Biological Invasions: a Global Perspective
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CHAPTER 11

Ecosystem-level Processes and the Consequences of Biological Invasions

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11.1 INTRODUCTION

Numerous studies demonstrate that biological invasions by exotic species can alter the population dynamics and community structure of native ecosystems (Elton, 1958; Mooney and Drake, 1986). However, considerably less information is available for the ecosystem-level consequences of biological invasions. In this paper, we define ecosystem-level changes as those that alter the fluxes of water and energy or the cycling and loss of material. Commonly studied characteristics such as primary productivity, decomposition, secondary production, mineral nutrient availability, and hydrological balances would be included in this definition, as would the type and frequency of dsiturbance. Changes in these properties can alter the conditions of life for all of the organisms in an ecosystem.

Our emphasis on ecoystem-level characteristics of invasions is based in part on the need to evaluate the potential impacts of invasions on ecosystems from the point of view of managing or mitigating those effects. However, we believe that this emphasis also addresses fundamental concerns in ecosystem-level ecology. For example, there is a considerable debate on the functional significance of individual species in ecosystems. We believe that a demonstration of widespread ecosystem-level consequences of biological invasions would constitute an explicit demonstration that species make a difference on the ecosystem level, and would further suggest ways in which to integrate the often disparate approaches of population biology and ecosystem-level ecology.

Limited research on ecosystem-level consequences of biological invasions has been carried out, and some of the generalizations that can be drawn from that work are summarized by Vitousek (1986). Exotic animals, especially mammals, clearly alter ecosystems in many areas (see Batcheler, 1983; Singer *et al.*, 1984). Determining the ecosystem-level consequences of invasions by plants is more difficult, although some clear examples of major effects are well documented (cf. Mueller-Dombois, 1973; Thomas, 1981; Neill, 1983; Halvorson, in press). In part, this distinction between the ecosystem-level effects of invading plants and animals probably reflects a real difference—most exotic animals have a larger effect on native ecosystems than do most exotic plants (Vitousek, 1986).

One reason for this difference may be that invading plants most often occupy disturbed habitats, especially in sites altered by humans. It can be difficult to separate the ecosystem-level effects of biological invasions from those of the disturbance that created the invaded habitats. The consequences of biological invasions in disturbed sites and secondary succession represent at once the most difficult and the most important area of research. It is here that the effects of invasions are most easily confounded with those of the massive, prolonged, or novel disturbances which often form the invaded habitat, here that economic effects on humans are most important, and here that changes in ecosystem-level characteristics are most rapid even in the absence of biological invasions.

In this chapter, we will briefly review the ecosystem-level consequences of biological invasions into intact native ecosystems and into primary succession. We will then develop a detailed case study of the effects of biological invasion into secondary successions initiated by shifting cultivation.

11.2 INVASIONS OF INTACT ECOSYSTEMS

The generalization that biological invasions are primarily successful in disturbed habitats (Allan, 1936; Egler, 1942) is well supported as it applies to plants, but exotic animals frequently invade intact native ecosystems and cause significant changes in ecosystem-level properties of the areas invaded. Pigs probably provide the best example. They invade intact forest and savanna ecosystems in 12 states within the *United States* (Wood and Barrett, 1979), including the most diverse forest area in North America, the Great Smoky Mountains National Park in North Carolina and Tennessee. Wherever they are abundant, they alter soil structure, soil nutrient availability, and even nutrient losses in streamwater (Singer *et al.*, 1984; Vitousek, 1986).

Many other examples of the effects of exotic animals have been documented. Goats remove vegetative cover and cause increased soil erosion on many oceanic islands (see Stone *et al.*, in press). Even exotic insects are likely to be important. The ant *Pheidole megacephala* totally changed the lowland invertebrate fauna (including many of the pollinators and organisms on the decomposer food chain) of Hawaii about 100 years ago, and the Argentinian ant (*Iridomyrmex humilis*) is now doing so at higher elevations (Medeiros *et al.*, 1986). Similar processes are important in the South African fynbos (Bond and Slingsby, 1984). Ecosystem-level effects of these invasions have not yet been studied.

Invasions by exotic plants into intact native ecosystems are less common, but they do occur. For example, Eurasian phreatophytes of the genus *Tamarix* invade both natural water courses and reservoir margins in the arid southwestern United States (Robinson, 1969). Their transpiration is much more rapid than that of native communities, and they can convert marshes which support surface water during part of the year into wholly dry areas. In one case, removal of

Tamarix led to regeneration of a marsh (Neill, 1983). The floating aquatic plant *Salvinia molesta* can change parts of tropical river systems into thick masses of live and dead plant material. Exotic grasses in seasonal montane forests or shrublands can increase fire frequency or intensity, thereby altering ecosystems in a way that favors increased dominance by the grasses (Parsons, 1972; Smith, 1985; Christensen and Burrows, 1986). Finally, exotic trees can invade certain native shrublands and woodlands (Chilvers and Burdon, 1983, Macdonald *et al.*, this volume), thereby altering rates of productivity and nutrient circulation.

Exotic plants can also interact with exotic animals in ways that facilitate invasions of disturbed habitats. Invasions of seemingly intact mature ecosystems by exotic plants often take place in close association with the activities of exotic animals (Merlin and Juvik, in press). For example, guavas (Psidium *guajava* and *Psidium cattleianum*) are common and serious invaders of oceanic islands worldwide. Their dispersal and success are closely tied to the movements and soil-disturbing activities of cattle and pigs. Similarly, feral pigs consume and disperse the exotic vine *Passiflora mollisima* in Hawaii, and then deposit the seeds within mounds of organic fertilizer in seedbeds cleared by the pigs' rooting activity. *Passiflora mollisima* then apparently affects patterns of mineral cycling in montane Hawaiian rainforests (Scowcroft, 1986).

Overall, detailed studies of the population biology and plant–animal interactions of that subset of invaders able to colonize intact native ecosystems would be most useful. To the extent that these species are able to alter ecosystem-level characteristics, they are likely to have impacts disproportionate to their numbers.

11.3 INVASIONS OF PRIMARY SUCCESSION

Primary succession involves the development of ecosystems on areas that are free of the influence of previous biotic communities (Clements, 1916). Primary succession can be initiated by glacial recession, eolian activity, river meanders, or vocanic activity; some human activities (such as strip mining) reproduce it quite closely.

The effects of biological invasions upon primary succession are relatively little-studied, in large part because primary succession does not occur over large areas at present. It is slower and often much simpler (fewer species in the early stages, more predictable patterns of soil-plant interaction) than secondary succession, however (Vitousek and Walker, 1987), so it may lend itself better to studies of the effects of biological invasions. For example, nitrogen availability is generally low early in primary succession (Walker and Syers, 1976): Robertson and Vitousek, 1981); Vitousek *et al.*, 1983). The exotic symbiotic nitrogen fixer *Myrica faya* is now invading young volcanic substrates in Hawaii and substantially altering nitrogen availability there (Vitousek *et al.*, 1987); it is likely to alter the course of soil development substantially. Australian species of *Acacia* may have a similar effect in South Africa (MacDonald *et al.*, this volume).

Casuarina equisetiifolia invades beaches in south Florida and in many oceanic islands. Its effects on nitrogen availability have been not studied, but it significantly alters the form of shorelines and patterns of beach erosion (Macdonald *et al*., this volume, LaRosa, in press).

11.4 INVASIONS OF SECONDARY SUCCESSION

Exotic species are prominent in disturbed sites throughout the world, on continents as well as islands and in the tropics as well as the temperate zone. The association between disturbed sites and invaders may be due to greater invasiveness on the part of successional species, or it may simply reflect the association between humans and disturbance which gives early successional species greater opportunities to invade. In either case, it is often difficult or impossible to determine how invaders have altered secondary succession because it is difficult to know what secondary succession was like before humans altered disturbance regimes and brought in exotic species.

Nevertheless, there are several documented cases in which biological invaders have altered ecosystem processes during secondary succession. The phenology of exotic *Andropogon* in some areas of Hawaii does not match the seasonal distribution of rainfall, and in consequence boggy conditions develop in invaded sites (Mueller-Dombois, 1973). The ice-plant *Mesembryanthemum crystallinum* invades degraded pastures in California and Australia (Vivrette and Muller, 1977; Kloot, 1983); once established it redistributes salt from throughout the rooting zone onto the soil surface, thereby interfering with the growth of other species and eventually increasing soil erosion (Halvorson, in press). In fact, invaders may alter ecosystem processes in secondary succession wherever they can obtain resources the natives cannot, or wherever they differ substantially from the natives in resource use efficiency (Vitousek, 1986)—but it is difficult to document the effects of many invasions for the reasons outlined above.

One type of disturbance which lends itself well to studies of the effects of invasion on secondary succession is shifting cultivation. It is practiced over large areas of the tropics, and in many of these areas it has been the major form of disturbance for millenia. The consequences of biological invasions in these relatively well-defined successional systems are therefore more understandable than is true in systems with novel disturbance regimes.

11.5 INVASIONS AND SHIFTING CULTIVATION—A CASE STUDY

In the humid tropics of Asia, Africa, and Latin America, shifting agriculture is a major land use and an important, frequent perturbation to forest ecosystems. Shifting agriculture involves clearing and burning forest vegetation, cropping for one to several years, and then abandoning the land for several to many years before another cycle of clearing and cultivation is initiated (Nye and Greenland, 1960; Walters, 1971; Ruthenberg, 1976; Ramakrishnan, 1985a). Today, exotic species along with natives are important components of early successional communities in the fallow phase of shifting cultivation in many areas. This section analyzes the consequences of invasion by exotic species, using the shifting agriculture systems in north eastern India as a case study.

11.5.1 Shifting agriculture and secondary succession

Slash and burn agriculture, locally known as 'jhum,' is extensively practiced by the tribal populations of the hill areas in the northeastern region of India. This practice consists of cutting down the vegetation at various stages of development on the hill slopes, allowing the slash to dry for a few months, burning it, and then cropping for 1 or 2 years. The average size of a plot varies from 1 to 2.5 hectares. The fallow period before the land is again cultivated is now short, around 4 or 5 years, but in the traditional system when population pressure was not so great the cycle was as long as 20–30 years (Ramakrishnan *et al.*, 1981). Longer cycles are occasionally encountered at present in more remote areas.

The soil of the region is highly leached because of average annual rainfall of 200 cm or more. The climate is seasonal, supporting a mixed subtropical humid forest at lower elevations (Singh and Ramakrishnan, 1982); high elevation sites have cooler climates with subtropical montane forests (Boojh and Ramakrishnan, 1983). Most of the rainfall occurs during the monsoon period, which is followed by a dry winter and a brief warm summer.

When a forest is cleared for cultivation, not only is its original vegetation destroyed, but the site is subject to continuing perturbations owing to fire, the introduction of crop species, weeding, hoeing, and other disturbances to the soil attendant on harvesting. These result in a progressive reduction in species diversity. Hence, early successional stages following the abandonment of cultivation contain few species, and the number of species increases gradually as secondary succession proceeds.

The pattern of secondary succession and the rapidity with which a forest community develops depend upon the degree of destruction of the prefarming vegetation and of its propagules in the soil. During the first few years of succession, when weeds of cultivated sites predominate, there is considerable variation in community composition according to the length of the agricultural cycle, weeding intensity, and the availability of seeds. For example, at least four different types of weed-dominated communities were observed at lower elevations of Meghalaya in northeast India (Toky and Ramakrishnan, 1983). Either the exotic species *Eupatorium odoratum* or *Mikania micrantha*, or the natives *Imperata cylindrica* or *Saccharum spontaneum* predominate under short agricultural cycles. At higher elevations of Meghalaya, however, the important exotic weed is *Eupatorium adenophorum*, which occurs with many natives such as *Imperata cylindrica* and *Pteridium aquilinum* (Mishra and Ramakrishnan, 1983c).

If the agricultural cycle is a short one of 4 to 5 years and is imposed continuously at the same site, succession is arrested at the weed stage (Toky and Ramakrishnan, 1983); Saxena and Ramakrishnan, 1984a). If the cycle is longer, however, vegetation changes rapidly from weed colonizers to bamboo (*Dendrocalamus hamiltonii*) and other shade-intolerant tree species at lower elevations. Bamboo itself is eliminated after about 25 years. A 50-year-old forest at the lower-elevation study site had broad-leaved tree species such as *Schima wallichii, Castanopsis indica, Shorea robusta, Millusa roxburghiana*, and *Artocarpus chaplasha* (Singh and Ramakrishnan, 1982). At higher elevations of Meghalaya the weeds are replaced by rapidly regenerating pine trees (*Pinus kesiya*) along with broad-leaved trees such as *Schima wallichii* (Mishra and Ramakrishnan, 1983c). A mature forest in the region would be a mixed broad-leaved forest dominated by species of *Quercus* and *Castanopsis*, such as now exists only in sacred groves (Boojh and Ramakrishnan, 1983).

11.5.2 Weed potential under shifting agriculture

As observed elsewhere, the species that form early successional communities are commonly found as weeds in agricultural plotts (Woodwell and Whittaker, 1968;

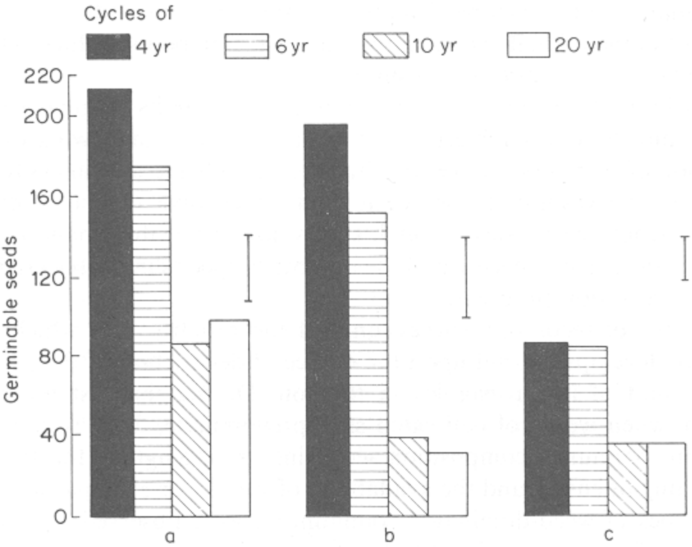

Figure 11.1. Germinable soil seed population of herbaceous species under different jhum cycles. Vertical lines represent least significant difference ($P = 0.01$): (A) just before slashing and burning; (B) uncropped sites; (C) cropped sites (from Saxena and Ramakrishnan, 1984a). Reproduced by permission of Blackwell Scientific Publications Ltd.

Perozzi and Bazzaz, 1978). Continuous imposition of short agricultural cycles has facilitated the establishment of herbaceous weeds characterized by high reproductive potentials, in contrast to later successional species such as *Oplismenus compositus*, *Centotheca lappacea*, and *Oryza granulata* with low reproductive potential.

The high reproductive potential of the early successional species leads to a high rate of propagule production during the fallow phase following cultivation. Also, short fallow cycles can only support a low intensity burn following land clearing, and short cycles may also be associated with comparatively lower losses of viability in buried seed banks. Overall, these processes cause significant differences in the germinable soil seed population under different agricultural cycles (Figure 11.1).

11.6 ADAPTIVE STRATEGIES OF NATIVES VERSUS EXOTICS: SYSTEM-LEVEL CONSEQUENCES

Several interacting factors contribute to invasion by exotic species and to the success of the exotics. Obviously, climatic and edaphic similarity between the original habitat of the exotics and their new habitat is one important factor (Holdgate, 1986). Humid tropical areas of Asia and Africa with highly leached soils are similar to the Latin American home of species such as *Eupatorium* spp. and *Mikania micrantha*, enabling them to invade and colonize appropriate sites on these two continents (Bennett and Rao, 1970; Nye and Greenland, 1960; Zinke *et al.*, 1978; Toky and Ramakrishnan, 1983; Mishra and Ramakrishnan, 1983c).

Under a shifting agricultural system, the initial perturbation by clearing and burning is further accentuated by cropping operations such as weeding and crop harvest (Toky and Ramakrishnan, 1981a; Mishra and Ramakrishnan, 1981). Tremendous losses of sediment and nutrients from steep slopes occur through runoff and infiltration water during the cropping phase (Toky and Ramakrishnan, 1981b; Mishra and Ramakrishnan, 1983a). Rapid uptake and reproduction which make efficient use of nutrients from these highly heterogeneous soils are critical to the establishment of successional vegetation, especially under the intense rain of the monsoon climate (Ramakrishnan, 1985b).

The exotic species which occupy sites after slash and burn have two sets of strategies which differ from those of early successional natives: (i) establishment largely through seeds (non-sprouting regeneration strategy) versus establishment largely through below-ground vegetative organs (sprouting strategy), and (ii) C_3 versus C_4 photosynthetic pathways.

11.6.1 Allocation and establishment

The non-sprouting regeneration strategy has been suggested to be successful under frequent perturbations through fire, whereas sprouting may be effective only under certain fire regimes (Keeley, 1981; Gill, 1975). Similar patterns have also been observed for shifting agriculture.

Exotics such as *Eupatorium* spp. have a high seed production potential (Kushwaha *et al.*, 1981; Ramakrishnan and Mishra, 1981) with a maximum seed production in a 3-year-old fallow. The survival of a species such as *Eupatorium odoratum* is favored by its rapid growth rate, rapid net assimilation, and allocation of many resources to the shoot system (Table 11.1). On the other hand, the slow growth of natives such as *Imperata cylindrica* and *Thysanolaena maxima* may result from initial allocation of energy and nutrients to below-ground parts, later followed by translocation of these resources for shoot growth during the early stages of regrowth (Figure 11.2).

Because a larger allocation of resources is made to below-ground organs in the sprouting species such as *Imperata cylindrica* and *Thysanolaena maxima*, they have less to allocate to sexual reproduction compared to a non-sprouting species (Keeley and Keeley, 1977; Saxena and Ramakrishnan, 1983). Thus, *Thysanolaena maxima* had much lower allocation of biomass and most nutrients to reproduction than *Eupatorium odoratum*. Both, however, allocated proportionately more nitrogen and phosphorus to reproduction in comparison with their allocation of energy. *Imperata cylindrica* did not flower in the first post-fire year. Clipping and burning promoted flowering (Kushwaha *et al.*, 1983), an observation also made by Schlippe (1956) for the effects of fire on this species. Gill (1975) reported similar observations on a number of successional shrubs in Australia.

While the success of exotic species such as *Eupatorium odoratum* and *E. adenophorum* depends upon heavy seed production (Kushwaha *et al.*, 1981; Ramakrishnan *et al.*, 1981), *Mikania micrantha* is an exotic that combines an effective seed-based reproduction with clonal propagation. *Mikania micrantha* also illustrates elegantly the importance of frequent perturbation such as fire (Swamy, 1986). This species responded to burning with increased birth and death

Table 11.1. Mean values ($\pm$ standard error of mean) of growth functions for four different species

Species	Growth function		
	Relative growth rate ($\mathrm{mg\,mg^{-1}\,day^{-1}}$)	Net assimilation rate ($\mathrm{mg(cm^2)^{-1}\,day^{-1}}$)	Leaf area ratio ($\mathrm{cm^2\,mg^{-1}}$)
Eupatorium odoratum	0.036 ± 0.015	0.302 ± 0.115	0.122 ± 0.031
Grewia elastica	0.008 ± 0.003	0.065 ± 0.014	0.121 ± 0.040
Imperata cylindrica	0.012 ± 0.004	0.133 ± 0.043	0.089 ± 0.016
Thysanolaena maxima	0.010 ± 0.004	0.108 ± 0.020	0.093 ± 0.018

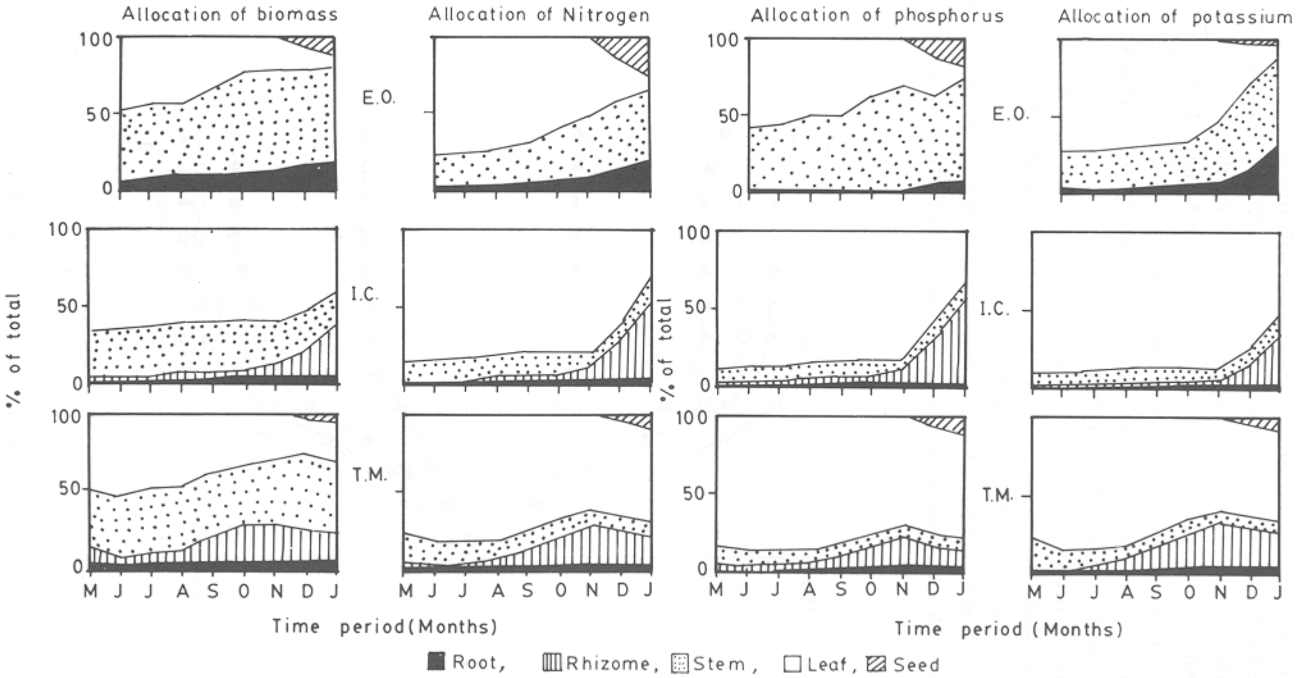

Figure 11.2. Allocation of biomass and nutrients to various compartments (expressed as a percentage of the total pool) during the growth of different species. E. O., *Eupatorium odoratum*; I.C., *Imperata cylindrica*; T.M., *Thysanolaena maxima*. (From Saxena and Ramakrishnan, 1983, reproduced by permission of the National Research Council of Canada)

rates of the total (seedling plus ramet population), more markedly so in 2-year-old and 4-year-old than in older fallows (Figure 11.3). Seedling recruitment in the younger fallows occurred only in burned sites, while seedling recruitment was observed in both burned and unburned portions of an 8-year-old site. However, none of the seedlings recruited in the unburned sites established rosettes in the following year. Allocation of biomass to seeds increased in burned sites of the older fallows, while it declined in unburned sites.

The response to fire by *Mikania micrantha* was most striking with respect to nutrient uptake and use (Table 11.2). In burned sites, the efficiency of nutrient uptake was generally higher than in unburned plots, and this difference increased with fallow age. Soil fertility status always increased after the burn, to a greater extent in older fallows because of increased fuel loads there. Consequently, the

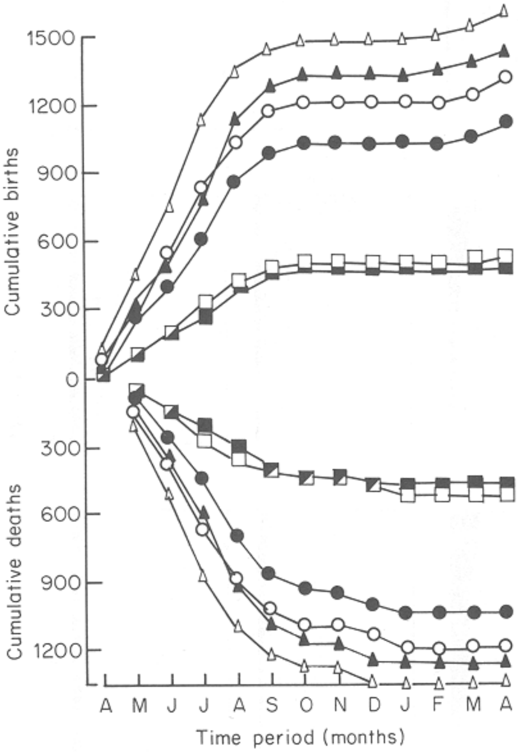

Figure 11.3. Cumulative births and deaths of *Mikania micrantha* populations in 2-year (circles), 4-year (triangles), and 8-year (squares) old fallows, after shifting agriculture. Burnt sites, closed symbols; unburnt sites, open symbols (from Swamy, 1986)

Table 11.2. Elemental uptake (mg nutrient absorbed per g root biomass) and use (mg dry matter produced per mg nutrient absorbed) efficiencies of *Mikania micrantha* in burnt and unburnt successional fallow plots after shifting agriculture. Values in parentheses are for nutrient use efficiencies (from Swamy, 1986)

Elemental efficiencies	Fallow age	Burnt	Unburnt
Nitrogen	2	108.1 (78.1)	85.2 (98.3)
	4	120.7 (75.6)	92.7 (100.4)
	8	128.0 (69.3)	45.1 (175.0)
LSD ($P = 0.05$)		10.6 (7.6)	7.3 (7.6)
Phosphorus			
	2	11.5 (699.3)	9.5 (895.7)
	4	13.6 (672.1)	9.3 (1005.8)
	8	14.5 (583.4)	4.4 (2029.9)
LSD ($P = 0.05$)		1.3 (24.9)	1.2 (157.0)
Potassium	2	133.8 (60.3)	114.6 (73.7)
	4	154.8 (56.5)	120.9 (77.1)
	8	166.1 (50.7)	81.2 (97.9)
LSD ($P = 0.05$)		14.6 (6.0)	11.0 (5.2)

LSD = least significant difference.

nutrient use efficiency in burned plots was generally lower than in unburned plots. Fire is an important process at various stages in the life cycle of this species, and the species itself is closely adapted to a ruderal environment subject to frequent perturbation (Swamy, 1986).

11.6.2 C_3/C_4 strategy and microdistribution

The C_3 species with large biomass contributions to secondary successional communities are all exotics, including the *Eupatorium* species and *Mikania* *micrantha*. On the otrher hand, all of the important native species, including *Imperata cyclindrica, Saccharum* spp., *Panicum* spp., and *Thysanolaena maxima*, have the C_4 photosynthetic pathway. Several less abundant C_3 species occur among the natives.

The biomass of C_3 species is higher than that of C_4 species in early succession (Saxena and Ramakrishnan, 1984b). The rapid growth of a species such as *Eupatorium odoratum* (Figure 11.4) is achieved partly through a larger light interception surface, and partly through its allocation of resources to the shoot system. Similar results were obtained for *Mikania micrantha* (Swamy, 1986). These results demonstrate that C_4 species are not always more productive than C_3 species (Caldwell, 1977); the productive potential of plants depends on factors in addition to photosynthetic rate per unit of leaf area (Black *et al*., 1969; Black, 1971).

Continuous imposition of short agricultural cycles of 4 to 6 years results in early successional communities monopolized by exotic C_3 species (Saxena and Ramakrishnan, 1984b). In contrast, long agricultural cycles impoverish the soil seed bank owing to a more intense fire effect (Saxena and Ramakrishnan, 1984a),

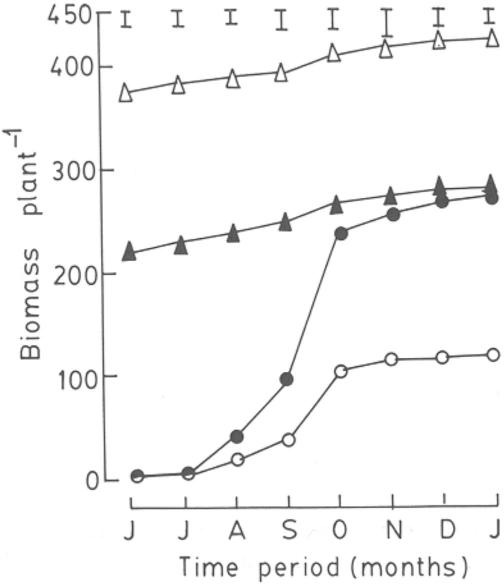

Figure 11.4. Growth curves of *Eupatorium odoratum* in different fallow fields. Recent fallow, after the burn and uncropped (●); soon after cropping (○); 2-year old (▲); 6-year old (△). Vertical bars represent LSD ($P = 0.05$) (from Saxena and Ramakrishnan, 1984a, reproduced by permission of Blackwell Scientific Publications Ltd.)

thereby affecting the seed-propagated C_3 species more than the vegetatively propagated C_4 species.

An important consequence of the different photosynthetic pathways is a temporal separation in peak photosynthetic production between the two groups, a difference that can contribute to their successful coexistence in some sites. Dry matter production by C_4 species occurred more efficiently during the early part of the growing season (April–June), when solar radiation was more intense and temperatures were higher. On the other hand, biomass accumulation by C_3 species was more pronounced during the latter part of the growing season (October–December) when solar, radiation and temperature were both less (Saxena and Ramakrishnan, 1981, 1984b), a situation when C_3 photosynthesis should be superior to C_4 (Ehleringer and Bjorkman, 1977).

Nitrogen is volatilized from the soil during fires, causing a decline in soil nitrogen status, and nitrification in the soil is inhibited in proportion to fire intensity (Saxena and Ramakrishnan, 1986). The high nutrient use efficiency of C_4 plants (Figure 11.5) may then allow them to grow more effectively during the early part of the growing season when nitrogen status is low. The input of detritus causes increased nutrient availability and nitrification later in the first growing season following burning, possibly favouring the growth of less nutrient efficient C_3 species (Ramakrishnan and Toky, 1981; Saxena and Ramakrishnan, 1986).

Under conditions of successive short agricultural cycles, nitrogen accumulation during the fallow period is inadequate to replace the amounts removed in harvest, volatilized during fires, or leached (Mishra and Ramakrishnan, 1984). Moreover, on steep slopes the loss of nutrients through leaching and erosion (Toky and Ramakrishnan, 1981b); Mishra and Ramakrishnan, 1983b) results in a heterogeneous distribution of soil nutrients after shifting cultivation (Ramakrishnan and Toky, 1981; Mishra and Ramakrishnan, 1983b). Under these conditions, the coexistence of C_3 and C_4 species is facilitated because C_3 species can colonize nutrient rich microsites while C_4 species occupy nutrient poor microsites (Saxena and Ramakrishnan, 1983, 1984b).

11.6.3 Nutrient conservation by exotic species

Exotic species contriburte a major fraction of the total biomass of early successional communities, and hence they may play a significant role in reducing losses of nutrients in run-off after cropped plots are abandoned (Table 11.3) (Toky and Ramakrishnan, 1981b; Ramakrishnan, 1984). The extent to which this function of exotic weeds would be replaced by natives if the former were not available is a moot point. However, with their C_3 photosynthetic pathway the exotics do have a systematically higher nutrient uptake (Swamy, 1986), and therefore they accumulate larger quantities of nutrients in plant tissue (Table 11.4). Under the present shortened agricultural cycles, it is likely that nutrient losses would be accelerated in the absence of exotic species.

The manner in which an exotic species can affect nutrient retention is

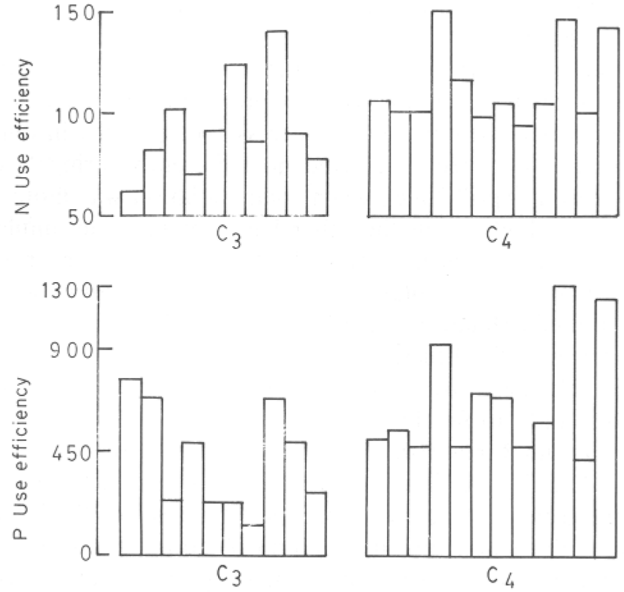

Figure 11.5. Nutrient use efficiency (expressed as mg dry matter production per mg nutrient absorbed) of different species coming after slash and burn. Different columns from left to right are: C_3 species: *Ageratum conyzoides*, *Boweria articularis*, *Cassia tora*, *Costus* sp., *Crossocephalum crepidioides*, *Erigeron linifolius*, *Eupatorium odoratum*, *Grewia elastica*, *Mimosa pudica*, *Mollugo stricta*; C_4 species: *Braclinaria distachya*, *Digitaria adscendens*, *Euphorbia hirta*, *Imperata cylindrica*, *Manisuris granularis*, *Panicum khasianum*, *P. maximum*, *Paspalidium punctatum*, *Rott boclia goalparer*, *Saccharum arundinaceum*, *Setaria palmifolia*, *Thysanoleana maxima*. Vertical bars represent standard error of the mean. (From Saxena and Ramakrishnan, 1984b.)

exemplified by the effect of *Mikania micrantha* on potassium cycling. Potassium is accumulated rapidly by vegetation up to 4 years into the fallow period—the enrichment quotient for potassium was the highest observed (Table 11.5). The bamboo species *Dendrocalamus hamiltonii* apparently functions in a similar way during the 10–25 year interval of longer fallows (Toky and Ramakrishnan, 1981b, 1983).

11.6.4 Weed extinction

As the shifting cultivation cycle lengthens, exotic weeds are suppressed during the natural progress of succession. Demographic analyses of invaders such as *Eupatorium odoratum* (Kushwaha *et al.*, 1981), *E. adenophorum* (Ramakrishnan

Table 11.3. Nutrient losses (kg ha^{-1} year^{-1}) through run-off and percolation water under a 10-year shifting agriculture cycle and a 5-year-old weed fallow in northeast India (from Toky and Ramakrishnan, 1981b)

	10-year cycle jhum plot		5-year fallow	
	Run-off	Percolation	Run-off	Percolation
Low elevation jhum:				
Nitrate nitrogen	4.2	10.7	0.8	1.1
Available phosphate	1.3	0.1	0.1	0.02
Potassium	91.2	21.2	0.9	0.5
High elevation jhum:				
Nitrate nitrogen	1.7	0.5	1.0	0.9
Available phosphate	0.9	0.1	ND	ND
Potassium	80.1	25.8	19.6	ND

ND = not detectable.

Table 11.4. Mean concentration of three nutrients (± standard error of the mean) during the growing season in leaf tissue of C_3 versus C_4 species. (From Saxena and Ramakrishnan, 1983, reproduced by permission of the National Research Council of Canada)

Species	Nutrient concentration (%)		
	Nitrogen	Phosphorus	Potassium
Eupatorium odoratum	2.92 ± 0.12	0.28 ± 0.06	3.60 ± 0.32
Grewia elastica	1.70 ± 0.14	0.21 ± 0.04	1.32 ± 0.24
Imperata cylindrica	0.85 ± 0.05	0.11 ± 0.02	1.46 ± 0.24
Thysanolaena maxima	1.40 ± 0.09	0.19 ± 0.04	1.54 ± 0.20

Table 11.5. Enrichment quotients (element held in vegetation element uptake) for *Mikania micrantha* and the vegetation in successional fallows developed after shifting agriculture in northeast India. Values in parentheses are for total vegetation (from Swamy, 1986)

Years	N	P	K	Ca	Mg
0–1	0.85 (1.14)	0.97 (1.25)	1.00 (1.32)	0.85 (1.08)	0.88 (1.17)
1–2	1.03 (1.42)	1.12 (1.74)	1.18 (1.60)	1.03 (1.33)	0.98 (1.29)
2–4	1.19 (2.12)	1.30 (2.67)	1.61 (2.74)	1.22 (1.90)	1.07 (2.41)
4–8	1.85 (2.63)	1.94 (5.62)	2.55 (4.01)	2.44 (2.64)	1.46 (3.20)
8–12	1.93 (3.08)	2.19 (4.64)	2.81 (6.15)	2.47 (3.58)	1.52 (3.34)

and Mishra, 1981), and *Mikania micrantha* (Swamy 1986) over a successional gradient suggest that they are eliminated after 5–6 years largely because of reduced light availability under the developing shrub and tree strata of the forest community (Kushwaha and Ramakrishnan, 1982). However, patterns of enregy and nutrient allocation could also contribute to their elimination. Whereas all individuals of *Eupatorium odoratum* in 1-year-old and 3-year-old fallows were fertile, only 50% of the plants in a 5-year-old fallow produced seeds and none did so in 10-year-old fallows.

11.7 CONCLUSION

We have summarized patterns of invasion, colonization, and extinction of exotic weeds following shifting agriculture in northeastern India. This example illustrates very well both the potential significance of biological invasions into secondary succession and the analytical difficulties inherent in demonstrating those effects.

Short agricultural cycles of 4–6 years are an important factor allowing the successful invasions that have largely occurred subsequent to the Second World War. Two species of *Eupatorium* and *Mikania micrantha* are now among the most aggressive weeds of the subcontinent. These species differ from most of the natives important early in secondary succession by having the C_3 photosynthetic pathway, reproduction primarily by seeds, and high nuitrient uptake. Thus, it is probable that invasion by these species has markedly altered myriad ecosystem properties, including productivity and nutrient budgets, in this succession. However, the success of these biological invaders is inextricably linked with a novel distrubance regime (short agricultural cycles), and it is difficult to separate the effects of the invaders *per se* those of that disturbance regime.

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