of forest.

The restoration of site quality during a fallow is biologically mediated. Earthworms, for example, are as agriculturally important in some tropical soils as they are in the temperate zone (137). Although earthworm populations decline when the soil is tilled or when the rate of input of readily decomposed organic matter decreases, they recover during the fallow period. Important in the phosphorus nutrition of almost all higher plants (101, 154, 225), mycorrhizal fungi also recolonize during the fallow (115). Trees that form ectomycorrhizae are far less common in the tropics than those that form vesicular-arbuscular mycorrhizae. Ectomycorrhizal species may, however, be particularly effective in site recovery because they are thought to be capable of both breaking down detritus and directly taking up the nutrients thereby released (116).

The restoration of nitrogen supplies is also biologically controlled and can be crucial, especially when a site has been cultivated so long that soil organic matter, and therefore the reserve of mineralizable nitrogen, has been reduced below about 50% of the steady-state amount (88). New supplies of nitrogen in forms available to higher plants come primarily from biological fixation, which is the conversion of dinitrogen to amino acids by microbes. Some work has been done on nitrogen fixation by symbiotic microorganisms (both bacteria and actinomycetes) in the tropics (64, 218), but such research is complicated by the fact that the nodules on some tropical-tree roots are very inconspicuous (55). There is also a need for much more work on nonsymbiotic, nitrogen-fixing autotrophs and heterotrophs in the tropics (73, 224).

Different plant life forms dominate the fallow at different times, and each life form affects the recovery process in a characteristic way. Forbs are often the most conspicuous colonizers of fields abandoned after shifting agriculture. Many of these are fast growing, short lived, and produce prolific amounts of seed. Forbs quickly fill the interstices between the larger woody plants that sprout from root systems that survive forest felling and burning. The ground cover of forbs facilitates colonization by the many longer-lived species whose seedlings die if they are not protected from the full force of the tropical sun (233).

Grasses, which tend to be long-lived and fierce in competition with annual crops, usually diminish during succession. In many places the length of the fallow period is determined by the time it takes for the grasses, especially notorious pests such as *Imperata cylindrica*, to disappear from the site. Although some grasses produce a fine network of roots that bind soil aggregates and improve soil structure (203), others provide lower levels of soil organic matter than woody vegetation and have few, if any, positive impacts

on site quality (163). Furthermore, the soil organic matter contributed by grasses is concentrated in the surface horizons, and the total biomass of a grass sward is far lower than that of a forest. This has led some agronomists, who have based their assessments on nutrient analyses of surface soils rather than total amounts of nutrients above- and below-ground, to conclude that forest-to-grassland conversions improve site quality (70, 235). Although this may indeed be the case with some well-managed pastures of succulent, readily decomposable grasses such as *Pennisetum purpureum*, there is no evidence that it is true of the more noxious perennial grasses, including many Andropogoneae, which invade areas where fallows are short and burning is common (163).

Woody plants are the key to the site-restoring powers of fallow vegetation in the humid tropics because of their deep, permanent root systems. In wet tropical climates where net water movement in the soil can be downward year-round, root uptake is the only mechanism available to pump deeply leached nutrients back to the surface. The subsoil is probably more important to the nutrition of trees and shrubs than it is to that of herbaceous crops such as alfalfa, cotton, maize, sugar beets, and many grasses, for which its role has been well documented (47). Results of one study in Africa indicated that perennial savanna species obtained more than 30% of their phosphorus from the subsoil, but short-term crops made less use of subsoil phosphorus (162). Coffee, cacao, and guava are the only woody tropical crops for which nutrient recovery from the subsoil has been measured (2, 110, 182, 205).

Deep roots are especially important in nutrient-poor substrates because they increase the volume of soil exploited by the vegetation (94, 95). Woody plants can also enrich the soil by being extremely effective at trapping, retaining, and recycling nutrients that enter in rain (93, 126, 128, 129). Through their permanence, the roots of woody plants bind the soil and reduce erosion, which is one of the major dangers that accompanies agriculture in the humid tropics (87, 63, 132, 163).

The harsh winter of the temperate zone controls pest populations, but the decline of pests during a fallow period in the humid tropics is governed more by the successional changes in plant species composition. This may be one reason why fallows of six years or more are commonly employed in the humid tropics.

Nematologists have been at the forefront in documenting population changes in agriculturally important pests during fallows (29, 121, 160), and they recognize vegetation change as an important control tool. Surprisingly little research, however, has been directed at quantifying or explaining the changes in insect or fungal populations that must also occur when land lies fallow (33), even though this must be one of the most potent control tools available.

Weeds are widely recognized as a major impediment to continuous cropping in the humid tropics, and fields are often abandoned more because uncontrollable weed populations are anticipated than because of declining fertility or pest buildups (9, 10, 151, 211, 226). Although most of the forbs that colonize immediately after land clearing are short-lived as adults, many of them have seeds that are long-lived in the soil (127). Seed viability of such species can be reduced by 50% or more by burning the vegetation that grows up during the fallow period (27, 65, 234), but as many as 80% of the surviving seeds might be expected to germinate afterwards (K. R. Young et al, submitted for publication). The resulting seedlings, plus their progeny, make up the weed populations that eventually outcompete annual crops. Although most weed populations decline during the fallow period, the process is sometimes accelerated by planting trees among pernicious species such as *Imperata cylindrica* (173).

PLANT NUTRITION

The maintenance of an environment that assures adequate plant nutrition is a key factor to be considered in designing agricultural ecosystems for the humid tropics. If soil scientists were to rank factors crucial to the maintenance of the fertility of deeply weathered and leached tropical soils, organic matter would likely head most lists. It is an important substrate for cation exchange (220); it is the warehouse of much of the nitrogen, phosphorus, and sulfur potentially available to plants; it is the main energy source for microorganisms; and it is a key determinant of soil structure. Although some scientists believe that the role of soil organic matter in tropical agriculture has been overstated (206), most probably subscribe to the view outlined by E. J. Russell in the early editions of his classic soils book (202, p. 654):

The basic principle of managing these [leached, tropical] soils is, therefore, to devise a system of farming that involves the minimum of clean cultivation—for this leaves the soil bare—and that maintains a high organic matter content in the surface soil—for this not only helps to hold bases against leaching and phosphate against fixation by the active iron and aluminum compounds present, but it is also a source of plant nutrients in itself and it helps to maintain the structure and permeability of the surface soil.

Virtually all agricultural operations have the potential to profoundly affect soil organic matter through changes in soil temperature, aeration, acidity, and the quality, quantity, and timing of root turnover and litter fall. Some traditional farming practices help preserve a high level of soil organic matter. Examples of such practices include the use of shade trees, mixed cropping of species that differ in phenology, weed control through crop rotation and dense spacing rather than through cultivation, mulching, manuring, and fallowing (204). Despite a wealth of empirical observations on organic matter in tropical

soils, however, the depth of understanding that might enable agronomists to prescribe optimum management techniques for specific situations has not been reached and is one of the major research needs in tropical agriculture. Advances in our understanding are likely to come from research that takes a holistic approach toward the study of soil microorganisms, the active fraction of soil organic matter, and nutrients (170).

Tropical soils that are low in organic matter and high in oxides of iron and aluminum have extremely low effective cation-exchange capacity, often less than 4 meq/100 g (206). Such soils are often severely deficient in cationic macronutrients—potassium, calcium, magnesium. Deficiencies of micronutrients can impede tropical agriculture as well: Zinc deficiency is common in rice and citrus; molybdenum frequently limits the productivity of forage legumes; and copper supplies are inadequate for the growth of many crops on reclaimed peat, for example (203, 206).

Nitrogen and phosphorus, however, tend to be in short supply for agriculture on almost all soils. Fertilizers are the normal solution to nitrogen and phosphorus deficiencies, but industrial chemicals are beyond the economic reach of most smallholders in the humid tropics. There is an alternative, however: Within limits imposed by climate and parent material, the quantities of these two nutrients that are available to crops can be controlled by manipulating the physiognomy and composition of the vegetation.

Nitrogen

The importance of nitrogen as a major limiting factor for plant growth is illustrated by the fact that its industrial fixation into forms suitable for application as fertilizers is the major energy expenditure in modern grain agriculture (177).

Most nitrogen in tropical, terrestrial ecosystems, both agricultural and natural, is in the soil organic matter, not in the biomass (123). The microbially mediated release of this organic nitrogen through ammonification and nitrification make it available for plant uptake. Thereafter it may be returned to the soil as dead roots, leaves, and branches, as root exudates, or as canopy leachate and frass, thus completing the cycle. But there are leaks in this circuit, and two of them—denitrification and leaching—are likely to be especially pronounced in the humid tropics.

Denitrification is the conversion of nitrate to nitrous oxide and dinitrogen. Direct measurement of denitrification is difficult, and most attempts to monitor it in the field have yielded inconclusive results (14, 41). Nevertheless, the prerequisites for denitrification—sources of nitrate and soil organic matter, plus poor aeration (28, 171)—are present in many tropical soils. Furthermore, denitrification is not a phenomenon that is unique to flooded soils, as was once thought to be the case (62). Rather, it can occur in locally saturated microsites, even in well-drained soil (28, 82, 222).

The second major leak in the nitrogen cycle is leaching. Nitrate is extremely mobile, and it is the major anion leached from agricultural soils in the humid tropics (86, 163). The problem is compounded by the fact that each ion of leached nitrate is accompanied by an equivalent of a cation—often potassium (163), itself an element that is required in prodigious quantities for the nutrition of both agricultural and natural ecosystems. Actively growing vegetation is one of the best defenses against nitrate leaching, even on soils with low anion exchange capacity (143).

Volatilization of ammonia is another way that nitrogen can be lost from the soil. In the acid soils that predominate in the humid tropics, however, the nonvolatile ammonium ion is the dominant form and ammonia is scarce, so volatilization is usually unimportant (249). It is likely to be important only when nitrogen fertilizers are applied as urea or ammonium, when rice fields are flooded, or when slash is burned prior to cultivation (65, 84, 149, 192).

If the nitrogen budget is to balance, the losses due to denitrification, leaching, volatilization, and crop harvests must be replaced by fertilization, atmospheric inputs, and/or nitrogen fixation. Nitrogen additions as fertilizer account for most of the increases in agricultural yields achieved this century (96, 200). Nitrogen fertilizer is expensive, however, and beyond the means of most farmers in the lowland humid tropics.

Atmospheric inputs of inorganic nitrogen (ammonium plus nitrate) amount to only 5–18 kg ha⁻¹ yr⁻¹ (103, 123, 198). These quantities may be significant in natural ecosystems, but they are small in comparison with the amounts harvested in most crops (74).

In an effort to free tropical farmers from the economic burden of purchasing industrially fixed nitrogen, much recent research has been devoted to the feasibility of incorporating nitrogen-fixing trees into agricultural systems. Many of the shade trees traditionally used over perennial crops are capable of fixing nitrogen. Under extensive management a site may acquire by nitrogen-fixing trees the amounts of nitrogen needed to offset or exceed the amounts removed in crop harvests (8, 210). Where management is intensive, however, the accrual rate falls far short of the amount needed (23).

Although there is no doubt that nitrogen-fixing trees have a place in some agroforestry systems (26, 158, 197, 236, 248), they are not a biogeochemical panacea for the tropics. Some species commonly thought to fix nitrogen may, in fact, fix none at times. For example, the nodules of one tree species commonly used to shade coffee in Mexico, *Inga jinicuil*, fixed > 40 kg N ha⁻¹ yr⁻¹, but another member of the same genus, *I. vera*, fixed none (196). Furthermore, the nitrogen thus fixed is taken up by the trees themselves, and most of it does not become available to other species in the community until the leaves drop and are decomposed. However, nitrogen-fixing trees that produce useful timber, fruits, or shade can be self-sufficient with respect to

nitrogen and noncompetitive with coinhabitants for other sources of this element.

Some experts feel that nitrogen fixation by free-living microorganisms will prove adequate to meet the need of many agricultural ecosystems and that there is little to be gained by planting symbiotic nitrogen-fixers such as leguminous trees (104, 136). Although we know little about rates of nitrogen fixation by free-living microorganisms in the tropics, the importance of such microorganisms in long-term nitrogen accrual has been clearly documented in at least one temperate-zone ecosystem (53) and strongly inferred by researchers at several tropical sites (111, 113, 163, 201).

The exciting discovery that nitrogen-fixing bacteria inhabit the rhizosphere of some tropical grasses (59, 60) gave rise to hopes that this parasymbiosis might prove agronomically useful (75). Reasonably well-defined relationships have since been established between various genera of bacteria and the roots of at least five species of higher plants, including sugar cane and rice (61), but the amount of nitrogen thus fixed, probably $< 30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, is unlikely to satisfy the requirements of most crops (64, 225). However, it may be important in pastures and in natural ecosystems.

Phosphorus

The amount of phosphorus in an unfertilized soil is determined primarily by the parent material. Phosphorus is extremely immobile (25, 244), so little is lost through leaching. Tropical rainwater delivers only modest amounts of phosphorus—less than $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in most places (103)—so there is little opportunity for soil enrichment from atmospheric sources. Changes do become apparent over the long term, of course, as phosphorus becomes immobilized in highly insoluble forms or is redistributed by erosion and human activities (54, 240). However, over the short term—decades at least—the total amount of phosphorus in the soil is likely to remain relatively constant.

A constant amount of phosphorus present, however, does not mean a constant supply available to plants. Some tropical soils are notorious for their ability to immobilize large quantities of phosphorus in chemical forms that are unavailable to plants. The worst offenders are some of the Andepts that contain variable charged clays (208, 232); Andepts are the same soils that are, in many other respects, among the most promising ones for agriculture in the tropics. In many moderately weathered acid tropical soils, most inorganic phosphorus is sorbed onto films of iron and aluminum oxide, where it is potentially, but not readily, available to plants (203). As weathering progresses, however, much of the phosphate eventually becomes bound inside precipitates of iron oxide, where it is virtually unavailable (203).

Much of the phosphorus that is available to plants in the tropics is in the soil organic matter. Organic matter normally accounts for up to 50% of the total

phosphorus in the surface horizons of tropical soils and may represent 60–80% of the total soil phosphorus in highly weathered Oxisols, Ultisols, and Alfisols (206). Organic phosphorus circulates rapidly between plant and soil via the litter, and its release through decomposition can be an important regulator of productivity (37, 102). Soil organic matter is well correlated with extractable phosphorus in surface soils but not in subsoils (24). This is probably because most organic matter that is deep in the soil has been partially decomposed and has already lost its readily extractable phosphorus.

Most of the identifiable fraction of organic phosphorus in the soil, which usually accounts for less than half of the total, is inositol phosphates (131). Microorganisms are directly involved in making this and other forms of organic phosphorus available to plants (42, 45, 76, 217). In addition, some of the microorganisms associated with roots may release phytohormones that stimulate plant growth, thus enabling the plants to reach more phosphorus (15). A substantial fraction of the soil organic phosphorus [3–19% in one recent study (31)] is in microbial biomass.

Once phosphorus is converted to forms that can be taken up by plants, mycorrhizae close the biogeochemical loop. Sometimes they short-circuit the soil and transfer phosphorus directly from litter to plant (105, 116). Although many important processes have been attributed to mycorrhizae, their role in phosphorus uptake is probably the most universal and important one. Phosphorus uptake is facilitated by mycorrhizae because the external mycelium creates an absorbing surface that is larger and better dispersed than that provided by uninoculated roots (209, 225).

A Chronology of Nitrogen and Phosphorus Limitations

Both nitrogen and phosphorus are obviously of great importance to ecosystem productivity. Which of the two is likely to be more limiting in tropical agroecosystems? I argue that the answer to this question will change with stand development: First phosphorus is likely to be most limiting, then nitrogen, and finally phosphorus again. My argument is based on the idea that an ecosystem can accrue nitrogen, but the amount of phosphorus present is dictated by the initial state of the soil. Thus, when a site has been occupied by vegetation for a long time, phosphorus is likely to become more limiting than nitrogen.

Our starting point is recently cleared soil of some agricultural potential—not an extremely depauperate soil nor a previously unvegetated site. Immediately after deforestation, nitrate is usually abundant. This is especially true if forest felling is followed by burning of the slash (17, 65). If the soil contains a reasonable amount of nitrifiable nitrogen, the first crops and early colonizing weeds are likely to be relatively well supplied with nitrate (58, 81, 175). The members of this first plant community, however, are likely to be

short of phosphorus because it is so immobile. The nitrate moves to the roots through diffusion and mass flow, but the roots must grow to the phosphorus (25).

The period when nitrogen is abundant does not last long, however. The amount of nitrate declines quickly—within weeks—because of ash erosion, leaching, and plant uptake (65). During the intensive cropping of short-lived plants that usually follows land clearing, soil organic matter and nitrogen continue to decrease (17, 58, 81, 83, 84, 88, 164, 231).

Nitrogen continues to be in short supply, even if land is allowed to lie fallow after a period of intensive cropping. The same would likely be true if agroecosystems that resemble successional forests were substituted for native vegetation. Nitrogen demand is high during the early stages of succession, as plants build nitrogen-rich foliage and accumulate biomass (184, 239). During this period of high demand, available forms are further depleted and competition between roots and soil microorganisms for nitrogen increases. Nitrogen availability is soon limited by the rate at which it is released by decomposers. At the same time, the mycorrhizal root systems permeate a greater volume of soil, thus gaining access to its available phosphorus reserves. At this stage, plant growth may become more limited by nitrogen than by phosphorus.

Eventually the plants take up and recycle most of the readily extractable phosphorus. If soil acidity increases during stand development, as it sometimes does (20), an increasing fraction of the inorganic phosphorus that is not taken up by plants can become bound on oxides of iron and aluminum, further decreasing phosphorus availability (206). Concurrently, nitrogen demand by vegetation decreases (44, 150), and the amount of nitrogen in the system increases owing to fixation of atmospheric nitrogen and retention of mineral nitrogen brought by rain. A sequence of changes similar to this is evident in data from tree plantations in Nigeria (39) and in a simulation of forest-floor dynamics in a temperate-zone forest (1).

As soil organic matter returns to its steady-state level, the nitrogen it contains is rapidly cycled through a continuous process of litter fall, root sloughing, ammonification, nitrification, and uptake. Work in grasslands and temperate-zone forests suggests that the rate of nitrification decreases with succession (187, 188), but most tropical research does not support this idea (35, 58, 133, 191). Although some tropical trees may use ammonium as well as, or perhaps in preference to, nitrate (124, 216), the low levels of nitrate in most lowland tropical forest soils probably result from rapid uptake rather than reduced nitrification. Because the nitrate is taken up almost as fast as it is produced, amounts in the soil are extremely small and almost no nitrate is lost through leaching. Bicarbonate, which increases in response to high temperatures and microbial respiration, may replace nitrate as the most abundant anion in the soil solution, provided the pH is not much below 5.0 (120, 144,

237). The scarcity of nitrate in soil solution at this stage can be exacerbated further on phosphorus-poor soils, where its rate of production can be limited because of the sensitivity of nitrite-oxidizing bacteria to phosphorus deficiency (181).

The total amount of aboveground nitrogen in circulation under these circumstances can be very high—150 to 200 kg ha⁻¹ or more (19, 161)—even though the turnover time of available nitrogen in the soil is short. At this stage of development, physiological processes are more likely to be phosphorus limited than nitrogen limited, an inference supported by the low phosphorus concentrations of fresh leaf litter in many tropical forests (238). Although nitrogen and its mineralization are still tightly linked to productivity at this stage, the nitrogen dynamics may, in the long run, be controlled by phosphorus (43, 169).

Whether an ecosystem is limited more by nitrogen or by phosphorus thus hinges on three factors: (a) the amounts of phosphorus and nitrogen initially present in potentially available forms, (b) the ecosystem's successional status, and (c) the degree of substrate weathering, which strongly influences its phosphorus-fixing mineralogy (206, 240).

Plant communities on tropical soils that never accumulate appreciable quantities of organic matter, such as some savanna soils subjected to periodic fires (81, 88, 163), are likely to be nitrogen limited throughout their development. There are two reasons for this. First, nitrogen is required in far greater quantities than is phosphorus; typical foliage concentration ratios for tropical trees are on the order of 17 or 20 to 1 (89, 146, 221). Second, under these circumstances, the nitrogen-starved vegetation never develops to the point where it is limited by any other element. Thus, a chronic nitrogen deficiency may mask shortages of phosphorus, but a nitrogen buildup is likely to presage phosphorus limitation.

This proposed chronology of nitrogen and phosphorus limitations implies that nutrient management should change as an agroecosystem ages. In the earliest stages of stand development, when nutrient demands are high and substantial amounts of nutrients leave the site in harvests of short-lived crops, it is likely that both nitrogen and phosphorus fertilizers would increase productivity. The faster that deep-rooted, mycorrhizal plants can be encouraged, however, the faster the community is likely to become phosphorus self-sufficient. During the intermediate stages of stand development—when the community consists of a mixture of herbs, shrubs, and small trees, for example—it may be most useful to concentrate on increasing nitrogen supplies. This might be accomplished by incorporating nitrogen-fixing plants into the species mix or by favoring species that produce readily decomposable litter. As the agroecosystem matures and its annual growth increment approximates yield, phosphorus is likely to be the most limiting nutrient. Phosphorus

fertilization—never a simple matter on acid, iron-and-aluminum-rich tropical soils (72, 206)—may not only remedy this deficiency but may also increase the availability of nitrogen.

CONSEQUENCES OF SPECIES RICHNESS

There are three potential ecological benefits to having several species in a ecosystem: full use of resources, pest protection, and compensatory growth. None of these is a universal outcome of diversity, but each is an attribute worth striving for in designing sustainable agricultural ecosystems.

That species should use resources differently is an appealing idea and the fundamental concept that underlies niche theory. But plant species do not necessarily use different resources as adults: They require the same suite of 17 elements, and they all use the same wavelengths of solar radiation in photosynthesis. Cohabitants may share the same habitat niche but coexist because of interspecific differences in regeneration niches (90). Thus, it is not surprising that increases in species richness do not always lead to more effective resource use (79, 141, 227). Nevertheless, in many multispecies plant communities, resource use is complementary rather than competitive (49, 227, 228, 246). Several agricultural examples of how species might be grown in useful mixtures based upon their “ecological combining abilities” (98) are described below.

There are several ways to combine plants so that solar radiation is fully used. Plants that reach maximum photosynthesis at different radiation levels make logical agricultural combinations (155, 229); plants that use the C_3 pathway of carbon fixation might be combined with C_4 species if light levels are adequate (130, 223); and leaf area and leaf density can be manipulated by combining species that differ with respect to stature, shade tolerance, and leaf angle (92, 112, 130).

Another way to facilitate complementary resource use in the same habitat is to combine species that differ in phenology (4, 108). A prominent example in tropical agriculture is the use of *Acacia albida* as an overstorey crop above grains and peanuts in Africa; the tree loses its leaves during the growing season of the annual crop (183). Resource use might also be enhanced by growing mixtures in which some species grow shoots at the same time that others are growing roots. Among perennial plants, allocations of photosynthate to shoots and roots differ seasonally and with age (22, 134, 230).

Nutrients and water are key resources, and their utilization might be enhanced by combining species whose roots exploit different parts of the soil (107). There is evidence that this is the case in many multiple-cropping schemes involving coconuts (157, 159), as well as in mixtures of annual crops (247). Also, nitrogen-fixing plants might be grown with others that do not fix

nitrogen; species that take up ammonium might be grown together with species that take up nitrate; and species that do not form mycorrhizae might be grown jointly with some that form vesicular-arbuscular mycorrhizae and others that form ectomycorrhizae.

In spite of these qualitative, temporal, and spatial ways that plants can partition resources, it still seems clear that tropical forests contain far more species than are required to use fully the available resources. It is the other two benefits that derive from species richness that make it worthwhile to consider building some redundancy into agricultural ecosystems.

The first of these is the pest protection that one species may receive by growing in association with others (11, 97, 195). Many mechanisms may be involved in conferring this protection (33, 174). These include: reduced apparency of a pest's target (71); diluting potential host species within a matrix of nonsusceptible species (51, 176, 195, 219); physically interfering with pest movements by dense vegetation comprised of various life forms (189); creating an environment unfavorable to pests (16); or creating an environment favorable to the enemies of pests (5, 195). Although crops in diverse communities are usually subjected to lower losses to pests than are crops grown in monoculture (190), high plant-species richness sometimes leads to an increase in such losses (33). This can occur either because pest populations flourish (16, 99), because a plant suffers from increased apparency by growing with species to which it is related (71), or because species suffer from associational susceptibility when they grow with ones that are especially attractive to polyphagous pests (21; B. J. Brown, J. J. Ewel, submitted).

Compensatory growth, the second desirable trait, results from having more species in a community than would be required to use a site's resources fully. If one species succumbs to disease, pest attack, weather, senescence, or harvest, another species is available to fill the void and maintain full use of available resources (174). Cover, leaf area, productivity, and nutrient cycles are thereby sustained over time and under different sets of environmental constraints, even though the relative abundance of species within the community may change dramatically (18, 32, 38, 145). An agriculturally important outcome of such resilience is that the risk of crop failure is spread among several cultivars.

Stands of cocoa, an understory tree before its domestication, sometimes break up earlier if grown as an unshaded monoculture than if grown beneath tree shade (3). The mechanisms involved are not well understood. This effect may be due to the fact that early growth is fast in the absence of shade and thus the species matures and senesces faster under these conditions than when grown in the understory. In this case, the polyculture does not so much provide resilience as it reduces the need for it.

LONGEVITY

Many of the purported ecological benefits of high species richness may have less to do with diversity than with the fact that many, although by no means all, species-rich communities are dominated by long-lived plants. Longevity and continuity of cover mean that nutrients circulate without interruption, nitrogen and organic matter build up to steady-state levels, and the internal environment of the ecosystem is ameliorated. By using perennials, one can construct a tropical agroecosystem having many of the same desirable functional attributes as a tropical forest, but with far fewer species.

Long-lived, woody dominants endow a plant community with a thick, complete canopy. In some cases, dense (agricultural) stands of one or two perennial species may have nearly as high an optical density and leaf area index as natural communities containing upwards of 50 species (68). A dense canopy can also protect the soil. Bare soil in the humid tropics is extremely susceptible to erosion, to compaction, and to decline of microbial populations and organic matter (52, 67). A dense stocking of perennial plants—whether trees, shrubs, or herbs—in an agroecosystem increases the likelihood that the soil will be covered continuously, moderating oscillations in temperature and humidity that can damage the soil. However, the role of trees in reducing the impact of rain has probably been overrated. Splash erosion in the humid tropics can be severe beneath cleanly weeded tree plantations because rainwater accumulates on foliage before coalescing into large drops, and these then strike the soil with great erosive force (243).

A second important structural feature of long-lived woody dominants is their dense, deep root systems. An extensive, permanent root system enables a plant community to exploit fully the surface soil, to retrieve leached cations and nitrate, to gain access to subsoil phosphorus, and to exploit newly weathered substrates. A tropical evergreen plant community with an extensive root system removes nutrients from the soil solution quickly and continuously; it further reduces leaching losses by drying the soil faster and deeper than does evaporation from bare soil. Whether or not the root systems of tree monocultures can exploit the soil as completely as mixed-species stands is not known.

The size of long-lived plants is a third structural attribute that may be agronomically important. Large plants might be expected to be more responsive to drought or defoliation than most small plants, but we know little about the stored energy reserves of tropical trees. One exception is tea culture, in which roots are routinely tested to determine whether the bushes have adequate starch reserves to tolerate pruning or foliage harvest. Defoliation of tropical trees is a common natural phenomenon (7, 119, 193). Most species refoliate quickly, but we do not know if they are more responsive than other life forms of tropical plants.

In addition to the three structural aspects discussed above, a fourth agronomically useful trait of long-lived plants is their potential resistance to herbivores. Trees may invest proportionally more of their available energy in defenses against polyphagous herbivores than do short-lived species (69, 153). The difference in pest susceptibility between short-lived crops and trees is further accentuated by the fact that herbivore defenses of annual crops, especially the reproductive parts that we eat, have often been made less effective through breeding. On the other hand, we often harvest tree parts specifically for the defense chemicals they contain: the caffeine of coffee seeds and tea leaves, the cocaine of coca leaves, and the latex of rubber stems, for example.

When pests do become a problem on tree crops, however, the situation can be far more serious than on annual crops because the breeding time of trees is far longer than that of their pests (117). It normally takes a decade or more to develop an annual crop variety for release to farmers, but the time required to prepare a perennial crop variety can be 30 years (in the case of rubber, for example) or more (179). Although tropical trees differ vastly in their susceptibilities to herbivore damage, there is a tendency for long-lived species to incur less damage than shorter-lived pioneers (46).

LIMITATIONS OF SPECIES-RICH, LONG-LIVED AGROECOSYSTEMS

The benefit of forest-like agroecosystems is low risk; the limitation is low yield. Perennial cropping systems that contain many species are found throughout the tropics of Asia, Africa, and the Americas (148, 168, 212), but invariably they are subunits of larger subsistence systems. Because yields from wooded gardens are low, a main subsistence crop such as rice, maize, or cassava is usually grown in the same vicinity, often by use of shifting agriculture.

The yield (mass per unit area per unit time) of annual crops is normally much higher—often an order of magnitude or more—than that of perennials. Furthermore, a large fraction of the total biomass of most annual crops is consumable, so when they are harvested the vegetation structure is demolished. On the other hand, only a small proportion of the total biomass of most perennial crops is used (134). In rubber, for example, I estimate that the yield is 0.5–2.3% of the biomass; in shaded cocoa it is about 0.3% (W. Hadfield, unpublished data); and in tea it reaches about 5.7% (91). Because the harvested product is such a small fraction of the total biomass of perennial crops, stand structure remains intact after harvest. Given the differences in the amounts of biomass harvested from the two kinds of ecosystems, it is not surprising that annual crops are often important for food, whereas perennials

are more likely to be cash crops: A kilogram of cocoa, coffee, or tea sells for at least ten times more than a kilogram of maize, rice, or yams.

Annual crops often have very high net primary productivity, much of which is allocated to the reproductive or storage organs we harvest for food (147). Photosynthesis in diverse, perennial agroecosystems can be as high or higher than that of annual monocultures (130). However, a greater proportion of the photosynthate is respired than is allocated to biomass production. This respiration drives many essential processes, just as it does in natural forests: decomposition, mycorrhizae-mediated phosphorus uptake, pollination, nitrogen fixation, and pest defense, for example.

Although it would be highly desirable to develop agroecosystems for the humid tropics that combine the ecological virtues of perennial polycultures with the high yields that are possible in monocultures of annuals, there are fundamental biological constraints to doing so. The very attributes that make forest mimics attractive—recycling of nutrients, freedom from dependence on large inputs of agricultural chemicals, reduced risk, and effective use of available resources—seem to have biological costs that are incompatible with high yield. The plant's photosynthetic energy may be allocated either to harvestable products or to the ecological functions that sustain complex ecosystems, but not to both simultaneously.

Design of appropriate farming systems for the humid tropics must be based on a thorough assessment of local resources, soil and climatic conditions, potentially available inputs, and the farmer's ability to take risks. Where resources and inputs are abundant and the farmer has adequate capital to be able to risk crop failure, a high-yielding monoculture or relatively simple polyculture is likely to be the agroecosystem of choice. Where resources and inputs are scarce and crop failure might be fatal, however, diverse cropping systems dominated by long-lived plants would probably be prescribed. In most situations, some system falling between these two extremes, or some combination of two or more kinds of systems, may be optimum. The use of several systems appropriate for specific areas and dependent on each farmer's constraints would result in a landscape mosaic of agroecosystems in various stages of succession.

LANDSCAPE MOSAICS

There are at least three potential agricultural advantages to maintaining a landscape as a mosaic of agroecosystems representative of various stages of succession. One of these is that the risk of complete failure is spread among, as well as within, cropping systems. This extends the concept of spreading agronomic risk among species in a polyculture while obviating the need to sacrifice high yield everywhere. Low-risk/low-yield patches, for example,

might be interspersed with high-risk/high-potential-yield patches. Furthermore, the landscape need not contain only the extreme agroecosystems—annual monocultures and diverse, wooded gardens—but it might consist of a mosaic of subunits that differ in age and diversity, just as tropical forests do (12, 30, 57, 100, 165, 186, 194).

A second potential benefit is the pest protection that may or may not accompany spatial heterogeneity (97, 213). In agricultural systems the type of pest control program envisaged will to some degree dictate the best type of within- and among-community structure. Although there is substantial enthusiasm, and some supportive evidence, for the idea that among-system diversity may enhance natural biological pest control (5, 6, 77), it is by no means clear that pest problems will be diminished in heterogeneous landscapes. For example, some organisms that are relatively benign inhabitants of forests have become serious pests in tropical monocultures (69). Discussing the relationships between agricultural systems and surrounding habitats of natural vegetation, Janzen (118, p. 37) points out that generalization is impossible:

While forest and other natural habitat remnants may harbor important parasites and predators, they may also harbor important pests during the dry season or other times when crop plants are unavailable. Which of these two roles is more important will vary from site to site and from crop to crop, and can be determined solely with respect to a particular situation. From a biological control viewpoint, we simply cannot say whether the loss of marginal habitats and lands to more intensive agriculture will result in a net gain or loss.

Well-established “integrated pest management” practices, such as spraying alternate rows and desisting until pest populations reach a predetermined density, are meant not only to avoid killing the enemies of pests but deliberately to maintain pest populations for pest enemies to live on (16). Theory indicates that some types of pests—including fast-reproducing species whose populations often explode in monocultures—may be easier to control in mosaics of habitats than in vegetation of uniform age and composition (50, 138, 139, 214, 215). The next logical step is to put theory to the test in the field, but this has not yet been done on a practical scale in the humid tropics.

The third possible advantage to having mosaics of community-types migrating amoeboid-fashion around the landscape is that this confers a potentially advantageous degree of temporal change. The benefits of change are of two types: those derived from being unpredictable, thereby reducing the likelihood of pest buildups, and those derived from being successional. An early successional phase implies high net primary productivity as well as all the rewards of a fallow period, discussed earlier. Many indigenous people in the humid tropics have long practiced such agricultural schemes by following crop monocultures or simple polycultures with managed fallow vegetation that yields useful products until it is rotated back into clean cultivation decades later (48, 56, 142, 167, 180, 245). Their systems, presumably

developed on the basis of successes and failures over very long times, can offer a great deal as models on which to base the design of sustainable agroecosystems for our most vulnerable and complex biome.

CONCLUSIONS

Agricultural systems must be both sustainable and independent of massive inputs of fossil-fuel derivatives if they are to be useful in most tropical countries. Four ecological attributes that address these constraints can be incorporated into the design of agroecosystems for the humid tropical lowlands: low requirements for nitrogen and phosphorus fertilizers; the ability to use fully the available nutrients, light, and water; protection from pests; and low risk. These features can be obtained by constructing mixed-species communities that imitate successional vegetation.

Nitrogen and phosphorus cycles are interdependent. Early in the development of a successional agroecosystem, phosphorus is likely to be in short supply, but this shortage may be alleviated as the site becomes dominated by deep-rooted perennials. During the middle stages of succession, an agroecosystem is likely to suffer nitrogen deficiencies. This is the time when nitrogen-fixing species and organic matter management may be most beneficial. Nitrogen supplies in the longer term are controlled by the phosphorus supply, so phosphorus fertilizers can increase the availability of both elements.

Species richness usually confers some pest protection. Also, the risk of complete crop failure in species-rich agroecosystems is low. However, floristically complex agroecosystems are hard to manage, so it is essential to reduce the species to the smallest number required. Herbs, shrubs, and trees differ in ecologically and agronomically significant ways, and each of these three life forms has a place in tropical agroecosystem design. Long-lived species obviate many of the problems associated with clean-cultivated monocultures of annual crops in the humid tropics. Stands consisting of one to a few species of perennials may use light, water, and nutrients as completely as more diverse mixtures. The yields from perennials tend to be low, however, so they are most attractive to farmers when they produce money rather than food.

One land-use scenario for the humid tropical lowlands consists of a mosaic of agroecosystems. High yields would come from annual crops, perhaps polycultures of three to four species that are ecologically compatible and complementary. Fields would change in composition, however, and eventually become dominated by long-lived plants. At the end of the rotation, the forest-like agroecosystem would be harvested for wood or destroyed, and the site would again revert to a cropping system dominated by annuals.

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Literature Cited

1. Aber, J. D., Botkin, D. B., Melillo, J. M. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* 8:306-15
2. Ahenkora, Y. 1975. Use of radioactive phosphorus in determining efficiency of fertilizer utilization by cacao plantation. *Plant Soil* 42:429-39
3. Ahenkora, Y., Akrofi, G. S., Adri, A. K. 1974. The end of the first cocoa shade and manurial experiment at the Cocoa Research Institute of Ghana. *J. Hort. Sci.* 49:43-51
4. Aitken, Y. 1974. *Flowering Time, Climate and Genotype*. Melbourne: Melbourne Univ. Press. 193 pp.
5. Altieri, M. A., Letourneau, D. K. 1982. Vegetation management and biological control in agroecosystems. *Crop Protection* 1:405-30
6. Altieri, M. A., Letourneau, D. K., Davis, J. R. 1983. Developing sustainable agroecosystems. *BioScience* 33:45-49
7. Anderson, J. A. R. 1961. Destruction of *Shorea albida* by an unidentified insect. *Emp. For. Rev.* 40:19-29
8. Aranguren, J., Escalante, G., Herrera, R. 1982. Nitrogen cycle of tropical perennial crops under shade trees. I. Coffee. *Plant Soil* 67:247-58
9. Aranson, T., Lambert, J. D. H., Gale, J., Cal, J., Vernon, H. 1982. Decline of soil fertility due to intensification of land use by shifting agriculturists in Belize, Central America. *Agro-Ecosystems* 8: 27-37
10. Ashby, D. G., Pfeiffer, R. F. 1956. Weeds, a limiting factor in tropical agriculture. *World Crops* 8:227-29
11. Atsatt, P. R., O'Dowd, D. J. 1976. Plant defense guilds. *Science* 193:24-29
12. Aubréville, A. 1938. *La Forêt Coloniale*. Académic des Sciences Coloniales. Annales, IX. Société d'Éditions Géographiques. Maritimes et Coloniales: Paris
13. Ayanaba, A., Dart, P. J., eds. 1977. *Biological Nitrogen Fixation in Farming Systems of the Tropics*. Chichester: Wiley
14. Ayanaba, A., Veldkamp, W. J. 1980. Denitrification in a toposequence. See Ref. 199, pp. 311-15
15. Barber, D. A. 1978. Nutrient uptake. In *Interactions Between Nonpathogenic Soil Microorganisms and Plants*, ed. Y. R. Dommergues, S. V. Krupa, pp. 131-62. Amsterdam: Elsevier
16. Batra, S. W. T. 1982. Biological control in agroecosystems. *Science* 215:134-39
17. Bartholomew, W. V. 1977. Soil nitrogen changes in farming systems in the humid tropics. See Ref. 13, 3:27-42
18. Benedict, F. F. 1982. *Structure, function, and stability of intercropping systems in Tanzania*. PhD thesis. Univ. Florida, Gainesville. 399 pp.
19. Bernhard-Reversat, F. 1977. Recherches sur les variations stationnelles des cycles biogéochimiques en forêt ombrophile de Côte d'Ivoire. Cah. ORSTOM Ser. Pédol. 15:175-89
20. Binkley, D., Richter, D. 1986. Nutrient cycles and H⁺ budgets of forest ecosystems. *Adv. Ecol. Res.* In press
21. Blanton, C. M., Ewel, J. J. 1985. Leaf-cutting ant herbivory in successional and agricultural tropical ecosystems. *Ecology* 66:861-69
22. Borchert, R. 1973. Simulation of rhythmic tree growth under constant conditions. *Physiol. Plant.* 29:173-80
23. Bornemisza, E. 1982. Nitrogen cycling in coffee plantations. *Plant Soil* 67:241-46
24. Brams, E. 1973. Soil organic matter and phosphorus relationships under tropical forests. *Plant Soil* 39:465-68
25. Bray, R. H. 1954. A nutrient mobility

- concept of soil-plant relationships. *Soil Sci.* 78:9-22
26. Brewbaker, J. L., Van Den Beldt, R., MacDicken, K. 1982. Nitrogen-fixing tree resources: Potentials and limitations. See Ref. 80, pp. 413-25
 27. Brinkmann, W. L. F., Vieira, A. N. 1971. The effect of burning on germination of seeds at different soil depths of various tropical tree species. *Turrialba* 21:77-82
 28. Broadbent, F. E., Clark, F. E. 1965. Denitrification. *Agronomy* 10:344-59
 29. Brodie, B. B., Murphy, W. S. 1975. Population dynamics of plant nematodes as affected by combinations of fallow and cropping sequence. *J. Nematol.* 7:91-92
 30. Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. In *The Ecology of Natural Disturbance and Patch Dynamics*, ed. S. T. A. Pickett, P. S. White, pp. 53-69. Orlando: Academic. 472 pp.
 31. Brookes, P. C., Powlson, D. S., Jenkinson, D. S. 1984. Phosphorus in the soil microbial biomass. *Soil Biol. Biochem.* 16:169-75
 32. Brown, B. J. 1982. *Productivity and herbivory in low and high diversity tropical successional ecosystems in Costa Rica*. PhD thesis. Univ. Florida, Gainesville. 292 pp.
 33. Brown, B. J., Marten, G. G. 1986. The ecology of traditional pest management in Southeast Asia. In *Traditional Agriculture in Southeast Asia: A Human Perspective*, ed. G. G. Marten, 12:241-72. Boulder, Colorado: Westview.
 34. Bykov, O. D., Koshkin, V. A., Catsky, J. 1981. Carbon dioxide compensation of C₃ and C₄ plants: Dependence on temperature. *Photosynthetica* 15:114-21
 35. Chandler, G. 1985. Mineralization and nitrification in three Malaysian forest soils. *Soil Biol. Biochem.* 17:347-53
 36. Chang, J. 1968. The agricultural potential of the humid tropics. *Geogr. Rev.* 58:333-61
 37. Chapin, F. S. III, Barsdate, R. J., Barèl, D. 1978. Phosphorus cycling in Alaskan coastal tundra: A hypothesis for the regulation of nutrient cycling. *Oikos* 31:189-99
 38. Chapin, F. S. III, Shaver, G. R. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66:564-76
 39. Chijicke, E. O. 1980. *Impacts on Soils of Fast-Growing Species in Lowland Humid Tropics*. FAO Forestry Pap. 21. Rome: FAO. 111 pp.
 40. Clark, F. E., Rosswall, T., eds. 1981. *Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts*. *Ecol. Bull.* 33. Stockholm: Swedish Nat. Sci. Res. Council. 714 pp.
 41. Colbourn, P., Dowdell, R. J. 1984. Denitrification in field soils. *Plant Soil* 76:213-26
 42. Cole, C. W., Elliott, E. G., Hunt, H. W., Coleman, I. C. 1978. Trophic interactions in soils as they affect energy and nutrient dynamics. V. Phosphorus transformations. *Microb. Ecol.* 4:381-87
 43. Cole, C. W., Heil, R. D. 1981. Phosphorus effects on terrestrial nitrogen cycling. See Ref. 40, pp. 363-74
 44. Cole, D. W., Rapp, M. 1981. Element cycling in forest ecosystems. In *Dynamic Properties of Forest Ecosystems*, ed. D. E. Reichle, 6:341-409. Cambridge: Cambridge Univ. Press. 683 pp.
 45. Coleman, D. C., Reid, C. P. P., Cole, C. V. 1983. Biological strategies of nutrient cycling in soil systems. *Adv. Ecol. Res.* 13:1-55
 46. Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53:209-33
 47. Comerford, N. B., Kidder, G., Mollitor, A. V. 1984. Importance of subsoil fertility to forest and non-forest plant nutrition. *Forest Soils and Treatment Impacts. Proc. 6th N. Am. For. Soils Conf.*, ed. E. L. Stone, pp. 381-401. Knoxville: Univ. Tenn. 454 pp.
 48. Conklin, W. C. 1957. *Hanunoo Agriculture. A report on an Integral System of Shifting Cultivation in the Philippines*. Rome: FAO. 209 pp.
 49. Conner, D. J. 1983. Plant stress factors and their influence on production of agroforestry plant associations. See Ref. 109, 27:401-26
 50. Conway, G. 1981. Man versus pests. In *Theoretical Ecology, Principles and Applications*, ed. R. M. May, 15:356-86. Oxford: Blackwells. 489 pp. 2nd ed.
 51. Cromartie, W. J. Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *J. Appl. Ecol.* 12:517-33
 52. Cunningham, R. K. 1963. The effect of clearing a tropical forest soil. *J. Soil Sci.* 14:224-345
 53. Day, J. M., Harris, D., Dart, P. J., Van Berkum, P. 1975. The Broadbalk experiment. An investigation of nitrogen gains from nonsymbiotic nitrogen fixation. In *Nitrogen Fixation by Free-Living Micro-Organisms*, ed. W. D. P.

- Stewart, 5:71-84. Cambridge: Cambridge Univ. Press
54. Deevey, E. S., Rice, D. S., Rice, P. M., Vaughan, H. M., Brenner, M. et al. 1979. Mayan urbanism: Impact on a tropical karst environment. *Science* 206: 298-306
55. de Faria, S. M., Franco, A. A., de Jesus, R. M., Menandro, M. de S., Baitello, J. B., et al. 1984. New nodulating legume trees from south-east Brazil. *New Phytol.* 98:317-28
56. Denevan, W. M., Treacy, J. M., Alcorn, J. B., Padoch, C., Denslow, J. et al., 1984. Indigenous agroforestry in the Peruvian Amazon: Bora Indian management of swidden fallows. *Interciencia* 9:346-57
57. Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12(Suppl.):47-55
58. de Rham, P. 1970. *L'azote dans quelques Forêts, Savanes et Terrains de Culture d'Afrique Tropicale Humide (Côte-d'Ivoire)*. Veröffentlichungen Geobot. Inst. 45 Heft. Zürich: Eidg. Techn. Hochschule. 124 pp.
59. Döbereiner, J. 1961. Nitrogen fixing bacteria of the genus *Beijerinckia* Dext in the rhizosphere of sugar cane. *Plant Soil* 14:211-17
60. Döbereiner, J. 1966. *Azotobacter paspali* n. sp. uma bacteria fixadora de nitrogênio na rizofera de paspalum. *Pesqui. Agropecu. Bras.* 1:357-65
61. Döbereiner, J., De-Polli, H. 1980. Diazotrophic rhizocoenoses. In *Nitrogen Fixation*, ed. W. D. P. Stewart, J. R. Gallon, 13:301-33. London: Academic Press. 451 pp.
62. Dubey, H. D., Fox, R. H. 1974. Denitrification from humid tropical soils of Puerto Rico. *Soil Sci. Soc. Am. Proc.* 38:917-20
63. El-Swaify, S. A., Arsyad, S., Krishnarajah, P. 1983. Soil erosion by water. *Natural Systems for Development: What Planners Need To Know*, ed. R. A. Carpenter, 3:99-161. New York: MacMillan. 485 pp.
64. Elmerich, C. 1984. Molecular biology and ecology of diazotrophs associated with non-leguminous plants. *Bio/Technology* 2:967-78
65. Ewel, J. J., Berish, C. W., Brown, B. J., Price, N., Raich, J. W. 1981. Slash and burn impacts on a Costa Rican wet forest site. *Ecology* 62:816-29
66. Ewel, J. J., Chai, P., Lim, M. T. 1983. Biomass and floristics of three young second-growth forests in Sarawak. *Malay. For.* 46:347-64
67. Ewel, J. J., Conde, L. F. 1980. *Potential Ecological Impact of Increased Intensity of Tropical Forest Utilization. BIOTROP. Spec. Publ. No. 11*. Bogor, Indonesia: SEAMO Regional Center for Tropical Biology. 70 pp.
68. Ewel, J. J., Gliessman, S., Amador, M., Benedict, F. F., Berish, C. W. et al. 1982. Leaf area, light transmission, roots and leaf damage in nine tropical plant communities. *Agro-Ecosystems* 7: 305-26
69. Evans, G. C. 1976. A sack of uncut diamonds: The study of ecosystems and the future resources of mankind. *J. Ecol.* 64:1-39
70. Falesi, I. C. 1976. *Ecosystema de Pastagen Cultivada na Amazônia Brasileira*. Belem, Brazil: Empresa Brasileira de Pesquisa Agropecuária CPATU. 193 pp.
71. Feeny, P. 1976. Plant apparency and chemical defense. In *Biochemical Interaction Between Plants and Insects*, ed. J. W. Wallace, R. L. Mansell, pp. 1-40. New York: Plenum. 425 pp.
72. Fenster, W. E., León, L. A. 1979. Management of phosphorus fertilization in establishing and maintaining improved pastures on acid, infertile soils of tropical America. In *Pasture Production in Acid Soils of the Tropics*, ed. P. A. Sanchez, L. E. Tergas, pp. 109-22. Cali, Colombia: CIAT
73. Fogg, G. E., Stewart, W. D. P., Fay, P., Walsby, A. E. 1973. *The Blue-Green Algae*. London: Academic Press. 459 pp.
74. Frissel, M. J., ed. 1978. *Cycling of Nutrients in Agricultural Ecosystems*. Amsterdam: Elsevier
75. Gaskins, M. H., Albrecht, S. L., Hubbell, D. H. 1984/1985. Rhizosphere bacteria and their use to increase plant productivity: A review. *Agriculture, Ecosystems and Environment* 12:99-116
76. Gerretsen, F. C. 1948. The influence of micro-organisms on the phosphate intake by the plant. *Plant Soil* 1:51-85
77. Gliessman, S. R., García E. R., Amador, A. M. 1981. The ecological basis for the application of traditional agricultural technology in the management of tropical agro-ecosystems. *Agro-Ecosystems* 7:173-85
78. Golley, F. B., ed. 1983. *Tropical Rain Forest Ecosystems: Structure and Function*. Amsterdam: Elsevier. 381 pp.
79. Gomez, A. A., Gomez, K. A. 1983. *Multiple Cropping in the Humid Tropics of Asia*. Ottawa, Canada: Int. Dev. Res. Ctr. 248 pp.
80. Graham, P. H., Harris, S. C. eds. 1982. *Biological Nitrogen Fixation Technol-*

- ogy for *Tropical Agriculture*. Cali, Colombia: CIAT
81. Greenland, D. J. 1958. Nitrate fluctuations in tropical soils. *J. Agric. Sci.* 50:82-92
 82. Greenland, D. J. 1962. Denitrification in some tropical soils. *J. Agric. Sci.* 58:227-33
 83. Greenland, D. J. 1977. Contribution of microorganisms to the nitrogen states of tropical soils. See Ref. 13, 2:13-25
 84. Greenland, D. J. 1980. The nitrogen cycle in West Africa—agronomic considerations. See Ref. 199, pp. 73-81
 85. Greenland, D. J., Hayes, M. H. B., eds. 1981. *The Chemistry of Soil Processes*. Chichester: Wiley. 714 pp.
 86. Greenland, D. J., Hayes, M. H. B. 1981. Soil Processes. See Ref. 85, 1:1-35
 87. Greenland, D. J., Lal, R., eds. 1977. *Soil Conservation and Management in the Humid Tropics*. Chichester: Wiley. 283 pp.
 88. Greenland, D. J., Nye, P. H. 1959. Increases in the carbon and nitrogen contents of tropical soils under natural fallows. *J. Soil Sci.* 9:284-99
 89. Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: With special reference to mineral nutrition. *Ann. Rev. Ecol. Syst.* 8:83-107
 90. Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* 52:107-45
 91. Hadfield, W. 1975. The effects of high temperatures on some aspects of the physiology and cultivation of the tea bush, *Camellia sinensis*, in North East India. In *Light as an Ecological Factor: II*, ed. G. C. Evans, R. Bainbridge, O. Rackham, 21:477-95. Oxford: Blackwells. 616 pp.
 92. Hadfield, W. 1981. Canopy architecture of some Ecuadorian cocoa populations with special reference to light penetration. *Proc. 7th Int. Cocoa Res. Conf., Douala, Cameroon*, pp. 109-20. London: J de Lafforest & Transla-Inter
 93. Harcombe, P. A. 1977. Nutrient accumulation by vegetation during the first year of recovery of a tropical forest ecosystem. In *Recovery and Restoration of Damaged Ecosystems*, ed. J. Cairns, Jr., K. L. Dickson, E. E. Herricks, pp. 347-78. Charlottesville: Univ. Press Va. 531 pp.
 94. Hardy, F. 1958. *Cacao Soils*. *Proc. Soil Crop Sci. Soc. Fla.* 18:75-87
 95. Hardy, F. 1974. Root room. *Trop. Agric. (Trinidad)* 51:272-78
 96. Hardy, R. W. F., Havelka, U. D. 1975. Nitrogen fixation research: A key to world food? *Science* 188:633-43
 97. Hare, J. D. 1983. Manipulation of host suitability for herbivore pest management. In *Variable Plants and Herbivores in Natural and Managed Systems*, ed. R. F. Denno, M. S. McClure, 18:655-80. New York: Academic. 717 pp.
 98. Harper, J. L. 1977. *Population Biology of Plants*. London: Academic 892 pp.
 99. Hart, R. D. 1975. A bean, corn and manioc polyculture cropping system. I. The effect of interspecific competition on crop yield. *Turrialba* 25:294-301
 100. Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. *Tropical Trees as Living Systems*, ed. P. B. Tomlinson, M. H. Zimmermann 26:617-38. Cambridge: Cambridge Univ. Press. 675 pp.
 101. Hayman, D. S. 1983. The physiology of vesicular-arbuscular endomycorrhizal symbiosis. *Can. J. Bot.* 61:944-63
 102. Hedley, M. J., Stewart, J. W. B., Chandon, B. S. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Sci. Soc. Am. J.* 46:970-76
 103. Hendry, C. D., Berish, C. W., Edger-ton, E. S. 1984. Precipitation chemistry at Turrialba, Costa Rica. *Water Resour. Res.* 20:1677-84
 104. Henzell, E. F., Vallis, I. 1977. Transfer of nitrogen between legumes and other crops. See Ref. 13, 6:73-88
 105. Herrera, R., Merida, T., Stark, N., Jordan, C. 1978. Direct phosphorus transfer from leaf litter to roots. *Naturwissenschaften* 65:208-9
 106. Holdridge, L. R. 1967. *Life Zone Ecology*. San José, Costa Rica: Trop. Sci. Ctr. 206 pp. 2nd ed.
 107. Huck, M. G. 1983. Root distribution, growth, and activity with reference to agroforestry. See Ref. 109, 32:527-42
 108. Huxley, P. A. 1983. Phenology of tropical woody perennials and seasonal crop plants with reference to their management in agroforestry systems. See Ref. 109, 31:503-26
 109. Huxley, P. A., ed. 1983. *Plant Research and Agroforestry*. Nairobi, Kenya: Int. Ctr. Res. Agrofor. 617 pp.
 110. Huxley, P. A., Patel, R. Z., Kabarra, A. M., Mitchell, H. W. 1974. Tracer studies with ³²P on the distribution of functional roots of *Arabica* coffee in Kenya. *Ann. Appl. Biol.* 77:159-80
 111. Isichei, A. O. 1980. Nitrogen fixation by blue-green algal soil crusts in Nigerian savanna. See Ref. 199, pp. 191-98
 112. Jackson, J. E. 1983. Light climate and

- crop-tree mixtures. See Ref. 109, 25:365-78
113. Jaiyebo, E. O., Moore, A. W. 1963. Soil nitrogen accretion under different covers in a tropical rain forest environment. *Nature* 197:317-18
114. James, W. O. 1953. *Plant Respiration*. London: Oxford Univ. Press. 282 pp.
115. Janos, D. P. 1980. Mycorrhizae influence tropical succession. *Biotropica* 12(Suppl.):56-64
116. Janos, D. P. 1983. Tropical mycorrhizas, nutrient cycles and plant growth. *Tropical Rain Forest: Ecology and Management*, ed. S. L. Sutton, T. C. Whitmore, A. C. Chadwick, pp. 327-45. Oxford: Blackwell. 498 pp.
117. Janzen, D. H. 1973. Tropical agroecosystems. *Science* 182:1212-19
118. Janzen, D. H. 1976. Additional land at what price?—Responsible use of the tropics in a food-population confrontation. *Proc. Amer. Phytopathol. Soc.* 3:35-39
119. Janzen, D. H. 1981. Patterns of herbivory in a tropical deciduous forest. *Biotropica* 13:271-82
120. Johnson, D. W., Cole, D. W. 1980. Anion mobility in soils: Relevance to nutrient transport from forest ecosystems. *Environ. Int.* 3:79-90
121. Johnson, A. W., Dowler, C. C., Hauser, E. W. 1975. Crop rotation and herbicide effects on population densities of plant parasitic nematodes. *J. Nematol.* 7:158-68
122. Jones, H. G. 1983. *Plants and Microclimate*. Cambridge: Cambridge Univ. Press. 194 pp.
123. Jordan, C. F. 1985. *Nutrient Cycling in Tropical Forest Ecosystems*. Chichester: Wiley. 190 pp.
124. Jordan, C. F., Todd, R. L., Escalante, G. 1979. Nitrogen conservation in a tropical rain forest. *Oecologia* 39:123-28
125. Kalpagé, F. S. C. P. 1974. *Tropical Soils: Classification Fertility and Management*. New York: St. Martin's. 283 pp.
126. Kellman, M. C. 1979. Soil enrichment by neotropical savanna trees. *J. Ecol.* 67:565-77
127. Kellman, M. C. 1974. The viable weed seed content of some tropical agricultural soils. *J. Appl. Ecol.* 11:669-78
128. Kellman, M., Hudson, J. 1982. Nutrition of *Pinus caribaea* in its native savanna habitat. *Plant Soil* 64:381-91
129. Kellman, M., Sanmugadas, K. 1985. Nutrient retention by savanna ecosystems. I. Retention in the absence of fire. *J. Ecol.* 73:935-51
130. Kira, T., Kumura, A. 1983. Dry matter production and efficiency in various types of plant canopies. See Ref. 109, 24:347-64
131. Kowalenko, C. G. 1978. Organic nitrogen phosphorus and sulfur in soils. In *Soil Organic Matter*, ed. M. Schnitzer, S. U. Khan, 3:95-136. Amsterdam: Elsevier. 319 pp.
132. Lal, R., Russell, E. W., eds. 1981. *Tropical Agricultural Hydrology: Watershed Management and Land Use*. Chichester: Wiley. 482 pp.
133. Lamb, D. 1980. Soil nitrogen mineralisation in a secondary rainforest succession. *Oecologia* 47:257-63
134. Ledig, F. T. 1983. The influence of genotype and environment on dry matter distribution in plants. See Ref. 109, 28:427-54
135. Lee, J. A., McNeill, S., Rorison, I. H., eds. 1983. *Nitrogen As An Ecological Factor. The 22nd Sym. Br. Ecol. Soc., Oxford, 1981*. Oxford: Blackwells
136. Lee, J. A., Stewart, G. R. 1978. Ecological aspects of nitrogen assimilation. *Adv. Bot. Res.* 6:1-43
137. Lee, K. E. 1983. Earthworms of tropical regions—some aspects of their ecology and relationships with soils. In *Earthworm Ecology*, ed. J. E. Satchell, 15:179-93. London: Chapman. 495 pp.
138. Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15:237-40
139. Levins, R., Wilson, M. 1980. Ecological theory and pest management. *Ann. Rev. Entomol.* 25:287-308
140. Linares, O. F. 1976. "Garden hunting" in the American tropics. *Hum. Ecol.* 4:331-49
141. Loomis, R. S. 1984. Traditional agriculture in America. *Ann. Rev. Ecol. Syst.* 15:449-78
142. Manner, H. I. 1981. Ecological succession in new and old swiddens of montane New Guinea. *Hum. Ecol.* 9:359-77
143. Marrs, R. H., Roberts, R. D., Skeffington, R. A., Bradshaw, A. D. 1983. Nitrogen and the development of ecosystems. See Ref. 135, 6:113-36
144. McColl, J. G., Cole, D. W. 1968. A mechanism of cation transport in forest soil. *NorthWest Sci.* 42:134-40
145. McNaughton, S. J. 1977. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. *Am. Nat.* 111:515-25
146. Medina, E. 1984. Nutrient balance and physiological processes at the leaf level. *Physiological Ecology of Plants in the Wet Tropics*, ed. E. Medina, H. A. Mooney, C. Vázquez-Yanes, pp. 139-59. The Hague: Dr. W. Junk. 254 pp.

147. Melillo, J. M. 1984. Net primary production, net ecosystem production and nutrient availability. *Options Méditerranéennes, Serie Etudes* 1984-1:95-110. Paris: Cte. Int. Hautes Etudes Agron. Méditerranéennes
148. Michon, G., Bompard, J., Hecketsweiler, P., Ducatillon, C. 1983. Tropical forest architectural analysis as applied to agroforests in the humid tropics: The example of traditional village—agroforests in West Java. *Agrofor. Syst.* 1:117-29
149. Mikkelsen, D. S., DeDatta, S. K., Obcemea, W. N. 1978. Ammonia volatilization losses from flooded rice soils. *Soil Sci. Soc. Am. J.* 42:725-30
150. Miller, H. G. 1981. Nutrient cycles in forest plantations, their change with age and the consequence for fertilizer practise. In *Proc. Australian Forest Nutrition Workshop, Productivity in Perpetuity*, pp. 187-99. Canberra, Australia: CSIRO, Div. For. Res. 302 pp.
151. Moody, K. 1974. Weeds and shifting cultivation. In *Shifting Cultivation and Soil Conservation in Africa*. *Soils Bull.* 24:155-66. Rome: FAO. 248 pp.
152. Mooney, H. A., Godron, M., eds. 1983. *Disturbance and Ecosystems*. Berlin: Springer-Verlag. 292 pp.
153. Mooney, H. A., Gulmon, S. L. 1982. Constraints on leaf structure and function in reference to herbivory. *BioScience* 32:198-206
154. Mosse, B. 1973. Advances in the study of vesicular-arbuscular mycorrhiza. *Ann. Rev. Phytopathol.* 11:171-96
155. Murray, D. B., Nichols, R. 1966. Light, shade and growth in some tropical plants. In *Light as an Ecological Factor*, ed. R. Bainbridge, G. C. Evans, O. Rackham, pp. 249-63. Oxford: Blackwells. 452 pp.
156. Myers, N. 1983. Conversion rates in tropical moist forests. See Ref. 78, 18: 289-300
157. Nair, P. K. R. 1983. Agroforestry with coconuts and other tropical plantation crops. See Ref. 109, 7:79-102
158. National Academy of Sciences. 1980. *Firewood Crops: Shrub and Tree Species for Energy Production*. Washington, DC: Natl. Acad. Sci. 237 pp.
159. Nelliatt, E. V., Bavappa, K. V. A., Nair, P. K. R. 1974. Multistoried cropping—new dimension of multiple cropping in coconut plantations. *World Crops* 26:262-66
160. Nusbaum, C. J., Ferris, H. 1973. The role of cropping systems in nematode population management. *Ann. Rev. Phytopathol.* 11:423-40
161. Nye, P. H. 1961. Organic matter and nutrient cycles under moist tropical forest. *Plant Soil* 13:333-46
162. Nye, P. H., Foster, W. N. M. 1961. The relative uptake of phosphorus by crops and natural fallows from different parts of the root zone. *J. Agric. Sci.* 56:299-306
163. Nye, P. H., Greenland, D. J. 1960. *The Soil Under Shifting Cultivation. Tech. Comm. No. 51*. Harpenden: Commonwealth Bur. Soils. 156 pp.
164. Nye, P. H., Greenland, D. J. 1964. Changes in the soil after clearing tropical forest. *Plant Soil* 21:101-12
165. Oldeman, R. D. A. 1983. The design of ecologically sound agroforests. See Ref. 109, 14:173-207
166. Osmond, C. B., Björkman, O., Anderson, D. J. 1980. *Physiological Processes in Plant Ecology*. New York: Springer-Verlag. 468 pp.
167. Padoch, C., Chota Inuma, J., DeJong, W., Unruh, J. 1985. Amazonian agroforestry: A market-oriented system in Peru. *Agrofor. Syst.* 3:47-58
168. Padoch, C., Vayda, A. P. 1983. Patterns of resource use and human settlement in tropical forests. See Ref. 78, 19:301-13
169. Pastor, J., Aber, J. D., McClaugherty, C. A., Melillo, J. M. 1984. Above-ground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65:256-68
170. Pavul, E. A. 1984. Dynamics of organic matter in soils. *Plant Soil* 76:275-85
171. Payne, W. J. 1981. *Denitrification*. New York: Wiley. 214 pp.
172. Peet, R. K. 1981. Changes in biomass and production during secondary succession. *Forest Succession*, eds. D. C. West, H. H. Shugart, D. B. Botkin, 20:324-38. New York: Springer-Verlag. 517 pp.
173. Pelzer, K. J. 1948. *Pioneer Settlement in the Asiatic Tropics. Special Publ. No. 29*. New York: Am. Geogr. Soc. 290 pp.
174. Perrin, R. M. 1977. Pest management in multiple cropping systems. *Agro-Ecosystems* 3:93-118
175. Pfadenhauer, J. 1979. Die Stickstoff Mineralisation in Böden subtropischer Regenwälder in Südbrasilien. *Oecol. Plant.* 14:27-40
176. Pimentel, D. 1961. The influence of plant spatial patterns on insect populations. *Ann. Entomol. Soc. Am.* 54:61-69
177. Pimentel, D., ed. 1980. *Handbook of Energy Utilization in Agriculture*, Boca Raton, Fla: CRC. 475 pp.

178. Pisek, A., Larcher, W., Moser, W., Pack, I. 1968. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter maximum der Netto-Photosynthese und Hitzeresistenz der Blätter. *Flora abt. B.* 158:110-28
179. Plucknett, D. L., Smith, N. J. H. 1986. Sustaining agricultural yields. *BioScience* 36:40-45
180. Posey, D. A. 1982. The keepers of the forest. *Garden* 6:18-24
181. Purchase, B. S. 1974. The influence of phosphate deficiency on nitrification. *Plant Soil* 41:541-47
182. Purohit, A. G., Mikherjaee, S. K. 1974. Characterizing root activity of guava trees by radiotracer technique. *Indian J. Agric. Sci.* 44:575-81
183. Raintree, J. B. 1983. Bioeconomic considerations in the design of agroforestry cropping systems. See Ref. 109, 19: 271-89
184. Reiners, W. A. 1981. Nitrogen cycling in relation to ecosystem succession. See Ref. 40, 33:507-28
185. Reiners, W. A. 1983. Disturbance and basic properties of ecosystem energetics. See Ref. 152, 33:83-98
186. Richards, P. W. 1952. *The Tropical Rain Forest*. Cambridge: Cambridge Univ. Press. 450 pp.
187. Rice, E. L. 1984. *Allelopathy*. Orlando: Academic. 422 pp. 2nd Ed.
188. Rice, E. L., Pancholy, S. K. 1972. Inhibition of nitrification by climax ecosystems. *Am. J. Bot.* 59:1033-44
189. Risch, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: An experimental test of two hypotheses. *Ecology* 62:1325-40
190. Risch, S. J., Andow, D., Altieri, M. A. 1983. Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. *Environ. Entomol.* 12:625-29
191. Robertson, G. P. 1984. Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. *Oecologia* 61:99-104
192. Robertson, G. P., Rosswall, T. 1986. Nitrogen in West Africa: The regional cycle. *Ecol. Monogr.* 56:43-76
193. Rockwood, L. L. 1973. The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* 54:1363-69
194. Rollet, B. 1983. La régénération naturelle dan les trouées. *Bois For. Trop.* 202:19-24
195. Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of col- lards (*Brassica oleracea*). *Ecol. Monogr.* 43:95-124
196. Roskoski, J. P. 1982. Nitrogen fixation in a Mexican coffee plantation. *Plant Soil* 67:283-91
197. Roskoski, J. P., Montano, J., van Kessel, C., Castilleja, G. 1982. Nitrogen fixation by tropical woody legumes: Potential source of soil enrichment. See Ref. 80, pp. 447-54
198. Rosswall, T. 1978. Exchange of nutrients between atmosphere and vegetation-soil. See Ref. 74, 7.4:296-302
199. Rosswall, T., ed. 1980. *Nitrogen Cycling in West African Ecosystems*. Stockholm: SCOPE/UNEP Int. Nitrogen Unit, Swedish Acad. Sci. 450 pp.
200. Rosswall, T., Paustian, K. 1984. Cycling of nitrogen in modern agricultural systems. *Plant Soil* 76:3-21
201. Ruschel, A. P., Vose, P. B. 1982. Nitrogen cycling in sugarcane. *Plant Soil* 67:139-46
202. Russell, E. J. 1961. *Soil Conditions and Plant Growth*. London: Longmans. 688 pp. 9th ed.
203. Russell, E. W. 1973. *Soil Conditions and Plant Growth*. London: Longman. 849 pp. 10th ed.
204. Ruthenberg, H. 1980. *Farming Systems in the Tropics*. Oxford: Clarendon. 424 pp. 3rd ed.
205. Saiz del Rio, J. F., Fernandez, C. E., Bellavita, O. 1961. Distribution of absorbing capacity of coffee roots determined by radioactive tracers. *Am. Soc. Hortic. Sci.* 77:240-44
206. Sanchez, P. A. 1976. *Properties and Management of Soils in the Tropics*. New York: Wiley. 618 pp.
207. Sanchez, P. A., Bandy, D. E., Villachica, J. H., Nicholaidis, J. J. 1982. Amazon basin soils: Management for continuous crop production. *Science*. 216: 821-27
208. Sanchez, P. A., Uehara, G. 1980. Management considerations for acid soils with high phosphorus fixation capacity. In *The Role of Phosphorus in Agriculture*, 17:471-514. Madison, Wis: Am. Soc. Agron. 910 pp.
209. Sanders, F. E., Tinker, P. B. 1973. Phosphate flow into mycorrhizal roots. *Pesticide Sci.* 4:385-95
210. Santana, M. B. M., Cabala-Rosand, P. 1982. Dynamics of nitrogen in a shaded cacao plantation. *Plant Soil* 67:271-81
211. Seavoy, R. E. 1973. The shading cycle in shifting cultivation. *Ann. Assoc. Am. Geogr.* 63:522-28
212. Soemarwoto, O., Soemarwoto, I. 1984. The Javanese rural ecosystem. In *An Introduction to Human Ecology Research*

- on *Agricultural systems in Southeast Asia*, ed. T. A. Rambo, P. E. Sajise, 16:254-87. Los Baños: Univ. Philippines
213. Stanton, M. L. 1983. Spatial patterns in the plant community and their effects upon insect search. In *Herbivorous Insects*, ed. S. Ahmad, 4:125-57. New York: Academic. 257 pp.
214. Stenseth, N. C. 1981. How to control pest species: Application of models from the theory of island biogeography in formulating pest control strategies. *J. Appl. Ecol.* 18:773-94
215. Stenseth, N. C., Hansson, L. 1981. The importance of population dynamics in heterogeneous landscapes: Management of vertebrate pests and some other animals. *Agro-Ecosystems* 7:187-211
216. Stewart, G. R., Orebamjo, T. O. 1983. Studies of nitrate utilization by the dominant species of regrowth vegetation of tropical West Africa: A Nigerian example. See Ref. 135, 8:167-88
217. Stewart, J. W. B., McKercher, R. B. 1982. Phosphorus cycle. *Experimental Microbial Ecology*, ed. R. G. Burns, J. H. Slater, pp. 221-38. Oxford: Blackwells. 683 pp.
218. Sylvester-Bradley, R., de Oliveira, L. A., de Podesta Filho, J. A., St. John, T. V. 1980. Nodulation of legumes, nitrogenase activity of roots and occurrence of nitrogen fixing *Azospirillum* spp. in representative soils of central Amazonia. *Agro-Ecosystems* 6:249-66
219. Tahvanainen, J. O., Root, R. B. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phylotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321-46
220. Talibudeen, O. 1981. Cation exchange in soils. See Ref. 85, 4:115-77
221. Tanner, E. V. J. 1985. Jamaican montane forests: Nutrient capital and cost of growth. *J. Ecol.* 73:553-68
222. Tiedje, J. M., Sextone, A. J., Parkin, T. B., Revsbech, N. P., Shelton, D. R. 1984. Anaerobic processes in soil. *Plant Soil* 76:197-212
223. Tieszen, L. L. 1983. Photosynthetic systems: Implications for agroforestry. See Ref. 109, 23:323-46
224. Thompson, J. P., Skerman, V. B. D. 1979. *Azotobacteraceae: The Taxonomy and Ecology of the Aerobic Nitrogen-Fixing Bacteria*. London: Academic. 417 pp.
225. Tinker, P. B. 1984. The role of microorganisms in mediating and facilitating the uptake of plant nutrients from soil. *Plant Soil* 76:77-91
226. Toky, O. P., Ramakrishnan, P. S. 1981. Cropping and yields in agricultural systems of the north-eastern hill region of India. *Agro-Ecosystems* 7:11-25
227. Trenbath, B. R. 1974. Biomass productivity of mixtures. *Adv. Agron.* 26:177-210
228. Trenbath, B. R. 1976. Plant interactions in mixed crop communities. *Multiple Cropping* (Spec. Publ.) 27:129-69. Madison, Wis: Am. Soc. Agron.
229. Trenbath, B. R. 1979. Light-use efficiency of crops and the potential for improvement through intercropping. *Proc. Int. Worksh. Intercropping, Hyderabad, India*, pp. 141-54. Hyderabad, India: Int. Crops Res. Inst Semi-Arid Trop.
230. Troughton, A. 1960. Further studies on the relationship between shoot and root systems of grasses. *J. Br. Grassl. Soc.* 15:41-47
231. Tulapitak, T., Pairintra, C., Kyuma, K. 1985. Changes in soil fertility and tilth under shifting cultivation. II. Changes in soil nutrient status. *Soil Sci. Plant Nutr.* 31:239-49
232. Uehara, G., Gillman, G. 1981. *The Mineralogy, Chemistry, and Physics of Tropical Soils with Variable Charge Clays*. Boulder, Colo: Westview. 170 pp.
233. Uhl, C. 1986. Factors controlling succession following slash and burn agriculture in Amazonia. *J. Ecol.* In press
234. Uhl, C., Clark, K. 1983. Seed ecology of selected Amazon Basin successional species. *Bot. Gaz.* 144:419-25
235. Vicente-Chandler, J., Caro-Costas, R., Pearson, R. W., Abruna, F., Figarella, J., et al. 1964. *The Intensive Management of Tropical Forages in Puerto Rico*. Univ. Puerto Rico Agric. Exp. Stn. Bull. 187.
236. Viemeyer, N. D. 1979. Tropical tree legumes: A front line against deforestation. *Ceres* 12:38-41
237. Vitousek, P. M. 1983. Mechanisms of ion leaching in natural and managed ecosystems. See Ref. 152, 3.6:129-44
238. Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285-98
239. Vitousek, P. M., Reiners, W. A. 1975. Ecosystem succession and nutrient retention: A hypothesis. *BioScience* 25:376-81
240. Walker, T. W., Syers, J. K. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1-19
241. Walter, H., Lieth, H. 1967. *Klimadiagramm-Weltatlas*. Jena: Fischer-Verlag
242. Wellman, F. L. 1968. More diseases on

- crops in the tropics than in the temperate zone. *Ceiba* 14:17-28
243. Wiersum, K. F. 1983. *Effects of various vegetation layers of an Acacia auriculiformis forest plantation on surface erosion at Java, Indonesia*. Pres. at Int. Conf. Soil Erosion and Conserv. Hawaii: Malama Aina. 15 pp.
244. Wild, A. 1981. Mass flow and diffusion. See Ref. 85, 2:37-80
245. Wilken, G. C. 1977. Integrating forest and small-scale farm systems in Middle America. *Agro-Ecosystems* 3:291-302
246. Willey, R. W. 1985. Evaluation and presentation of intercropping advantages. *Exper. Agric.* 21:119-33
247. Willey, R. W., Rao, M. R. 1981. A systematic design to examine effects of plant population and spatial arrangement in intercropping, illustrated by an experiment on chickpea/safflower. *Exper. Agric.* 17:63-73
248. Wilson, G. F., Kany, B. T. 1980. Developing stable and productive biological cropping systems for the humid tropics. *Biological Husbandry: A Scientific Approach to Organic Farming*, ed. B. Stonehouse, pp. 193-203. London: Butterworth. 352 pp.
249. Wollum, A. G., Davey, C. B. 1975. Nitrogen accumulation, transformation, and transport in forest soils. In *Forest Soils and Land Management. Proc. 4th N. Am. Forest Soils Conf.*, ed. B. Bernier, C. H. Winget, pp. 67-108. Laval, Quebec: Les Presse Univ. 454 pp.
250. Young, A. 1976. *Tropical Soils and Soil Survey*. Cambridge: Cambridge Univ. Press. 468 pp.



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