Agroforestry Systems **45**: 1–21, 1999.

Natural systems as models for the design of sustainable systems of land use

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Key words: agriculture, climate, fertility, humid tropics, life zones, succession

Abstract. Natural ecosystems, whose components are the results of natural selection, are sustainable; most are productive, responsive to pests, and retentive of nutrients. Thus, they are appropriate models on which to base the design of new systems of land use. Abiotic and biotic stressors are related non-linearly; the nadir of total stress being mid-way along a gradient of environmental harshness. Superimposing the stress functions on Holdridge's life zone chart yields four broad categories of environments for agriculture: climates where annual rainfall is similar to potential evapotranspiration, plus three other categories that are either too cold, too arid, or too wet. Extremely cold lands have no potential for agriculture. Lands that are arid or infertile can be used successfully, although the cost of compensating for environmental limitations increases exponentially with increasing abiotic stress. Grazing animals (which act as trophic buffers between people and environment) have proven successful in dry and infertile environments. The humid tropical lowlands epitomise environments of low abiotic stress but overwhelming biotic intricacy. Here it pays to imitate natural systems rather than struggle to impose simplicity on ecosystems that are inherently complex. The keys to success are to (i) channel productivity into outputs of nutritional and economic importance, (ii) maintain adequate diversity to compensate for losses in a system simple enough to be horticulturally manageable, (iii) manage plants and herbivores to facilitate associational resistance and not associational susceptibility, and (iv) use perennial plants to maintain soil fertility, guard against erosion, and make full use of resources.

1. Introduction

Different environments require different solutions in the quest for systems of land use that are ecologically, socially, economically, and politically sustainable. This paper is an attempt to simplify that search through development of a theoretical basis for categorising landscapes and analysis of the kinds of solutions that might be sought for each category. The humid tropical lowlands are given special emphasis because they constitute today's agricultural frontier. Significant tracts of tropical forests – our doomed warehouses of global biological diversity – can only be saved if people make a swift transition from short-term exploitation to sustainable land use: mimicry of nature is one potential solution.

Why seek new models for agriculture? More specifically, why pursue the development of agricultural systems that imitate the structure and function of natural ecosystems? There are three important reasons. First, much high-yield agriculture is not sustainable because its practice consumes non-renewable environmental capital, especially soil and ancient groundwater. A century of petroleum-driven agriculture has yielded some striking mismatches between land use and environment. Many global transfers of agricultural practices were, in fact, little more than the cultural baggage of early colonists, with more basis in history than agronomy: extensive grain monocultures to the humid tropics are one example, and Spanish sheep to the dry subtropics are another. Native ecosystems are time-proven survivors, and it is logical to learn from them and imitate their useful traits.

Second, modern agronomy carries a cultural burden imparted by our system of education: most students are provided with little knowledge of evolution and ecology, at least not at a scale that extends beyond a particular cultivar or perhaps a cultivar and the insects and diseases that attack it. Naturally occurring ecosystems are long-term products of evolution and the accommodation of organisms to environment: they change with time, as both environment and biota change, and they run on solar power, thus making them self-sustaining. Modern agriculture, in contrast, is completely dependent upon fossil energy – fuels, machinery, fertilisers, pesticides, and all the industries that support them. Nevertheless, there is no doubt that affordable supplies of fossil energy – a non-renewable resource on any time scale relevant to humans-are dwindling (e.g. see Hatfield, 1997). Reduced supplies inevitably will be accompanied by increased costs to consumers, including farmers. Nature's solar powered systems make eminent sense for the future of food production, making it all the more regrettable that most agricultural scientists are ill-equipped to take advantage of the knowledge these systems offer.

And third, most farmers (e.g. those in much of India, Africa, and China) have not benefited significantly from the technological innovations that led to soaring agricultural productivity elsewhere in this century. Furthermore, population growth forces socially marginalised people to use agriculturally marginal lands. It is on such landscapes – places where water and nutrients are in short supply, or where high rainfall and temperatures promote competition from weeds, pest outbreaks, and nutrient leaching – that new approaches are needed. Here again, the most logical approach is surely to look to natural ecosystems as models for the design of sustainable systems of land use.

But natural systems are immensely more complex than the simplified plant-animal assemblages that humans exploit for food production. To attempt to generalise about such complexity is a risky undertaking, as any generalisations are certain to be riddled with exceptions. Nevertheless, generalisation is the only prospect for cosmopolitan solutions: with two or three decades of cheap fossil fuel remaining (Hatfield, 1997), coupled with the prospect of a doubling of the world's population in that same time frame, we simply cannot afford the luxury of solving agricultural problems solely on a hectare-by-hectare basis. We do need that site-specific detail, but decision-makers also need to be able to evaluate that detail against a global context. Thus, despite the risks and inevitable exceptions, this essay begins with an examination of the relationship between environment and biotic complexity, and it puts this relationship in a theoretical context relevant to land use. Building on that theory, landscapes are then assigned to four broad categories, each having different suitability for agricultural production. Next is a detailed analysis focused on the humid tropics, where people are still groping for sustainable systems of land use. This is followed by examples of how ecological research can provide useful information for the design of sustainable agroforests. The examples are based on highlights of research in the humid tropics, involving construction, monitoring, and assessment of fast-growing, diverse successional communities that imitate the structure of naturally occurring communities.

2. Agriculture across environmental gradients

2.1. *Theory*

From a biophysical perspective, the difficulty of achieving agricultural production may be viewed as the sum of two types of stresses: abiotic and biotic. The first involves environmental factors such as water, temperature, and soil fertility; the second, competition, herbivory, and disease.

Mitscherlich's (1923) model for crop yield is a useful starting point. He proposed that, if no factors were limiting to growth, a certain maximum yield (Ym) would be obtained, and that the response to additions of the limiting factor were proportional to the difference between current and maximum yield: i.e. the more limiting the factor, the greater the response (Eq. 1).

$$\text{Mitscherlich's Function: } \frac{\mathrm{d}Y}{\mathrm{d}X} = (Ym - Y)k \qquad (1)$$

where Y is yield at some level of the limiting factor, X; Ym is the maximum yield obtainable; and k is a constant that describes the response of yield to increments of the limiting factor.

If we assume that the difference between maximum yield and yield at a given level of a limiting factor is a measure of abiotic stress, i.e. stress that would be alleviated if the limiting factor were incremented, then the resulting curve of abiotic stress as a function of level of environmental factor X is described by Eq. 2.

$$\text{Abiotic stress: } \frac{\mathrm{d}S_a}{\mathrm{d}X} = -k_a S_a \qquad (2)$$

where S_a is abiotic stress, induced by absence of a limiting factor (or excess of a debilitating environmental factor); X is the amount of the limiting (or debilitating) factor; and k_a is a constant that describes the decrement in stress per unit increment in X. The further one goes to the right along this exponentially decreasing curve (Figure 1a, dashed line), the less the abiotic restriction to growth.

The corollary is that, as abiotic factors become less constraining, the opportunity for more kinds of organisms to thrive increases: add water to a desert and get more kinds of plants, microorganisms, and herbivores, for example.

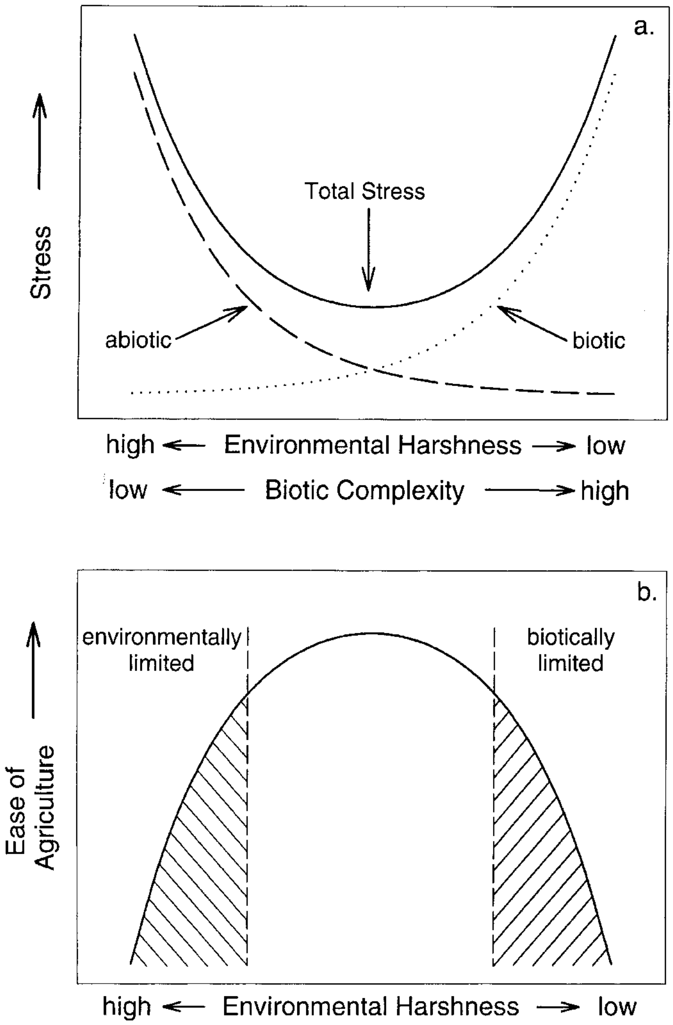

Figure 1. Stress and agriculture as a function of environment. a) Biotic and abiotic stress respond in opposite ways, and non-linearly, to environmental and biological gradients. Total stress is the sum of biotic and abiotic stresses. b) Appropriateness of different environments for agriculture. This function is the inverse of the total-stress curve in (a).

The relationship between such biotic stress and environmental factor X is described by Eq. 3.

$$\text{Biotic stress: } \frac{\mathrm{d}S_b}{\mathrm{d}X} = -k_b S_b \tag{3}$$

where S_b is biotic stress, induced by the competitors and consumers that thrive as limiting factor X increases, and k_b is a constant that describes the increment in biotic stress per unit increment in X. The further one goes to the right along this exponentially increasing curve (Figure 1a, dotted line), the greater the biotic impediments to agriculture. Thus, biotic impediments to agriculture (and the biotic simplicity it entails) increase as the abiotic constraints decline, and *vice versa*.

The key point is that the responses are not linear tradeoffs. Taking the sum of the responses (i.e. the sum of the dotted line and the dashed line in Figure 1a) to be the total constraint or impediment (shown as solid line in Figure 1a), we find that it is at the two endpoints that stresses are greatest. At the left-hand end of the graph, the constraints are primarily abiotic; at the right-hand end they are primarily biotic. The inverse image of this graph describes the ease with which agriculture can be accomplished in a particular environment (Figure 1b).

2.2. *Application*

It is feasible to nest global environments into categories according to their suitability for agriculture, ranging from those that are severely limited by abiotic stressors to those that are limited by biotic stressors, in accordance with the theory outlined above. One approach to broad-scale categorisation is to superimpose the concepts outlined above onto Holdridge's life zone chart (Figure 2a). Life zones are bioclimatic units determined by mean annual biotemperature and rainfall (Holdridge, 1947, 1967; Tosi, 1964). They have been used for assessment and planning at many scales, ranging from determination of local climates appropriate for specific crops (e.g. Hunter, 1959) to national descriptions of vegetation (e.g. Holdridge et al., 1971) to global assessments of the distribution of carbon and nitrogen (e.g. Post et al., 1982, 1985). There are more than 100 life zones on the earth's surface, but they can be aggregated into four clusters for an overview of appropriateness for agriculture (Figure 2b).

2.2.1. *Forgiving environments*

First, there are those life zones that have proven most propitious for agriculture, the ones clustered around the apogee of the ease-of-agriculture parabola (Figure 1b). These are (with few exceptions) the life zones in which annual rainfall does not deviate greatly from potential evapotranspiration (Figure 2); irrigation water, if needed at all, is required in only modest amounts, yet

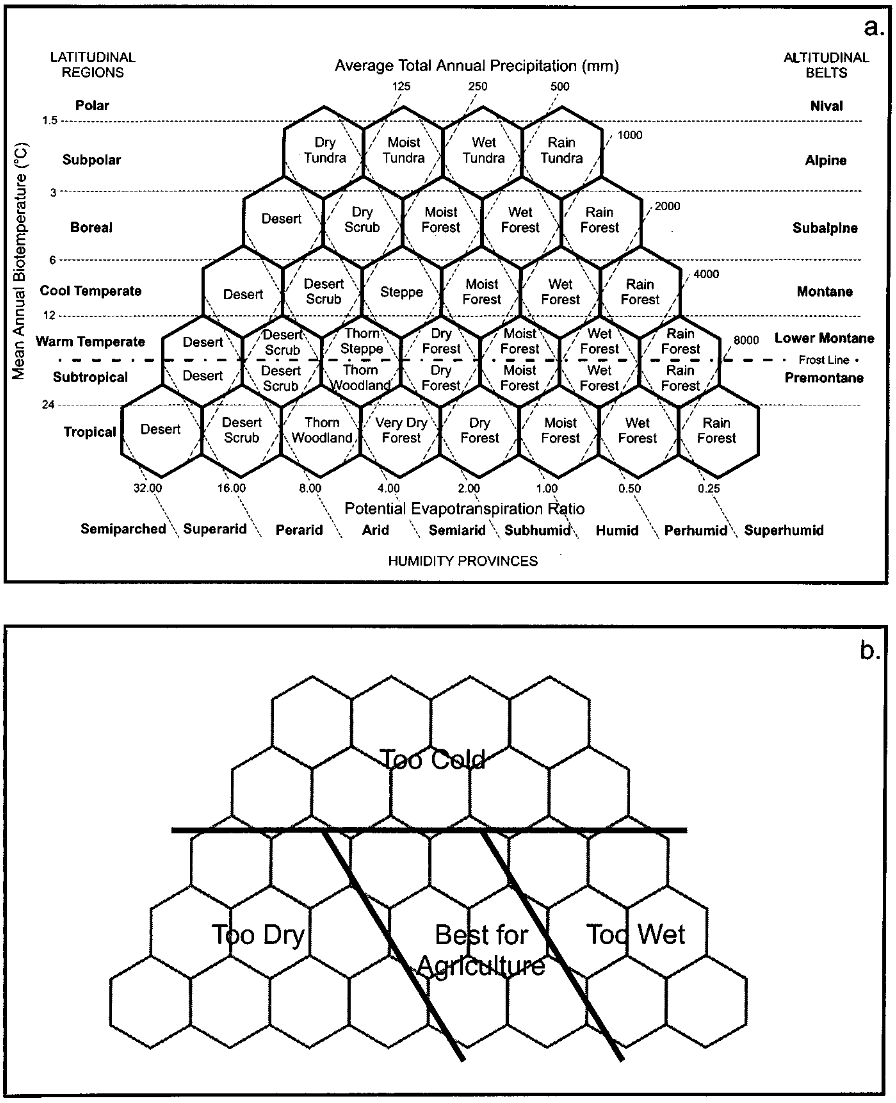

Figure 2. Categorisation of climates, and their suitability for agriculture. (a) The life zone classification scheme of Holdridge (1947, 1967). This two-dimensional figure illustrates the 38 Tropical life zones. Additional figures would be required to specifically illustrate the life zones of the six other latitudinal regions (named along the left edge of the chart); each successively more-polar region loses the lowest tier of life zones of the next most equatorial region. (b) Holdridge's life zones divided into four categories, each having different suitability for agriculture because of the stresses described by Figure 1.

rainfall is not so high that pests and nutrient leaching are overbearing problems. Not accidentally, these are the life zones of densest human settlement in many parts of the world (e.g. Tosi and Voertman, 1964). Where soils are inherently fertile (or where fertility is readily corrected, as in much of Australia), agriculture has thrived in these life zones, which encompass everything from the huge grain-producing farms of the temperate zone to tiny but prosperous mixed-crop farms of tropical and subtropical mountains. Some of the successful agroecosystems in these forgiving environments superficially resemble the natural systems they replaced. The grain monocultures of North America's Great Plains are low-diversity, short-lived versions of the native grasslands which makes the resemblance only superficial, as native grasslands are diverse and composed of perennial plants (Jackson, 1985), and orchards grown on lands that once supported native woodlands. Most, however, are products of human invention and cultural transplants.

2.2.2. *Too cold*

Of the other three clusters of life zones, all of which are more problematic, those that afford least agricultural utility are the ones that are permanently cold. From high in equatorial mountains they track a thermal decline in elevation, reaching sea level toward the poles. They lend themselves to little agricultural use other than subsistence transhumance (or, in more polar regions, seasonal hunting). The strategy in these zones is to harvest the grazers and browsers, whether domesticated or wild, which themselves harvest the meagre plant biomass produced in these inhospitable climates, just one step removed from permanent ice and snow.

2.2.3. *Too dry*

The second of the three problematic clusters consists of lands too arid to sustain agriculture without employing one, or some combination, of three tactics: (i) irrigate, (ii) schedule short-rotation crops to synchronise exactly with rains, or (iii) use grazers or browsers. Irrigation, especially in zones of high solar radiation and favourable temperatures, supports some of the highest population densities in the world. Nevertheless, it is not a panacea for agricultural development in arid zones because of the irony that irrigation is most feasible where least needed. The drier the climate, the more water required to meet the demands of evapotranspiration, the more likely the salinisation of surface soils, and the more the expenditure on infrastructure and maintenance. Inevitably, the most heavily irrigated, lowest-rainfall areas will experience or now experience salinity problems.

Timing crops to short rains is the global lottery of dryland agriculture. It is from such areas that news reports are filed annually with accounts of crop failure, sometimes accompanied by famine. One year it is Africa's Sahel, another year it is the warm-temperate end of the North American grain belt, and still another it is monsoonal South Asia. Recent change in global climate is the current scapegoat (if not the culprit), a situation that seems headed for exacerbation in the near future.

The third tactic employed in arid regions is to use large mammals to harvest, convert, and store plant biomass (Breman and de Wit, 1983; Coughenour et al., 1985). The cow (or camel, or sheep, or goat) covers a large area, harvesting and converting the primary production of natural ecosystems, its own mass rising and falling with availability of fodder. Sometimes their nomadic human shepherds live trophically downstream from the grazers and browsers, eating the animals or their metabolites (e.g. milk and blood); in other cultures the ungulates are used as draft animals in irrigated plots (Harris, 1965; Odend'hal, 1972). In both cases humans are buffered from the vagaries of rainfall by the large-biomass herbivores (Odum, 1967). In a sense, this system mimics nature, still to be seen today in East Africa's remnant herds of migrating wildebeest, gazelles, zebras, and their predators. Like so many of nature's models, this one seems doomed to extermination before we learn enough about it to facilitate even our own survival (Carr, 1964).

Southwestern Australia's wheat belt and its native vegetation, covered in detail elsewhere in this volume (Lefroy and Stirzaker, Hatton and Nulsen, Hobbs and O'Connor, and Dunin et al.), is an intriguing, if counter-intuitive, example of the imminent collapse of grain agriculture in one such semiarid climate. It has one element in common with other dry regions where failure has occurred, as the introduction of grain agriculture here was as much cultural as agronomic, having arrived with farmers who had been successful wheat growers elsewhere. But it has some unique features as well, chief among them its long geological history, during which time salts rained onto the landscape as wind-born, oceanic aerosols. Leached down into the soil profile, these salts were kept at bay by the transpirational pumping of fresh groundwater into the atmosphere by deep-rooted trees and shrubs: by pulling the freshwater out from depth over spring and summer, the salts remained harmlessly combined in the clays deeper in the profile. Each winter the groundwater was recharged with rainwater percolating rapidly to depth along low-resistance pathways such as root channels (Specht, 1957; Nulsen et al., 1986). Exchanging deep-rooted plants for shallow-rooted wheat, however, has proven disastrous. No deep pumping means water accumulates at depth, dissolving the stored salts as water tables rise; as more groundwater accumulates year after year, the salts rise closer to the surface, and when those salts reach roots of annual crops or pasture grasses, farming ends.

2.2.4. *Too wet*

Finally, there is the cluster of problematic life zones that make up today's agricultural frontier: the humid lowlands of the tropics. Where nature is so lush, why is farming so difficult? The problems are basically twofold. First, there is the biological problem of the crop being subsumed by the trophic complexity of the local biota: weeds, fungi, insects, viruses, nematodes, bacteria, and rodents flourish; among these, the relatively defenceless crops suffer. Second, there is the problem of much more water coming into the system than departing via evapotranspiration. The excess moves downward through the soil or runs off across the surface, and essential elements that are not sequestered in vegetation or tightly bound in the soil are vulnerable to leaching. People have coped with environments of high biotic stress, such as tropical moist forests, in many ways, ranging from wood mining to mimicry of forest structure, and it is those solutions that are addressed in much of the remainder of this paper.

3. Humid tropical lowlands

Much use of these areas of intensive biotic interaction has been, and in some areas continues to be, primarily exploitative. This involves the harvesting of palm stems for the manufacture of rattan furniture, the tapping of trees for latex destined to become aeroplane tires, the trapping of primates for biomedical research, and the harvesting of dozens of other naturally occurring resources, some for subsistence and some for sale. Fortunes are still being made from timber exploitation, a process that will probably come to a close within a few decades as the resource is exhausted and forests are conserved for other values.

The other principal land use in warm, high-rainfall areas is shifting agriculture, which, in the context of the theory outlined above, can be regarded as moving the agricultural plot to new land in anticipation of the arrival of the stressors, i.e. before the grasses and grasshoppers invade, or before the soil becomes completely impoverished through occupation by shallow-rooted, short-lived plants. In areas of low human-population density shifting agriculture works well, but it cannot be sustained where population pressures significantly shorten rotations.

Other, potentially more sustainable, land use systems are prominent, or becoming so, in the humid tropics, especially as timber exploitation and shifting agriculture become less and less tenable. One of these is the welcome re-discovery of natural-forest silviculture, a discipline that almost disappeared after World War II, when globalisation of markets and high demand for wood led to indiscriminate harvesting; this supplanted sound forest management throughout the tropics. New life is now being breathed into silviculture, as sustainable forestry regains international credibility as an appropriate land use for the humid tropics (e.g. National Research Council, 1993; Wadsworth, 1998).

A second system, one that deviates significantly from the structure of the natural forest, is plantation agriculture – cacao (*Theobroma cacao*), coconut (*Cocos nucifera*), rubber (*Calotropis procera*), and oil palm (*Elaeis guineensis*), for example. These perennials, unlike short-lived plants, afford uninterrupted protection of soil from erosion and nutrient leaching, especially when species are aggregated into judiciously selected multiple life-form combinations (Ewel and Bigelow, 1996). Such systems yield modest amounts of biomass, but produce large revenues per unit of mass harvested.

A third system, one that has thrived for centuries in the humid tropics, is the diverse, structurally complex home garden, or agroforest, dominated by perennial plants (e.g. Falanruw, 1994; Pinedo-Vásquez and Padoch, 1996; Michon, 1997). Characterised by continuous and diverse yields, these most-complex of agroecosystems provide a broad range of products for home consumption as foods, medicines, and building materials, as well as high-value outputs for market-vanilla beans from Tabasco, durians from Sarawak, allspice from Zanzibar. Such agroforests are ecologically sustainable, but they are labour intensive and require skilful management. Furthermore, they involve a trade-off between high diversity of products and low yield. Structurally and functionally they are probably the closest mimics of natural forest yet attained.

Agroforests and shifting agriculture are often partnered land uses in the same society: the shifting agriculture field provides the main subsistence crop, such as maize, rice, cassava, sorghum, sweet potato, banana, or taro, and the agroforest provides an essential diversity of fruits, herbs, pharmaceuticals, ornamentals, and spices. Sometimes the agroforest is derived successionally from the shifting agriculture fields (Seavoy, 1973; Manner, 1981; Denevan et al., 1984), sometimes the two are intermingled across the landscape, and sometimes the shifting agriculture field is remote from the residence whereas the agroforest is literally the dooryard garden (Alvarez and Banal, 1984; Fernandes et al., 1984).

Given that, on most soils in the wet tropics, continuous grain monocultures are non-sustainable without massive subsidies of pesticides and fertilisers (cf. Sanchez and Salinas, 1981; Sanchez et al., 1982; Sanchez and Benites, 1987), what options are available? Forestry is one possibility, and plantations of export crops is another, but both of these are beyond the economic reach of most smallholders. Agroforests offer a definite possibility, but little is known of their ecological functioning. It was that lack of knowledge, coupled with concern about the modest productivity of many wooded gardens, that motivated a study involving horticultural mimicry of the fast-growing successional vegetation that follows shifting agriculture.

4. Mimicry of successional ecosystems

For five years my co-workers and I constructed plant communities designed to imitate the structure and, we hoped, the functional properties, of the successional communities that blanket the land when agricultural fields are abandoned in the humid tropical lowlands. Successional communities were chosen as models because they offered three traits of potential value to agriculture: (i) high responsiveness (resistance and resilience) to pest attack, (ii) high productivity, and (iii) high retention of soil nutrients.

The design consisted of six replications of each of four treatments:

1. natural successional vegetation (the model system) that developed without investigator intervention following slashing and burning of the existing vegetation (Ewel et al., 1981),
2. the investigators' attempt to build a mimic containing the same mix of life forms that appeared in the successional vegetation, but which consisted of species alien to the site, selected and planted by the scientists (naturally occurring colonists being weeded out),
3. a sequence of four monocultures, each consisting of a species having the same life form that dominated the successional vegetation during a particular interval: maize, *Zea mais* (when the successional vegetation was dominated by herbaceous vegetation); a second planting of maize; cassava, *Manihot esculenta* (when the successional vegetation was dominated by shrubs); and a tree, *Cordia alliodora* (when the successional vegetation was dominated by trees); and
4. a species-enriched treatment, in which vast quantities of seeds were regularly added to natural successional vegetation in an effort to assess invasibility and the functional responses of further enrichment of diversity.

The first three treatments are relevant to this discussion, and it is data from those three treatments (succession, imitation, and monocultures) that are summarised here.

The response variables assessed fell into three broad categories that together define the ecological underpinnings of sustainability: responses to pests, productivity, and soil fertility. The findings have been published in more than 20 articles and book chapters; the following discussion cites some of those results but includes some previously unpublished data as well.

4.1. *Responses to pests*

Over all, the imitation (system 2) fared only moderately worse than the model with respect to leaf tissue lost to herbivorous insects (Ewel et al., 1982; Brown and Ewel, 1987); each lost, on average, 0.2 g m^{-2} ground area d^{-1} (although the imitation did lose a significantly greater proportion of its leaf area). Some species suffered disproportionately high amounts of herbivory, but this did not lead to a community-level reduction in productivity or leaf area. This highlights an extremely important point about diverse communities – their ability to compensate for the loss of individual species. In a diverse system, the resources freed by the loss of one species are taken up by another, thereby maintaining system-wide performance.

One example of a plant-herbivore interaction illustrates a second point, and that is the impact of community structure on biotic interactions in complex systems. There is a general perception that diversity confers protection from herbivores, and indeed there is ample evidence that this is sometimes the case. Nevertheless, the opposite is sometimes true, as exemplified by the consumption of cassava by leaf-cutting ants (*Atta cephalotes*). As anticipated, cassava was heavily attacked by the ants when grown in monoculture (Blanton and Ewel, 1985; Brown and Ewel, 1987), but we did not anticipate that it would be even more heavily attacked when grown as part of the diverse mixture of species (more than 100 per plot) in the imitation. Thus, just as structural complexity can confer associational resistance to herbivores, so too can it confer associational susceptibility. In this case, the ants may have responded to the shaded environment of the imitation, to the complex structure of the imitation that may have facilitated their mobility (using other plants as trellises, for example), or to something about the imitation that made it freer of predators. The main point is that diversity cannot be counted upon to afford protection from herbivores, and sometimes it can have the opposite affect.

4.2. *Productivity*

Net primary productivity (Figure 3) was estimated by determining net biomass increments at frequent intervals by cutting subplots of the vegetation and by adding the rate of biomass death (measured as rates of litter fall, plus death of tissue that was not abscised, plus herbivory) to those increments. Two findings merit attention here.

First, the imitation was not as productive as the successional vegetation. This was probably due, in large part, to the horticultural complexity of building and maintaining such complex communities. The natural succession (the model) was always ahead of the mimic, and this was true for floristic complexity and canopy development, as well as productivity.

Second, the short-lived, herbaceous crop, maize, contributed the two extremes of productivity (Figure 3e), once being the highest (Figure 3a) and once being the lowest (Figure 3b). Is it any wonder that grain monocultures are an attractive farming venture? By the same token, it should not be any surprise that their adoption is fraught with risk.

4.3. *Soil fertility*

Changes in fertility were assessed through frequent measurements of essential elements and organic matter (Ewel et al., 1991; Raich et al., 1985), and the loss process itself was investigated through studies of leaching (Russell and Ewel, 1985) and roots (Berish, 1982; Berish and Ewel, 1988). The two main trends had been predicted beforehand: (a) the monocultures were (with one important exception, described below) much less retentive of nutrients than were the more species-rich treatments, and (b) both the natural succession and the imitation of succession were very retentive of nutrients, the model being only moderately better than the mimic.

The exception (referred to above) was the striking increase in nutrient retention by the tree monoculture over a three-year period (Figure 4). During its first year, the *Cordia* plantation was just as vulnerable to nutrient leaching as

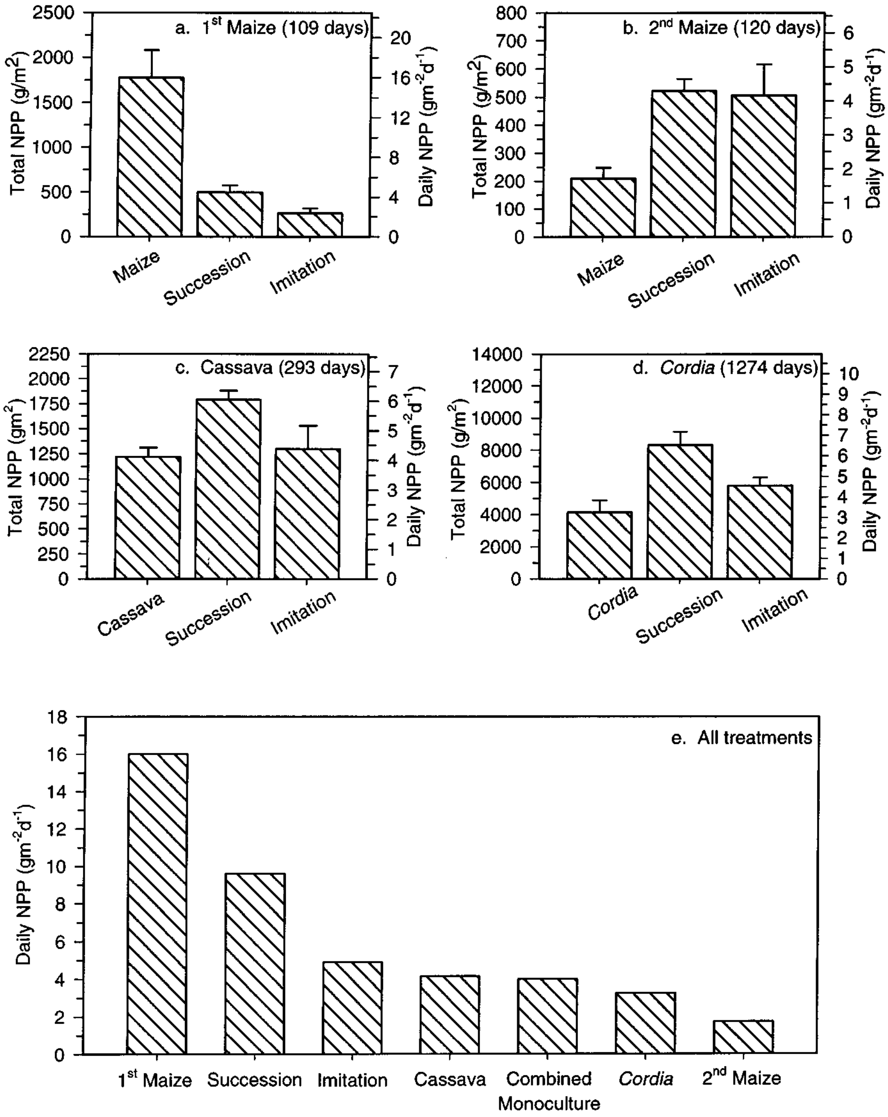

Figure 3. Above-ground net primary productivity of six ecosystems at La Selva, Costa Rica. Two of these, succession and imitation, were very species-rich, and four were monocultures. The smaller panels compare the three treatments over the same time intervals (e.g. a. compares the first maize with succession and imitation, for the 109 days when the monoculture was planted to the first maize crop), and the larger panel (e) compares productivity among all treatments, each for the time it occupied the site: five years for succession and imitation, and shorter periods for each of the four monocultures.

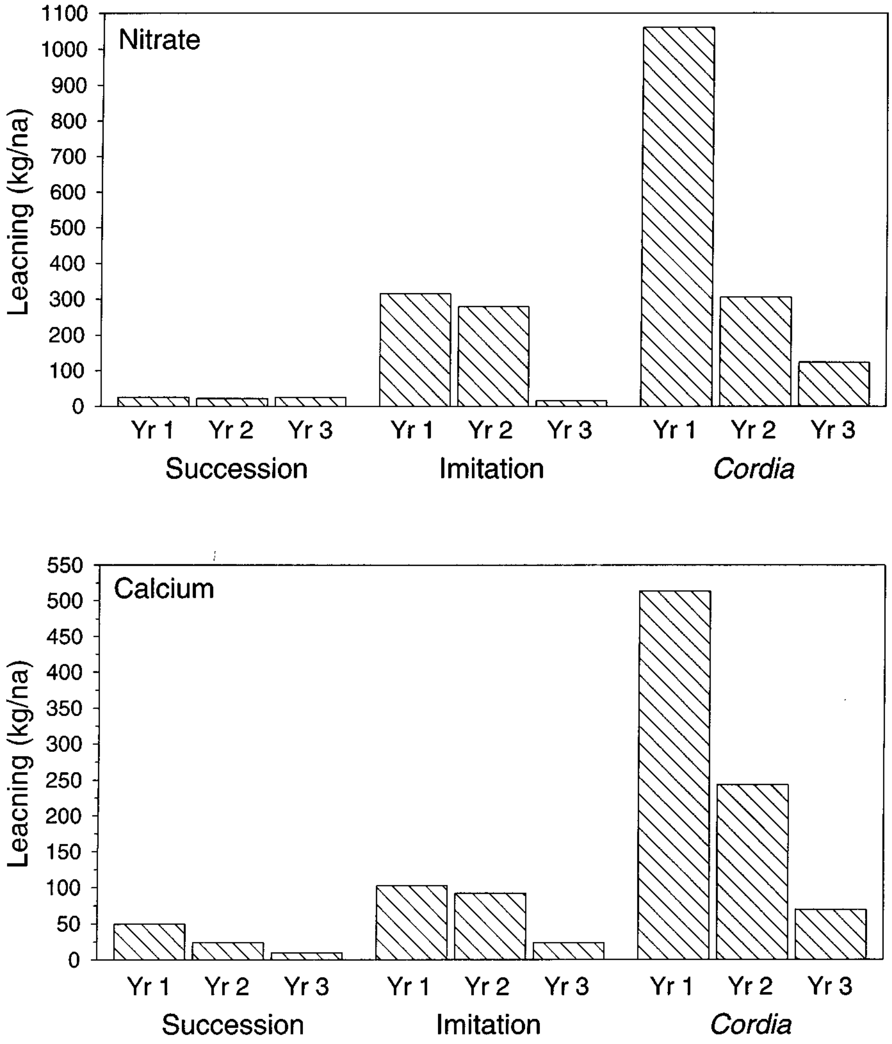

Figure 4. Annual leaching losses of nitrate (upper) and calcium (lower) from species-rich ecosystems and a monoculture of *Cordia alliodora* trees over a three-year period at La Selva, Costa Rica. Note the dramatic improvement in nutrient retention in the monoculture over the course of the three years.

the other monocultures had been; the second year, it improved substantially; and by the third year, it held nutrients almost as tightly as did the succession and its imitation. Here was a three-year-old, single-species plant community that was extremely effective at retaining nutrients – almost as effective as neighbouring communities containing more than 100 species each.

Two factors account for this remarkable capability of the tree monoculture to prevent nutrient leaching in a high-rainfall environment that loses about

1500 mm of water per annum to deep infiltration. First, it happened to be a very successful monoculture. The tree was well matched to the site; it grew quickly, and it was not heavily attacked by herbivores or disease. Had the *Cordia* trees performed poorly overall, or had patches of it succumbed to root pathogens, for example, there is no doubt that it would have proven to be every bit as susceptible to nutrient leaching as had the shorter-lived monocultures. Second, continuity of occupancy led to the development of an extensive, deep network of fine roots that effectively captured nutrients from soil solution before they could be leached (Figure 5). Longevity, as much as diversity (e.g. see Hobbs and O'Connor, this volume), is the key to nutrient retention in the humid tropics. It is this same difference in internal processes that marks the difference between the perennial native grasses of the North American prairies and their functionally deficient imitation by annual grain crops (Jackson, 1985; Soule and Piper, 1992).

5. Overview and conclusions

5.1. *Where to invest*

Blinded by past agricultural successes, society placidly ignores the agricultural crisis soon to be faced, when fossil energy becomes priced in proportion to the leverage it exerts in our global economy. No longer will we be able

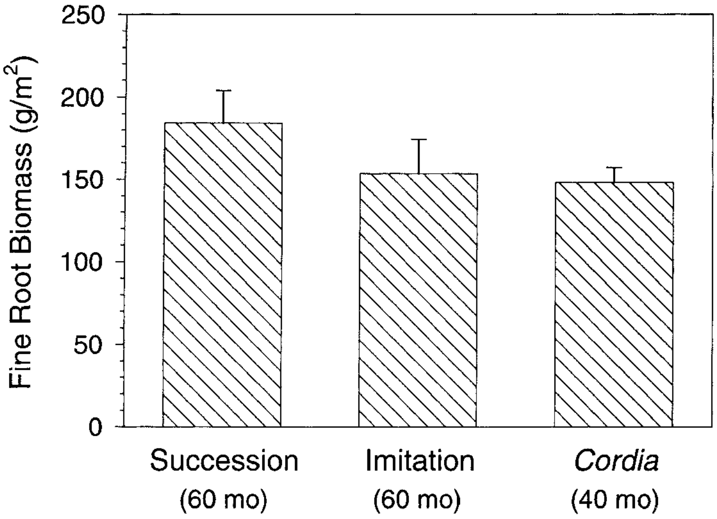

Figure 5. Comparative biomass of absorptive roots in two species-rich ecosystems (at age 5 y) and a monoculture of *Cordia alliodora* (at age 3.3 y) at La Selva, Costa Rica. It was this rapid development of a permanent network of fine roots that led to excellent nutrient retention by the tree monoculture (Figure 4).

to afford to move agricultural systems from one part of the globe to another without first giving due consideration to their ecological fit. Where can remaining reserves of fossil energy best be invested in intensive, high-technology agriculture?

Such investment makes sense in three environments. One is on reasonably fertile soils within that set of life zones where the annual water balance is neither too dry nor too wet, i.e. the very environments where agriculture has enjoyed a long history of success. To understand why this is the case, view agriculture as the human-mediated conversion of solar energy (which is dilute and abundant) to chemical energy. Investments of fossil energy merely facilitate that conversion. Greatest leverage of fossil-energy infusions is to be achieved where the conversion is least constrained by either abiotic or biotic forces because the inputs can then be focused on the conversion process itself rather than on alleviation of constraints such as water shortages or pests.

There are two other useful investments to be made, both involving displacements along the environmental gradient (Figure 1b), from either end toward the centre. Consider the example of flooded rice, or *padi*, in the humid tropics. In an environment where biotic forces might otherwise make a crop monoculture a poor competitor, flooding has the effect of increasing abiotic stress, i.e. inducing a shift from the right-hand side of the axis toward the centre. Furthermore, the *padi* system is often employed on recent alluvium and on young volcanic soils, where it concentrates water and nutrients (save nitrogen, accrued through biological fixation) from a much larger landscape. The result is high yields (and high human population densities) that, in some parts of Asia, have been sustained for centuries without significant modifications to the technology. Modest infusions of fossil-energy (in the form of high yielding varieties, nitrogen fertiliser, appropriately scaled machinery, etc.) into such systems have paid off handsomely in some instances, but in others they have led to disaster (Brown, 1970; Paddock, 1970; Wilkes and Wilkes, 1972; Harris, 1972, 1973).

Shifts in the other direction, i.e. from the left-hand, or environmentally harsh, side toward the centre of the environmental gradient (Figure 1b), are commonly achieved through intensive management of soil fertility and water supplies. A classic example from the temperate zone is the Central Valley of California, USA, which has a dry (thus low-pest, high solar radiation) climate, but where surrounding mountains provide water for irrigation. Although agricultural economists (and farmers) calculate Central Valley yields on the basis of land area cultivated, would not a more accurate assessment include the vast area of mountains that scour water out of the westerly winds sweeping inland from the ocean? It is those forested mountains that make agriculture possible in this semiarid valley.

Most other environments probably do not warrant such intensive investment. The low-temperature life zones, for example, offer little hope for agriculture, subsidised or not. The same is true for most areas in the wet tropics lowlands where, even when soil fertility constraints are alleviated through fertiliser applications, insects, diseases, and weeds overwhelm attempts at simplification. Except when value-inflated crops such as bananas and illegal drugs are grown for export, the massive inputs required to achieve biological simplification in the wet tropics are seldom warranted: heroin, cocaine, and marijuana may well become scarce in the international marketplace when petroleum is priced commensurate with its true value.

5.2. *Roles for mimicry*

It is far easier to mimic, or employ natural substitutes for, specific ecosystem processes than to try to duplicate all the complexity of nature. This strategy is likely to have potential applicability in many situations: deep-rooted, non-indigenous plants to pump groundwater in southwestern Australia (Lefroy and Stirzaker, this volume) and perennial grasses to protect soil in the Midwestern USA (Jackson, 1985) are examples. Herbivore resistance, effective display of light-capturing foliage, and symbiotic links with beneficial microorganisms can be, and have been, achieved by agronomists and crop breeders; they can also be achieved through effective mimicry – process by process – of natural ecosystems.

The other, more complex, approach is to design new land use systems using natural ecosystems which have withstood the test of evolutionary time as models. Such mimics, like their models, can be productive, pest resistant, and conservative of nutrients. But they are not without problems and risk; they can also be patchy, selectively attacked, and horticulturally complex (Ewel, 1986). Furthermore, they are sometimes accompanied by interesting side effects. For example, to achieve highest yields of many crops requires high levels of fertiliser, and those dosages tend to switch off microbially mediated input and cycling activities such as nodules, mycorrhizae, and proteoid roots. When imitating nature, therefore, it is important to reduce nutrient inputs and in the process be prepared to accept lesser – but biologically sustainable – yields. As one component within a landscape mosaic that combines intensive cultivation of short-lived crops, grazing and browsing ruminants, silviculture, and forested reservoirs for genes and water, diverse agroforests and prairie mimics can play an essential role – perhaps not a substitute for other modes of agriculture, but a complement to them.

Can these mimics of natural ecosystems provide the yields we have come to expect from modern agriculture? Not yet, and perhaps never; there are two reasons why that is the case. First, only a small fraction of large stature, perennial plants is harvested from the forest mimic; the bulk of the biomass is what sustains the protective structure of the ecosystem, and the more that is harvested the more we deviate from nature’s model. Human removal of latex and large-seeded fruits that have evolved to be dispersed by animals mean that only a small fraction of the agroforest’s biomass is removed i.e. it has a harvest index of 10 per cent or less. This contrasts sharply with the high harvest indices (approaching 50 per cent) of the world’s big-yielding crops, mostly composed of smaller seeds (primarily grasses) and below-ground storage organs. An old, diverse agroforest might have a high gross primary productivity, but much of that gross production is consumed by respiration that sustains the huge metabolic investment in structure.

The second reason why complex, perennial systems may be destined to lower yield concerns the presumed evolutionary trade-off between reproduction and permanence. Most plant biologists would contend that allocation of photosynthate involves mutually counteractive investment alternatives, with carbon allocated to stature and perennial organs being unavailable for reproduction (i.e. for the seeds we eat) and *vice versa*. Nonetheless, there are some encouraging preliminary results to the contrary; Jackson and Dewald (1994), working with a native North American grass, showed that perennialness (the property that sustains the ecosystem in the long run) and seed set (the part that sustains the farmer in the short run) were not mutually exclusive trade-offs. This exciting finding opens the door to the prospect of perennial grass agriculture, but whether the example studied has general applicability to other species remains to be tested.

Tropical forests and temperate grasslands are not the only appropriate models by any means. For example, a search might be directed profitably toward the permanent culture of perennial plants that produce large storage organs. There are examples of such systems, though they are not widespread. For example, some Micronesians harvest only a modest portion of the mass of *Cyrtosperma* taro tubers at one time, and some indigenous peoples in South America do the same with cassava; the tuber in the ground is food in the larder. This contrasts sharply with modern production of potatoes (a short-lived perennial forced into an annual growth mode as part of its domestication), whereby the entire agroecosystem is uprooted at harvest, and the larder is a fossil-energy-cooled warehouse.

At the level of the individual species or process, mimicry of form or function makes good ecological sense, for morphologies and processes are shaped by evolution: as such, they are proven survivors in the environment that shaped them. Mimicry of the entire complexity of natural ecosystems is more problematic, but although it may be ill-suited to some situations, it is certain to be well-suited to others. The increased willingness of some modern agricultural scientists to contend with biotic complexity is especially encouraging. Witness, for example, the international boom in integrated pest management. But current efforts are insufficient, and we are not moving forward fast enough. It behoves scientists to anticipate the near-future needs of agriculture through improved understanding of how complex systems – both models and mimics – work. Agricultural ecosystems that mimic the structural and functional complexity of nature have the potential to play a crucial role for all societies. They already do so in many developing, tropical countries, and it may be those of us who have been spoiled by an excess of fossil-energy riches that are going to need them most.

6. Acknowledgements

The ideas presented in this paper were developed over a period of many years, primarily in conjunction with research supported by the U.S. National Science Foundation, most recently under award DEB 9318403. I thank the following for very helpful suggestions that improved the manuscript: Becky Brown, Ankila Hiremath, Ted Lefroy, Henry Nix, Chin Ong, and John Pate. I thank Becky Brown and Cory Berish for two years of data on productivity and nutrient concentrations in leachate, respectively, and Larry Battoe for calculation of leaching losses. Tom Cole produced the figures, and Kris Kogan compiled and formatted the manuscript.

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