

## CHAPTER ONE

# Plant–plant interactions in tropical forests

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### Introduction

Some interactions between plants are uniquely conspicuous elements of certain tropical forests; the giant lianas that wind through the canopy and the epiphyte-laden branches of cloud forests are striking examples. Nevertheless, the fundamental processes involved are no different from those in extra-tropical communities, even though diverse, sometimes uniquely tropical, mechanisms may be involved. An individual of one plant species interacting with an individual of a second plant species can lead to any of the same five outcomes at any latitude, and these consist of all combinations of negative, positive and neutral effects (except the non-interaction described by the mutually neutral interaction, 0/0). But interactions among plants in forests seldom involve such simple one-on-one relationships. More commonly, multiple players are involved and the interactions change with time: the liana binds crowns of several trees, the fallen palm frond damages multiple seedlings, and the solum is shared by roots of many species. Furthermore, positive and negative interactions occur simultaneously, so the observer sees only an integrated net effect of multiple interactions (Holmgren *et al.* 1997).

Most symbiotic (mutually positive) interactions in tropical forests involve relationships between plants and animals or between plants and microbes – fungi, bacteria, algae – described elsewhere in this volume. What, if anything, distinguishes plant–plant interactions from plant–microbe, plant–animal or animal–animal interactions? Even though they employ different biotic services (pollination, dispersal; see Ghazoul, Chapter 10, this volume; Muller-Landau & Hardisty, Chapter 11, this volume), higher plants (with a handful of exceptions) all use the same abiotic resources: water, carbon dioxide, photosynthetically active solar radiation and the same suite of 13 mineral elements. Furthermore, the sporophyte is immobile, precluding spatial shifts to accommodate changing

conditions. Not surprisingly, then, most plant–plant interactions result in negative net impacts on at least one of the players as they compete in place for a common set of resources. Although recent years have witnessed a resurgence of interest in cooperative plant–plant interactions that benefit both participants, most examples concern physically harsh environments and are related to disturbance (Bertness & Callaway 1994).

Identification of interactions is relatively straightforward, but quantitative assessment of their ramifications is much more difficult. The approach we have used to assess consequences of interactions involved construction and 12 years of observation of communities on a fertile soil in the humid lowlands of Costa Rica. The experimental communities contain few species, representative of the life forms that have proven most evolutionarily successful in forests of the humid tropical lowlands. Unlike most studies of interspecific plant interactions, ours involve perennial species having different stature at maturity. Fast growth gives quick results, long-term observations provide an opportunity to assess changes, and perennial plants representative of successful life forms in natural forest give a semblance of real-world relevance. Three tree species (*Hyeronima alchorneoides*, *Cedrela odorata* and *Cordia alliodora*) are grown in monoculture and together with two monocots, one a perennial giant herb (*Heliconia imbricata*) and the other a palm (*Euterpe oleracea*) (Fig. 1.1). We and our colleagues have used this approach to assess invasibility (Gerwing 1995; Hummel 2000; Merwin *et al.* 2003), productivity (Haggar & Ewel 1994; 1995; 1997), stand structure (Ewel & Bigelow 1996; Menalled *et al.* 1998; Kelty 2000), and nutrient use (Ewel & Hiremath 1998; Heneghan *et al.* 1999; Hiremath 2000; Hiremath & Ewel 2001; Hiremath *et al.* 2002; Reich *et al.* 2003; Bigelow *et al.* 2004; Russell *et al.* 2004), in addition to a number of topics involving abiotic factors or intertrophic interactions.

In this chapter we restrict consideration to interactions among established plants – seedlings (or sporlings) through adults. First, we briefly review the mechanisms involved in some prominent, tropical plant–plant interactions, both physical and biogeochemical. Next, drawing primarily on 12 years of research using the experimental communities of low life-form diversity, we turn to manifestations of plant–plant interactions at the stand level, particularly the consequences of using a common resource base. We assess the results of resource use and partitioning in terms of competition, compensation and complementarity, and we consider their implications for ecosystem functioning. We then turn to the often-ignored temporal dynamics of plant interactions, particularly resource use, and discuss time-dependent changes in plant–plant relationships as they affect individuals, communities and systems of the future. Overall findings are then interpreted in terms of implications – positive, neutral, and negative – for the maintenance, restoration and management of tropical ecosystems.



**Figure 1.1** Three-life-form community at age 8 years, with tree overstorey (*Cedrela odorata*, in this example), palm mid-storey (*Euterpe oleracea*) and perennial-herb understorey (*Heliconia imbricata*). La Selva Biological Station, in the humid Atlantic lowlands of Costa Rica.

## Mechanisms

### Physical interactions

Perhaps second only to the striking diversity of tropical forests, physical interactions among plants are one of the most conspicuous features of tropical forests: the fallen tree trunk that leads to a row of seedlings germinating upon it, the right-angle bend in the stem of a treelet temporarily flattened years ago by a fallen palm frond, the tree crowns festooned with epiphytes, the tangles of lianas using one another as paths to the canopy, and crown shyness due to abrasion. At one extreme, a plant can be a passive participant. For example, an important yet easily overlooked interaction among plants is detritus-fall from large individuals that breaks, bends or kills smaller ones. Although this can occur in any forest, it is an especially important phenomenon in fast-turnover tropical forests. The agent may be branches or fronds, a rain of heavy detritus that damages an average of 10 to 20 per cent of a given cohort of seedlings (Aide 1987; Clark &

Clark 1991; Mack 1998; Drake & Pratt 2001) and therefore can affect future composition. At the other extreme, some interactions involve intricate mechanisms and processes, illustrative of the potential of plant evolution. Tropical forests are rich with examples, such as relationships between hemiparasites and their hosts.

In some plant–plant interactions, one member is a passive player in an interaction that is beneficial to the second member. The protection from direct sunlight afforded by a tall plant to a shorter one is an example. Although solar radiation commonly limits plant growth, many plants cannot thrive if exposed to direct sunlight. There are a number of potential causes: a plant may not be able to dissipate the heat accumulated by direct exposure to sunlight; it may lack the shielding that prevents chlorophyll degradation; or it may be unable to sustain an internal water balance when faced with high transpiration demand. Nevertheless, although many species survive and grow in light shade, few of them do better as shade intensity increases; most plants, including tropical trees, respond positively to increasing light.

Some plants are able to detect shifts in radiation wavelengths caused by neighbouring plants and follow that detection with a rapid growth response (Ballaré *et al.* 1990; Schmitt *et al.* 1999). Although the phytochrome mechanism involved has not been widely tested, growth responses to shifts in red-to-far-red ratios among tropical seedlings (Lee *et al.* 1996) indicate that this is probably a common phenomenon.

In most plant–plant interactions, the costs and benefits are less well defined than those just described. Epiphytes, hemiepiphytes, vines and hemiparasites, for example, all involve one plant providing physical substrate, and sometimes nutrition, for another (usually, but not always, of a different life form). The dependence of one life form on another for physical support is a common phenomenon in the tropics, and the wide range of scaffolding, substrates and trellises available, coupled with life forms capable of exploiting them, enrich tropical ecosystems: diversity breeds diversity. The most common forms of some large families are epiphytic (e.g. Orchidaceae, Bromeliaceae), and the local species richness of epiphytes can rise to 200 species or more, constituting up to half the flora (Nadkarni *et al.* 2001). The consequences of provision of support by one species for another can range from positive to nil to fatal.

Epiphytes that colonize tree limbs benefit from being perched in the canopy (the obligate habitat of many of them), often without apparent harm to the host. This is a reasonably clear case of facilitation (+/0). In some cases, however, heavy epiphyte loads increase the risk of phorophyte breakage (+/–). The relationship may also be mutually beneficial (+/+), for example if epiphytes slow the passage of atmosphere-borne nutrients that would otherwise pass through the system quickly and be lost before being captured by tree roots (Nadkarni 1981).

Many epiphylls, the leaf-colonizing subset of epiphytes, are capable of fixation of atmospheric nitrogen (e.g. Goosem & Lamb 1986), although the degree to which this nitrogen becomes available to the host is unclear. Epiphylls are generally thought to have a negative impact on their hosts because they capture solar radiation that might otherwise energize the leaf they are growing on or because they hold water that fosters the growth of pathogens (Coley & Kursar 1996). They might also filter incoming direct-beam radiation, reducing the likelihood of chlorophyll-bleaching in the host. Nevertheless, epiphyll growth is far more common in the understorey than in the canopy, which argues against such a sun-screening role being widespread. The abundance of epiphylls on shaded leaves may simply be a consequence of the drought vulnerability of epiphylls, most of which are non-vascular plants.

Hemiepiphytes, which are uniquely tropical, shift their growth habit with age. These plants (principally members of the Moraceae, Clusiaceae, and Araliaceae) begin life as epiphytes but become self-supporting and soil-rooted as adults, a feat that requires substantial morphological, anatomical and physiological plasticity (Holbrook & Putz 1996). By starting life in the crowns of trees, hemiepiphytes circumvent severe competition for light as seedlings. During their epiphytic phase they use the nutrient-rich humus that accumulates in the crown of the host tree (Putz & Holbrook 1989). A small subset of hemiepiphytes is commonly dubbed 'stranglers', although they might more accurately be called 'suicide facilitators', for it is the host tree that continues to enlarge when enveloped by such a hemiepiphyte, eventually leading to its death – a distinct disadvantage of having vascular cambium.

Among the most intricate plant-plant interactions are those between hosts and their hemiparasites or parasites. In the case of the hemiparasitic mistletoes (Loranthaceae, Viscaceae, others), both host and parasite photosynthesize, but the mistletoe has invasive haustoria that penetrate the host's branches, tapping its water supply and, in some cases, its photosynthate (Calder 1983; Lamont 1983; Marshall & Ehleringer 1990). Some parasites show little outward evidence of parasitism, as with the widespread (and valuable) sandalwood (*Santalum* spp.) and Australia's *Nuytsia*, both of which look superficially like other trees, but whose roots invade those of non-conspecific hosts (often other trees) on which they depend (Calladine & Pate 2000). In still other cases the parasite has lost its capacity to photosynthesize, thereby becoming entirely dependent upon the host. The most renowned example may be Southeast Asia's *Rafflesia*, notorious because it produces the world's largest (and one of its most foul-smelling) flower.

Vines are a notoriously successful life form in the tropics and, like obligate epiphytes, dependent upon other life forms for support. Seasonal shutdown of water flow leads to high risk of cavitation in plants having large vessels. It is not uncommon for lianas to have vessels with diameters of 200  $\mu\text{m}$  or more (Ewers

*et al.* 1991), and diameters as high as 700  $\mu\text{m}$  have been recorded (Tyree & Ewers 1996), so it is not surprising that lianas are a much more species-rich life form in the humid tropics than in cold or dry biomes. The impacts of vines on the host plants that provide them with structural support are invariably negative. These impacts include mass load on tree crowns (Putz 1991), interception of solar radiation (Dillenburg *et al.* 1995) and competition for water (Pérez-Salicrup & Barker 2000; Pérez-Salicrup 2001). In experiments in which trellises of varying diameters were provided or removed at ground level, Putz (1984) concluded that vine growth and survival can be trellis-limited, demonstrating once again the dependence of one life form upon the same or another life form. Twining vines cannot climb large-diameter trellises, so vines themselves become a common path to the canopy for other vines.

### Biogeochemical interactions

Although inconspicuous (and hard to measure), chemical interactions among plants can dictate local success, diversification or extinction. They involve common use of elements that are often in short supply relative to plant demand, sharing of water supplies and the production of chemicals by one species that either impact directly or serve as signals to neighbours.

The mineral nutrients contained in plant detritus generally become fair game for any plant in the neighbourhood once they are released by decomposition of the organic matrix. Some plants, however, shortcut the process by capturing detritus behind leaf bases (e.g. some palms: Raich 1983; Putz & Holbrook 1989) or in baskets or tanks formed by leaves (e.g. bromeliads and basket-forming ferns). The ability to intercept detritus can be nutritionally significant; Reich *et al.* (2003), for example, found that bromeliads switched from atmospheric to host-tree litter sources of nitrogen as their tank diameters, and therefore their detritus-capturing capacity, increased with age.

The provision of nitrogen-rich detritus that can nourish co-occurring species is an example of a passive action by one species that benefits another. Although this phenomenon occurs across a wide range of latitudes, it is especially common in the tropics, where legumes are prominent components of many forests. Nitrogen fixation in the tropics is not restricted to those legumes (primarily in the subfamilies Papilionoideae and Mimosoideae) that have symbiotic associations with bacteria capable of reducing the diatomic nitrogen of the atmosphere. The non-legumes include plants symbiotic with actinomycetes or cyanobacteria that fix nitrogen: e.g. *Myrica* (Myricaceae) and *Casuarina* (Casuarinaceae), both symbiotic with *Frankia*; *Parasponia* (Ulmaceae; symbiotic with *Bradyrhizobium*); *Psychotria* (Rubiaceae; symbiotic with *Klebsiella*), and *Gunnera* (Gunneraceae, symbiotic with *Nostoc*).

Even though nitrogen-fixing tree species commonly resorb about half of their foliar nitrogen prior to abscission, the concentrations achieved in leaves are so

high, often 4 per cent or more, that a considerable quantity reaches the forest floor. Once there, it enters the detrital food chain and some of it becomes available to co-occurring plants (e.g. DeBell *et al.* 1989; Binkley 1992). In time, this inadvertent provision of growth-stimulating nitrogen to competitors presumably can prove detrimental to the nitrogen-fixer. Nevertheless, trees that host nitrogen-fixing bacteria may exhibit their highest rates of fixation when young (e.g. Pearson & Vitousek 2001), so the benefits to competitors may be short-lived.

With relaxation of constraints caused by low nitrogen, other nutrients eventually limit growth. In stands comprising a relative-abundance gradient of a non-nitrogen fixing (*Eucalyptus saligna*) and a nitrogen-fixing tree species (*Albizia falcataria* [syn. *Falcataria moluccana* and *Paraserianthes moluccana*]), Kaye *et al.* (2000) found that although available soil nitrogen increased with increasing relative abundance of *Albizia*, available soil phosphorus declined, presumably because of uptake by trees. Whereas sequestration of nitrogen in above-ground biomass increased with increasing relative abundance of the nitrogen-fixing tree, sequestration of phosphorus in biomass peaked at a *Eucalyptus:Albizia* mix of 1:2, the same as carbon.

Water, like nitrogen, can be made available to a second species through the actions of a first. Hydraulic lift, whereby water taken up by deep roots flows at night from shallow roots into the surrounding soil, occurs in savannas (Scholz *et al.* 2002) and probably in other tropical ecosystems. Once in the surface soil, the water potentially becomes available to the plant that expelled it, to a competitor or to evaporative loss.

Unlike nitrogen, which can accumulate in plants and soil through biotic processes, phosphorus is limited from the start by parent material (except for the modest amounts that might enter through atmospheric deposition or flooding). As phosphorus is taken up and sequestered in vegetation, the available supply in the soil declines, until it can eventually limit plant growth. In their classic monograph on shifting cultivation, Nye and Greenland (1960) suggested that extraction of phosphorus by tree roots deep in the soil could lead to replenishment and maintenance of phosphorus in surface soils. Setting out to test this hypothesis, Kellman and Hudson (1982) severed the tap roots of pine trees in a tropical savanna, and after five years of study Kellman (1986) concluded that the tap roots had no effect on the concentrations of foliar phosphorus (or cations). Thus, the best tropical test to date of the intuitively appealing deep-pumping hypothesis has yielded null results.

Allelochemicals are an important means of interaction not only between plants and animals (see Massey *et al.*, Chapter 14, this volume), but also between plants; they constitute an exciting and very active area of chemical ecology (Dicke & Bruin 2001; Callaway 2002). Examples of chemically mediated communications between plants include wounded-plant-to-neighbours (Baldwin *et al.* 2002), root-to-root (Schenk *et al.* 1999), pollen-to-stigma (Ottaviano *et al.* 1992),

and plant-smoke-to-seed (Keeley & Fotheringham 1997). Although plant communication research has not had a strong tropical component (and is unlikely to have one soon as the field becomes increasingly focused on molecular biology; e.g. Kessler & Baldwin 2002), it is inconceivable that tropical plants will not possess the full suite of signals and detectors discovered in plants of the temperate zone; they are likely, in fact, to offer some exciting surprises as well.

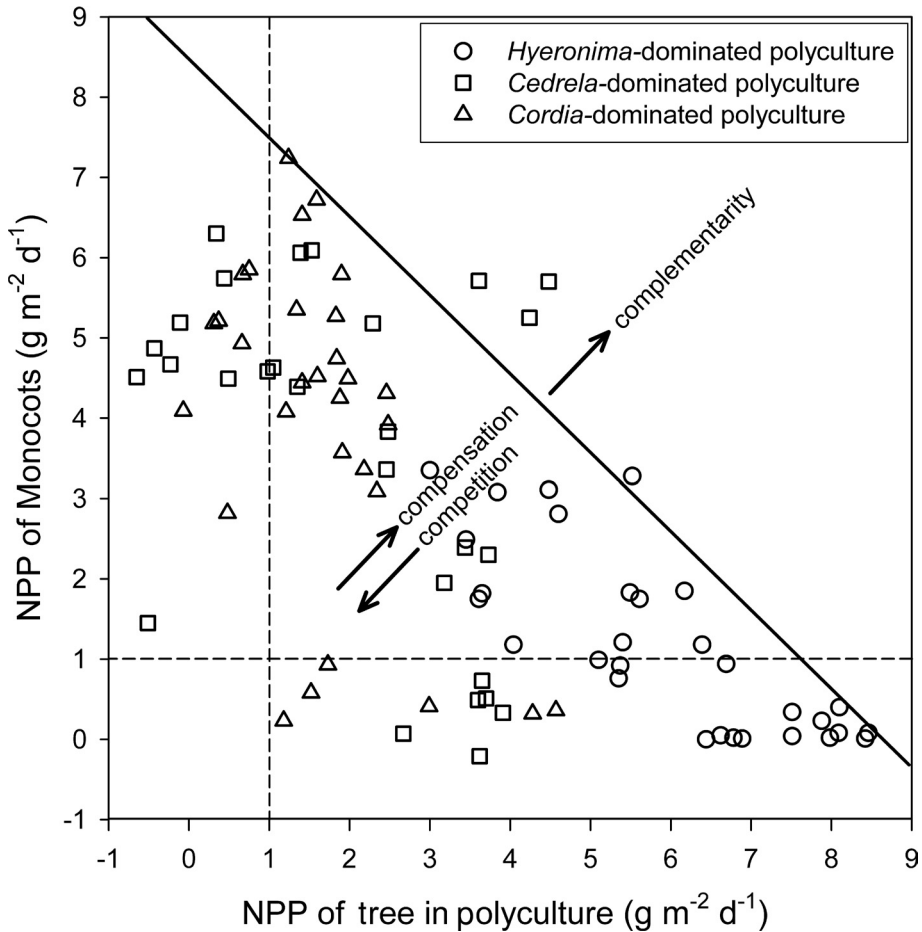
Support for widespread existence of allelopathy as a mechanism of plant-plant interaction has waned in the past couple of decades. Williamson (1990), however, makes a strong case for the fact that allelopathy is held to a higher standard of proof than are most interactions between plants, and he marshals evidence for both the direct production of allelochemicals by plants and the allelopathic properties of substances resulting from breakdown of non-allelopathic exudates. The species-rich genus *Eucalyptus*, widely planted throughout the tropics and subtropics, has borne the brunt of popular accusations that it is allelopathic, but the evidence is equivocal (Willis 1991). In any event, the production of allelochemicals and their exudation into the soil to impede colonization by competitors would be an expensive defence mechanism in the humid tropics, where the flow-through of soil water can easily be 75 per cent or more of rainfall; prodigious rates of chemical production would be required to keep up with losses. If allelopathy is a tropical phenomenon, it seems more logical to seek it in the dry tropics than in rainforests.

### Outcomes: the three 'C's of plant interactions

The results of competition-density experiments containing two or more species can vary from no interaction between the species to complete dominance by one of them. The intermediate results, i.e. those situations in which two presumed competitors coexist, are of particular interest to community ecologists because they offer clues regarding concomitant use of resources, and therefore mechanisms that promote diversity.

Additive experiments, whereby a fully stocked stand of one species is interplanted with one or more additional plant species, are useful tools for assessing resource availability and invasibility (Snaydon 1991). The continuum of possible results from such experiments can be broken down into three broad categories: (1) competitive dominance of the stand by one species whose growth is not affected by a second species that contributes little to total productivity; (2) compensatory productivity, whereby the growth of both species is slowed by competition, but the sum of their productivity is greater than that achieved by either species in monoculture, and (3) complementarity, in which two species share resources in ways that enable at least one of them to be as productive as it would be in monoculture and resulting in total productivity greater than that achieved by either species in monoculture. In the Costa Rican experiments we have encountered all three outcomes: competition, compensation





**Figure 1.2** Productivity of trees and monocots when grown together in an additive design. Each data point represents one replication for one year. Ninety community-years of productivity are plotted: 3 polycultures  $\times$  3 replications  $\times$  10 years. The dashed lines differentiate low NPP values (i.e. a year of productivity at an average rate  $\leq 1 \text{ g m}^{-2} \text{ d}^{-1}$ ) from higher values. The diagonal connects the highest observed annual average monocot and tree NPP values ( $7.2$  and  $8.7 \text{ g m}^{-2} \text{ d}^{-1}$ , respectively).

and complementarity. Furthermore, we learned that the response depended on when observations were recorded, as relationships among species changed with age.

Ninety community-years of data (3 polycultures  $\times$  3 replications  $\times$  10 years following crown closure at age 2) are arrayed on Fig. 1.2, where the net primary productivity (NPP) of interplanted monocots (a perennial herb, *Heliconia imbricata*, and a palm, *Euterpe oleracea*) is shown in relation to NPP of the tree species on the same plot. All stands plotted were at least 2 years old and had closed canopies and root systems. The diagonal is maximum anticipated combined NPP

based on the highest values of NPP observed for monocots ( $7.2 \text{ g m}^{-2} \text{ d}^{-1}$ ) or trees in monoculture ( $X$ -axis intercept =  $8.7 \text{ g m}^{-2} \text{ d}^{-1}$ ). Moving away from that diagonal toward either the horizontal axis (where monocot NPP  $\leq 0$ ) or the vertical axis (where tree NPP  $\leq 0$ ), competition intensifies, and one life form or the other dominates stand productivity. Moving from the origin toward the diagonal, compensatory growth increases; competition-induced productivity decrements in one life form are more than offset by the contribution of the other life form to whole-system productivity. Those few productivity combinations that surpass the diagonal demonstrate complementarity.

If one (arbitrarily) takes an NPP of  $\leq 1 \text{ g m}^{-2} \text{ d}^{-1}$  for either trees or monocots (demarcated by the dotted lines in Fig. 1.2) as evidence of strong competition between life forms in our systems, roughly half of the 90 data points on Fig. 1.2 fall into that category. Nevertheless, competition was manifested in stands dominated by the different tree species in very different ways. *Hyeronima*, clustered toward the lower right-hand portion of Fig. 1.2, proved to be a far more competitive tree species than the other two, and this competitive superiority was sustained throughout the study. It grows fast, has a dense canopy, is evergreen and develops a dense root system. *Cordia* and *Cedrela* each accounted for about a third of the data points that demonstrate competition, but their data points are about equally split between those close to tree NPP of 0 and those close to monocot NPP of 0: early in stand development the tree proved to be the stronger competitor, and now the palm is the stronger competitor. Thus a five-year study would have yielded conclusions quite contrary to those resulting from a ten-year study.

Most of the remaining data points (Fig. 1.2) still fall below the diagonal but illustrate combinations of NPP  $> 1 \text{ g m}^{-2} \text{ d}^{-1}$  for both life forms. Competition plays a role, but its effects are more than offset by the productivity of the additional species. In the case of the highly competitive *Hyeronima*, the only monocot that contributed substantially to productivity was the palm, and it developed much later there than in stands dominated by other trees. In stands of *Cedrela* and *Cordia*, early compensatory growth was provided by the herb, a role that was later usurped by the palm.

Complementarity should be a relatively rare phenomenon among immobile organisms that require the same suite of resources, and indeed only four (of 90) data points fall above the diagonal in Fig. 1.2. Three of those instances involved young ( $< 5$  yr old) stands of *Cedrela* at a time when *Heliconia* contributed substantially to stand-level NPP but did not compete measurably with the tree. The fourth instance involved a stand dominated by *Hyeronima* that was in its tenth year. In this case, the complementary productivity was contributed by the palm.

What mechanisms can account for complementarity? There are three classes of possibilities: resource substitution, spatial segregation of resource acquisition and temporal differentiation of use (cf. Trenbath 1974).

### Resource substitution

The restricted set of resources required by higher plants contrasts sharply with the dietary diversity of animals (although the dietary diversity of animals may be as much a reflection of packaging as basic chemical composition). One opportunity for using different forms of an essential resource involves nitrogen; the other involves use by understorey plants of those wavelengths of solar radiation that make it through the canopy after taller plants have skimmed the peaks off the action spectrum for photosynthesis.

The most apparent opportunity for resource substitution among terrestrial plants is the use of geochemically distinct sources of nitrogen: fixation of the diatomic form from the atmosphere by microbial symbionts, uptake of oxidized (nitrate) or reduced (ammonium) forms of mineral nitrogen, or uptake of organic nitrogen (Neff *et al.* 2003), from soil solution. Nitrogen-fixers and non-fixers use different biogeochemical pathways to acquire their nitrogen, required in prodigious quantities by both kinds of species.

Even though higher plants vary little in the quality of solar radiation that drives their photosynthesis, some plants are better adapted than others to take advantage of the shifted spectrum that reaches the forest floor. The radiation reaching the understorey of a tropical forest typically exhibits about a three-fold reduction in the red:far-red ratio (Chazdon *et al.* 1996). The fact that leaves of many understorey plants are relatively enriched in chlorophyll *b* hints that they may be able to use the red-depleted spectrum more effectively than leaves of canopy plants (Björkman 1981), although the ecological implications have not been quantified.

### Spatial separation

Differential exploitation of soil depths (e.g. Jackson *et al.* 1999) for water or nutrients may be the primary mechanism that leads to resource-partitioning among plants. In recent years substantial progress has been achieved in documenting this phenomenon using stable isotopes (Dawson *et al.* 2002). Presumably all species benefit by concentrating their roots in zones of most abundant resources, making it almost impossible to determine whether differential rooting depths are inherent traits of the life forms observed or induced by competition. Growing in a semi-solid medium as they do, roots (unlike tree crowns, for example) have escaped an overriding selection for self-support. This permits an architectural flexibility that enables plants of many life forms to exploit water and nutrients from different soil depths, thereby achieving complementary resource use. Preliminary data indicate that the complementarity we observed between *Hyeronima* and *Euterpe* (Fig. 1.2) came about because the palm developed a root system capable of extracting nutrients from greater soil depth than the tree.

Nevertheless, root-system development is not entirely free of genetic constraints, even in humid tropical forests (Jeník 1978): many perennial herbs in

the understorey have sparse root systems, often consisting of soft, thick roots that do not penetrate the soil very deeply; palms have cable-like roots with a very modest degree of branching and no secondary thickening; and some trees (e.g. *Cedrela odorata*, whose shoots are subject to attack by *Hypsipyla grandella*) have roots laden with starch, which enables them to recover from insect attack (Rodgers *et al.* 1995). In the seasonal tropics, variations in root systems may be especially striking because their development is influenced by requirements for storage, uptake of ephemeral surface water or water at extreme depth, and the ability to re-sprout after fires.

Unlike the trees and palms that reach the canopy, most understorey life forms studied to date, both perennial herbs and shrubs, have shallow root systems (e.g. Becker & Castillo 1990; Grainger & Becker 2001), and this may lead to some partitioning of soil resources. Nevertheless, an understorey growth response to trenching (Coomes & Grubb 1998) suggests that differential rooting alone is inadequate for partitioning of soil resources and that nutrients may be limiting in the understorey owing to the competitively superior overstorey, at least on infertile soils. Furthermore, there are interesting exceptions to the shallow-rooted understorey generalization, as in the case of *Jacquinia sempervirens*, a shrub found in neotropical dry forests that is wet-season deciduous but fully leafed in the dry season, when its long taproot exploits water deep in the soil.

Solar radiation presents resource-acquisition challenges and opportunities of a different nature. For one thing, light is a pass-through resource that is not storable unless converted to chemical energy; for another, all higher plants require the same wavelengths, so there is limited opportunity for qualitative partitioning (e.g. Lee 1997).

Optimization of light capture is closely tied to uptake and utilization of limiting mineral elements, particularly nitrogen, but also phosphorus in some situations. There is an internal tradeoff involved for an individual capable of overtopping its neighbours. The relative gains to be had from investing more nitrogen in a well-illuminated leaf must be balanced against the gains of distributing that nitrogen among many leaves including those receiving less solar radiation (Field & Mooney 1986). Some species are obligate investors in fully illuminated foliage. These include the thin-crowned, fast-growing pioneer trees (e.g. *Ochroma*, *Musanga*, *Octomeles*) as well as most nitrogen-fixing legumes. Other species sustain deep, densely foliated crowns, presumably by being effective at nitrogen acquisition or by being unable to achieve the extremely high rates of photosynthesis that make deployment of all available nitrogen to fully lighted leaves an optimal investment. Examples include *Flindersia*, *Garcinia* and *Manilkara*.

What about the space between the forest floor and tall, well-illuminated plants? Here the greater light capture that could potentially be achieved with increased stature comes at a carbon cost of investing in non-photosynthetic support tissue, an inefficient proposition in low-light environments (Chazdon 1986). It is not surprising, therefore, that the understorey of many tropical forests

(particularly in the humid lowlands) is dominated not by the seedlings of plants of tall potential stature but by a guild of short-stature plants that survive in the shadows, usually by being extremely effective at photon capture. Barely at the limits of the euphotic zone, these plants often exhibit morphological or anatomical features that would be penalized if they were exposed to full sunlight and to wind, such as high specific leaf area and thin palisade parenchyma (e.g. many Rubiaceae, Melastomataceae, Piperaceae) traits often accompanied by large leaves (e.g. many Araceae, Arecaceae, Cyclanthaceae, ferns, Heliconiaceae), in contrast with their sparse root systems. Many understory plants have non-overlapping phyllotaxy, ensuring that no leaf shades another. Still others have the thylakoid-packed leaves that greatly enhance their light-harvesting capacity, imparting an ability to sustain carbon gain in the shade, while at the same time taking advantage of ephemeral sunflecks (Chazdon 1988; Pearcy 1990). Further reducing light requirements, understory plants commonly have low rates of dark respiration, enabling them to sustain a positive carbon balance with low rates of photosynthesis (e.g. Björkman 1981; Chazdon 1986). In the extreme understory specialization, the abaxial anthocyanin layer in leaves of many understory species may help in the scavenging of every last photosynthetically active photon, reflecting it back up to the light-absorbing pigments (Lee 1979).

### **Temporal differentiation**

In the tropics, as in the temperate zone, much complementarity involves differential phenology, which enables two or more species to tap the same pool of resources at different times. The resource for which temporal sharing is most obvious is solar radiation, whereby understory life forms receive more light during seasons when overtopping plants are at least partially leafless.

Water demands at the tops of tall trees can be difficult to meet because of a combination of the length and associated resistances of the path that water must be transported internally, the greater vapour-pressure deficit and enhanced air speed with increasing height above the ground, and the force of gravity (Zimmerman 1971). Thus, as water supplies in the soil diminish and become held under increasingly greater tension, the necessary gradients cannot be sustained. The result is a top-down onset of deciduousness that, in many tropical forests, does not extend below the canopy dominants. One consequence is that during the portion of the year when the uppermost canopy trees are leafless, shorter-stature plants not only receive more solar radiation but also have exclusive access to nutrients and to any soil water that might become available through dry-season showers (Fig. 1.3).

### **In the fullness of time**

Ecological change is an unchallenged given, yet many of us still interpret the natural world in terms of what we observe today, giving short shrift to history or to future trajectory. Our relatively short-term run (12 years) of repeated



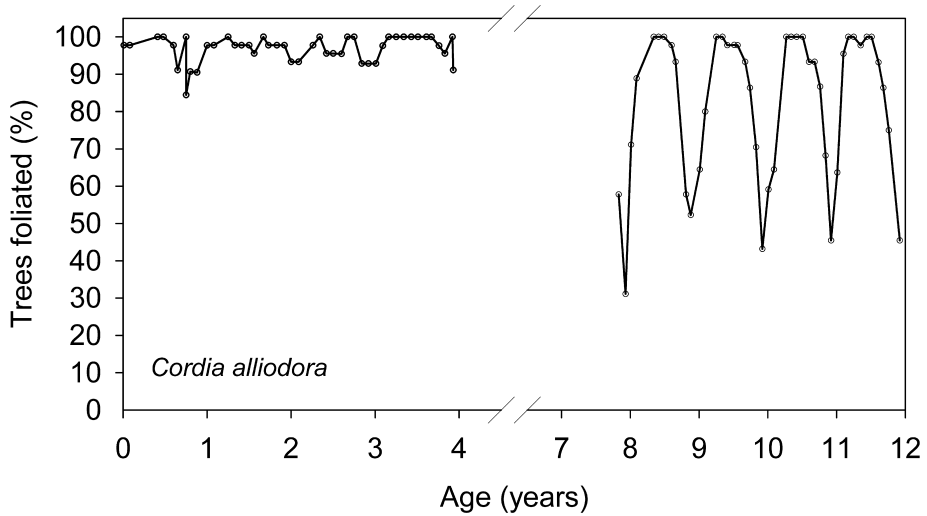
**Figure 1.3** Deciduous overstorey of *Cedrela odorata* above evergreen palm (*Euterpe oleracea*) and perennial herb (*Heliconia imbricata*) illustrates a common mechanism of resource-partitioning in the tropics. Stand age = 5 years. When the tallest components are leafless the lower-stature plants receive more solar radiation and have exclusive access to water and nutrients.

measurements on fast-growing experimental communities has provided surprises and insights, as we have witnessed predictions being overturned, trajectories redirected and answers reversed. There is no better environment for gaining time-dependent insights into the consequences of plant interactions than the humid tropical lowlands, where results come quickly. Because of the accelerated development that occurs where growth is unimpeded by harsh seasons it is feasible to observe changes within a few years that might take decades to manifest in the temperate zone.

Sustained observations of selected organisms, ecosystems and chronosequences will provide adequate data for understanding place-specific observations of short- to mid-duration phenomena (years to decades). Other approaches including modelling, palaeoecology, geochemistry and remote sensing will be needed to achieve understanding of ecological phenomena operating at longer time scales.

### **Changes in individuals**

Changes in interactions accompany increases in plant age, sometimes dramatically so, and this leads to changes in the consequences of plant-plant

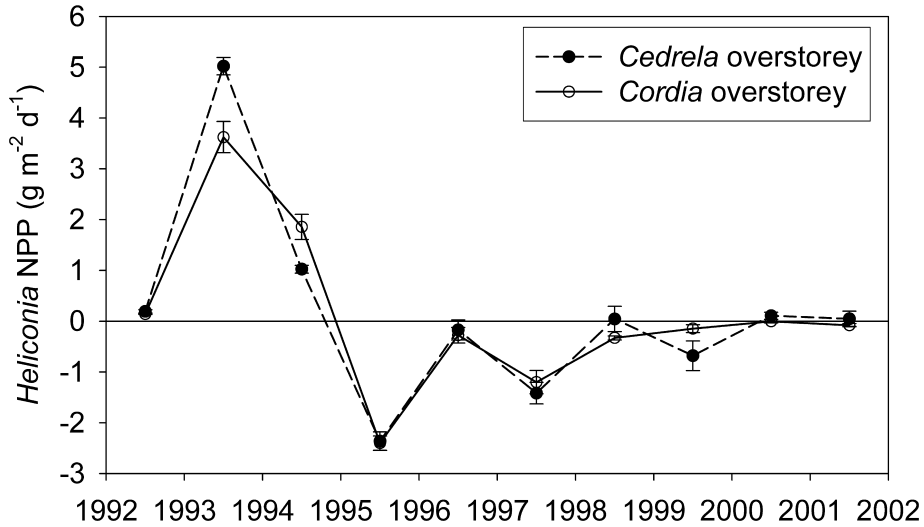


**Figure 1.4** Phenological shift with age by *Cordia alliodora*. Until age 4 years, this tree is almost entirely evergreen, but once it reaches reproductive maturity, between ages 5 and 7 years (and a height of about 20 m), it becomes seasonally deciduous. A foliated tree was one carrying  $\geq 50$  per cent of its full complement of leaves.

interactions. Leaf phenology is one such example. Many tropical tree species are evergreen or nearly so when young, but become deciduous when older. For example, we found that two of four species whose phenology we observed monthly for four years, *Cordia alliodora* and *Cedrela odorata*, metamorphosed from evergreen to predictably deciduous. In the case of *Cordia*, the onset of deciduousness occurred between ages 5 and 7 years (Fig. 1.4), coincident with its age of flowering.

The stature of plants having a basal meristem and no cambium (e.g. Cyperaceae, Heliconiaceae, Musaceae, Strelitziaceae, Zingiberaceae, most Cyclanthaceae and Poaceae, and many others) is biomechanically limited, and this too can impose age-dependent constraints on their roles in the community. Although such plants can be effective competitors against plants of similar stature, they lose dominance once they are overtopped by trees and palms. For example, in two of our experimental communities containing three life forms of plants – tree (*Cordia* or *Cedrela*), palm, perennial herb – the herb (*Heliconia imbricata*) grew as tall as 6 m and contributed more than 50 per cent of NPP in the first three years following establishment. But by the fifth year, when it was overtopped by the tree and the palm, its NPP plummeted to negative values, as its losses of tissues through death and respiration exceeded its carbon gains through photosynthesis (Fig. 1.5). Thereafter its NPP rebounded, oscillating around zero as it survived, but did not thrive, in the understorey.

Development of the root system can also lead to changes in species interactions over time. Dicotyledonous trees and palms that potentially compete for soil



**Figure 1.5** Time course of the contribution of the perennial herb, *Heliconia imbricata*, to aboveground net primary productivity (NPP) in three-life-form communities dominated by *Cordia alliodora* or *Cedrela odorata*. Early in stand development the herb contributed more than 50 per cent of total NPP, but, limited biomechanically by its basal meristem, its productivity plummeted once it was overtopped by the tree and palm, *Euterpe oleracea*.

nutrients provide an example. Many palms have geotropic stems, a behaviour that is often interpreted as an adaptation to fire or herbivores: the young palm's bud is safely below ground until a root system is well established, at which time a rapid spurt of height growth raises the bud above the height that would have made it vulnerable. In our experimental plantations we observed a similar developmental sequence by *Euterpe oleracea*, a palm of Amazonian flood plains: roots followed by stem. In this case, however, the driver is probably not fire or herbivory but delayed access by the palm to nutrients below the reach of more shallowly rooted trees.

Changes in light availability lead to physiological changes that manifest themselves in plant form, structure and functioning. Etiolation, whereby plants develop high ratios of stem height to diameter (Went 1941), is one response, and increased density of chlorophyll is another. Most plants acclimatize to some extent to changes in photon flux density in both directions, i.e. as conditions change from low light to high light (Langenheim *et al.* 1984; Demmig-Adams & Adams 1992) or from high light to low light (Björkman 1981), although low- and high-light specialists often have different capacities for accommodation. The time involved in acclimatizing typically falls in the range of weeks to months; Newell *et al.* (1993), for example, found that three species of *Miconia* adapted to high light within about four months. Like others who have studied acclimatization, they found that acclimatization required production of a new



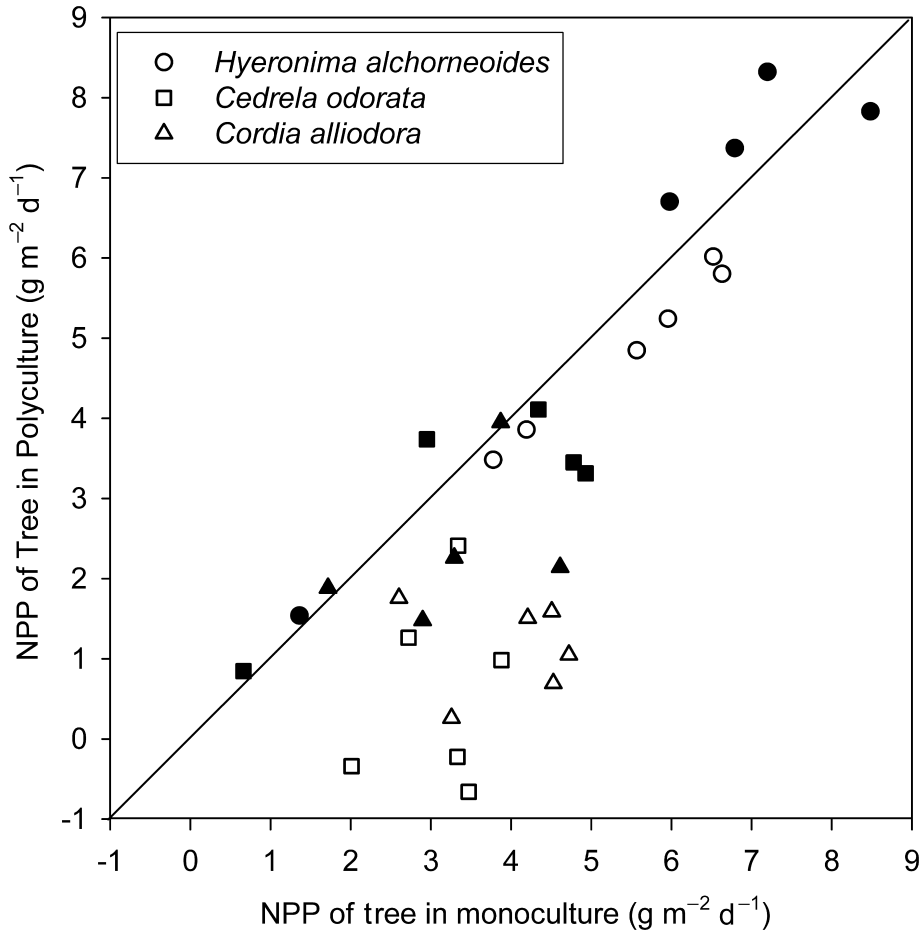
cohort of leaves, replacing those that had previously been adapted to lower light intensities. Thus, a plant capable of a particular rate of photosynthesis in one environment can often, with time, photosynthesize at a very different rate if the light environment to which it is exposed changes – a common phenomenon in tropical forests.

### Changes in communities

Just as spatial patterns in soil nutrient availability can affect the spatial distribution of species with varying efficiencies of nutrient use, so too temporal patterns in soil nutrient availability may alter the outcome of species interactions by imparting different competitive abilities on co-occurring species having different nutrient-use efficiency. Species' differences in nutrient-use efficiency can arise one of two ways: they can differ in their productivity per unit of nutrient in the plant (i.e. nutrient productivity; Ågren 1983) or in the length of time that nutrients are retained in the plant. There may be evolutionary trade-offs between plant traits associated with these two components of nutrient use (Berendse & Aerts 1987), and interspecific differences in these traits can confer varying abilities to deal with nutrient limitation. Thus, species with high nutrient productivity tend to be at an advantage in fertile environments, where faster growth may be the key to rapid resource capture and there is little benefit to be derived from a conservative use of plentiful nutrients. Species with longer nutrient retention, on the other hand, tend to be at a greater advantage in resource-poor environments, where conservation of scarce nutrients (rather than rapid growth) may be the key to a species' success.

Natural distributions of the three tree species that were included in the Costa Rica study bear out this reasoning (Hiremath *et al.* 2002). *Cedrela odorata*, which has high nutrient productivity but low retention, is most often found on fertile flood plain soils. *Hyeronima alchorneoides*, with relatively high nutrient productivity and much longer nutrient retention, would be expected to occur on a wider range of soils. In fact, *Hyeronima* grows rapidly in plantations on fertile soil, but also occurs, although growing slowly, in low-resource environments (Clark & Clark 1992). *Cordia alliodora* has low nutrient productivity, but this is a consequence of high concentrations of nutrients in tissues, rather than low productivity. It also has intermediate nutrient retention. Therefore, it would be expected to grow rapidly on fertile soils but to do poorly on less-fertile soils. In fact, *Cordia* does grow vigorously on abandoned agricultural fields having fertile soils but grows only slowly on degraded soils (Butterfield 1994). In our experimental plantations the nitrogen-demanding *Cordia* was the first to manifest the effects of nutrient limitation as a consequence of competition from the co-planted monocots (Haggar & Ewel 1997).

The differential competitiveness of the three tree species in the company of the two monocots is illustrated in Fig. 1.6, where tree productivity in



**Figure 1.6** Relative above-ground net primary productivity (NPP) of stands of three tree species grown in monocultures and in three-life-form polycultures. Each point is the mean of three replications, and each of the 11 points graphed per species represents a different year-long interval from age 0 to 12 years. Filled symbols represent ages 0 to 5 years; open symbols are ages 6 to 12 years. The NPP of *Hyeronima*, arrayed along the diagonal, showed little impact of the two other life forms in the polycultures. The other two tree species showed little effect early in stand development but eventually declined in NPP in response to competition.

monoculture is compared with that of polyculture. Neither *Cordia* nor *Cedrela* ever achieved a sustained (i.e. average over a year or more) NPP greater than about  $5 \text{ g m}^{-2} \text{ d}^{-1}$ , and their productivity in polyculture was consistently lower than in monoculture except during the first few years of growth (filled symbols, Fig. 1.6). *Hyeronima*, on the other hand, achieved average NPP over a year in excess of  $8 \text{ g m}^{-2} \text{ d}^{-1}$ , and there was little difference between its productivity in polyculture and in monoculture.

The temporal aspects of these trends merit special note. First, there was a dramatic change in vulnerability to competition with time. Early in the experiment both *Cordia* and *Cedrela* had years when their productivity in monoculture did not differ from that in polyculture, but once the monocots increased in biomass their impacts on resource availability were reflected strongly by a decline in tree productivity. Second, the competition in these systems was clearly dominated by below-ground processes, for tree growth slowed markedly even while the trees overtopped the monocots. At this well-watered site ( $\sim 4$  m of rain per annum) competition centred on nutrients; declines in foliar nitrogen-to-phosphorus ratios (Hiremath *et al.* 2002) caused by high leaching losses of nitrate (Bigelow *et al.* 2004) indicate that the nutrient in shortest supply was nitrogen.

### Legacies

Site history is easy to ignore, especially in the tropics where recovery is often fast and the impact of past occupants inconspicuous. Nevertheless, plants of the past can have an impact on soil fertility and plant-regeneration patterns observed today. Further exploration of this phenomenon is likely to prove fruitful in the tropics, just as it has in the temperate zone.

Plants (especially trees) of the past can leave a lasting imprint on the forest. This phenomenon has been studied especially well in forests dominated by large conifers, particularly in the northwestern United States, where the trunks of dead trees last many years. But *post mortem* impacts of tree death should be no less important in the tropics, even in the humid lowlands where decay rates are high. What kinds of legacies might be expected? The best-studied of these in the tropics is plant regeneration. Many tropical trees produce competition-tolerant seedlings, and these constitute the advance regeneration that captures the resources vacated by the death of the parent (e.g. Brokaw 1985). Long-dead pioneer trees such as *Trema* can affect regeneration for decades because of the large number of viable seeds they leave behind in the soil (Alexandre 1989). Gap dynamics, which gained momentum as a topic of study in the 1970s (e.g. Denslow 1987), is one of the best examples of south-to-north transfer of ecological knowledge. It is gap formation that aids niche-partitioning, particularly in the regeneration phase, among plants having different requirements for light, dispersal and (possibly) nutrient availability. Less well studied, but probably important, are the roles of dead wood in providing safe sites for regeneration of some species. In Hawaii, for example, *Metrosideros polymorpha* (the dominant tree species) regenerates predominantly on logs in alien grasslands, presumably because of lessened competition (Scowcroft 1992).

Plants sometimes change soil properties, and in doing so influence the propitiousness of a site for its own or other species. In a study of 23- to 36-year-old plantations and primary forest in the Brazilian Amazon, Smith *et al.* (1998) reported

that different species modified nitrogen availability such that mineralization rates were inversely proportional to efficiency of nitrogen use. In Micronesian mangrove swamps, Gleason *et al.* (2003) found that the soil beneath *Sonneratia* was more highly reduced than the soil beneath *Rhizophora* and *Bruguiera*. This apparently occurred because the roots of *Sonneratia* conducted less oxygen into the otherwise anaerobic substrate, thereby lowering the redox potential, which in turn improves availability of phosphorus.

### Global change

On longer time scales, present landscapes may be ghosts of conditions past, and the rapid global change that we are undergoing now will probably result in a future landscape very different from the one we know today. For example, a large part of now-forested West Africa may have been a much drier C<sub>4</sub> grassland during the mid-Pleistocene as a result of lower sea-surface temperatures off the African coast (Schefuss *et al.* 2003). So also, the reverse: the disappearance of trees from South Africa's savannas during the last glacial has been linked to low atmospheric CO<sub>2</sub> concentrations (in addition to fire), conditions under which the growth of fire-vulnerable trees is likely to have been slowed relative to fire-carrying grasses (Bond *et al.* 2003).

Grasses that possess the C<sub>4</sub> photosynthetic pathway have a distinct advantage over C<sub>3</sub> trees under warm, arid conditions, as their ability to concentrate CO<sub>2</sub> with only minimal stomatal opening enables them to tolerate extremes of drought. And where grasses and fire-vulnerable woody plants co-mingle, it takes only an ignition source to tilt community composition toward the grass (Budowski 1956). This conversion of forest to grassland, commonly triggered by agricultural activities and logging, has affected hundreds of thousands of hectares throughout the tropics. The process is reversed only when the ignition source is removed and taller-stature woody vegetation eventually suppresses the grasses through competition. In addition to low-stature monocots that fuel fires (primarily grasses and sedges, but in seasonally dry marshes including families such as Marantaceae and Typhaceae), palms often survive this conversion sequence (e.g. Anderson *et al.* 1991). Palms lack fire-vulnerable vascular cambium and their apical meristem is protected by its surrounding tissues, height above the ground or depth below the soil surface.

The grass  $\rightleftharpoons$  fire feedback is thought to underlie the widespread occurrence of the grassland-forest mosaics characteristic of many mountainous areas in the tropics. These mosaics are maintained by frost (Meher-Homji 1967), periodic drought (Wesche 2003), fires resulting from human activity (Ellenberg 1979; Corlett 1987), or interactions among them. Human activity is not a requisite for all such mosaics, as evidence of those in southern India goes back to at least the last glacial maximum, a period of widespread aridity (Sukumar *et al.* 1993) and a time well before any evidence of people in these areas (Misra 2001).

The increasing severity of El Niño events in the last three or four decades has resulted in increasingly more widespread fires in humid tropical forests, a result of severe drought compounded by logging, conversion to agriculture, and fragmentation (e.g. Laurance & Williamson 2001). Fires in Kalimantan in the late 1990s burned over five million hectares of wet forest, easily five times the area of forest burned in a similar El Niño period two decades before (Siegert *et al.* 2001). Although fires are by no means unprecedented in tropical wet forests (Goldammer 1992), palaeoecology and history tell us that they have been relatively infrequent phenomena, making such forests poorly adapted to fires. Even extremely low-intensity fires can result in widespread tree mortality (Cochrane 2003), very quickly leading to a landscape dominated by grasses and other fire-tolerant life forms such as palms (Anderson *et al.* 1991). With the possibility of a warmer, drier world, such forest transformations are likely to become a growing reality.

Warming-and-drying is but one potential scenario in a changing world. The reality is likely to be far more complex, with some regions becoming wetter as others become drier (e.g. Menon *et al.* 2002), and some regions becoming cooler as the globe grows warmer (Intergovernmental Panel on Climate Change (IPCC) 2001). Models based on ocean surface temperatures and circulation predict that the aerial extent, frequency and intensity of tropical storms and hurricanes could increase in some regions, leading to a greater abundance of disturbance-adapted life forms such as palms and lianas (Laurance *et al.* 2001; Pérez-Salicrup *et al.* 2001b). Palms, particularly, are well built to withstand storms, with dispensable fronds that can be shed to avoid toppling by cyclonic winds, with little damage to their ability to recover (Murphy 1916; Bannister 1970). The converse, a decline in the occurrence of tropical storms, is equally possible for some regions. This reduction in frequency of disturbance could lead to an increase in the extent of those tropical anomalies, the monodominant forests (Hart *et al.* 1989; Sheil & Burslem 2003), although there is also some evidence to suggest that monodominant forests may trace their existence to past catastrophic disturbance (e.g. Read *et al.* 1995).

Some vegetation shifts induced by climate change will undoubtedly be much more subtle than fire- and drought-induced conversions of forest to grassland, or the disturbance-wrought alterations of large landscapes. It is likely that closed-canopy forests will experience shifts in relative dominance and species composition due to changes in temperature, moisture and nutrient fluxes. Each of these abiotic factors, in turn, will influence the relative strengths of species with regard to competition, compensation and complementarity. For example, early successional species may be better able to use increased soil nutrients relative to late successional species (Huante *et al.* 1995). Similarly, rising atmospheric CO<sub>2</sub> may shift the balance of competition between trees and life forms such as lianas (Granados & Körner 2003). Nevertheless, because trees are long-lived,

they are better buffered than most life forms against short-term fluctuations in climate.

Climate is not the only global change of ecological consequence: the human-mediated homogenization of the world's biota is an unprecedented phenomenon, one certain to have irreversible impacts on ecosystem structure and functioning. Perhaps the greatest cost will be to less-competitive species: those most likely to be displaced, some to extinction, by non-indigenous invaders. In one sense, the result of the great eco-mix in the tropics will be intriguing ecosystems containing species that are extremely effective at what they do – vines in ecosystems that have never seen climbers, shade-tolerant shrubs in once open-understorey forests, nitrogen-fixing pioneers that redirect succession, and a greater range of specialization among epiphytes, canopy dominants, and every other structural and functional niche available. Such ecosystems are likely to be as effective as the originals, and in some cases to excel, at certain functional attributes such as carbon fixation and nutrient cycling. The tragic cost of mixing, however, is the loss of unique products of evolution. With them goes much of the diversity of interspecific interactions that add great richness to tropical forests. Uniformity and functionality come at a price, one that society should not be willing to pay.

### **Implications for management**

Interactions between plants are important not only to tropical forest diversity and functioning, but to matters of practical importance such as forest utilization, ecosystem restoration, implementation of conservation plans and the design of sustainable systems of land use. Sometimes the resource manager strives to augment certain interactions, and at other times the objective is to reduce their intensity.

Although we use value-laden terms (harmful, tolerate, etc.) below, we do not think their application is completely inappropriate in this context because it is the will of the human manager, whether a forester, a conservation biologist or a farmer, that is imposed. Nature may serve as model, but once humans become involved, natural trajectories inevitably are deflected as we tend to mould nature to our own images of what it ought to be and do.

Plant interactions sometimes lead to impacts that resource managers consider harmful. For example, loggers lament the fact that lianas tie together the crowns of multiple trees, making felling difficult and dangerous for workers, or damaging neighbouring trees, and then impeding regeneration and growth afterwards. It is not surprising, therefore, that liana-cutting has long been a standard silvicultural practice in tropical forests managed or exploited for timber (e.g. Fox 1969; Ewel & Conde 1980). Nevertheless, the costs and benefits of

climber-cutting are controversial, from both economic and ecological perspectives (Pérez-Salicrup *et al.* 2001a; Schnitzer & Bongers 2002). It appears likely that, for the time being at least, this practice will be evaluated on a case-by-case basis depending on local abundance of vines, cost and effectiveness of labour, value of the residual stand and impacts on wildlife.

A common and ecologically interesting case arises when managers find it useful to substitute one life form for another. This typically happens when, in restoring forests to land dominated by grasses, establishment of a tree cover proves essential to break the cycle of burning and grassland expansion (e.g. MacDicken *et al.* 1995). Even in wet climates where fire is not a threat, tree establishment sometimes, but not always, accelerates forest recovery in grasslands. In the humid lowlands of Costa Rica, for example, surveys of replicated plantations of seven tree species and pasture plots revealed the presence of 550 plant species – a remarkably rich local flora (Powers *et al.* 1997). While some of the tree plantations had more than twice the number of species as the abandoned pasture, others were no more effective at facilitating restoration than was the grass- and fern-dominated pasture.

Plants that share a common environment sometimes tolerate one another to the detriment of neither. This can lead to enhanced species richness and to complementarity. For example, by combining plants that differ inherently in rooting depths the manager can achieve complementary resource use while enriching local diversity. Application of the rooting-depth concept is currently limited, however, because of lack of data on the rooting patterns of perennial tropical plants and the degree to which observed differences are genetic, or environmentally induced. A useful first approach might be to identify broad rooting patterns among life forms: dicotyledonous trees, palms, shrubs, vines and perennial herbs.

Combinations of plants having non-synchronous leafing phenology also offer promise for complementary resource use and risk abatement (by spreading it among several species). Where rainfall quantity and equity of distribution permit evergreen species to survive, however, the opportunity for temporal partitioning of resource use is lost (although the benefits of risk abatement still hold). In such situations, a fast-growing evergreen species almost invariably dominates a fast-growing deciduous species of similar potential stature simply because its annual period of growth is longer. We observed this in four-genus combinations in Costa Rica, where two evergreens (*Hyeronima* and two species of *Euterpe*) had better survival than either *Cedrela* (dry-season deciduous) or *Cordia* (wet-season deciduous). There were some exceptions, though, and 12 years after planting a handful of the two deciduous species still thrive in the combination.

The sharing of above-ground space provides a third opportunity to combine plants in ways that maximize resource use and augment local diversity.

As an ephemeral, pass-through resource, solar radiation lends itself to the simultaneous use of three-dimensional space by multiple species. Above-ground plant parts are subject to much greater biomechanical constraints than roots (because of the low density of air), so crown architecture is under more genetic control than is that of root systems. The resource steward can take advantage of this in two ways. First, species to be combined can be selected on the basis of stature, crown morphology and requirements for photosynthesis. This will enable them to make optimal use of available space and light, thereby enhancing diversity whether for purposes of conservation or risk reduction (or both). Second, species can be combined so that different heights and crown architectures lead to a desired bole form. For example, when slow-growing trees with dense crowns and fast-growing, light-demanding trees are growing together, the dense foliage of the shorter trees will lead to rapid limb shedding and straighter stem form of the fast-growing trees (e.g. Jennings *et al.* 2003).

In still other situations, plants can be combined such that one species aids the growth of another. The provision of nitrogen by overstorey trees (e.g. *Inga*, *Erythrina*, *Falcataria*, *Casuarina*) to an understorey crop such as coffee or cocoa is a common interaction that has been incorporated into land use for centuries, long before farmers understood the mechanism whereby the trees enhanced growth of the crop. In many parts of Spanish-speaking tropical America, the nitrogen-fixing tree *Gliricidia sepium* is called *madre de cacao*, or 'mother of cocoa.' The crop benefits both from the nitrogen released and the light shade cast by the tree. Nevertheless, management of the overstorey tree for timber may damage the crop when the trees are felled and extracted. As a result, shade trees in plantations are often pollarded, which allows high inputs of solar energy to the understorey until the tree re-branches, rather than tended for their value as lumber.

Although nitrogen-fixing legumes are used occasionally as nurse crops for high-value tree species, sometimes it is a high-value tree itself that fosters colonization by other species, thereby hastening within-stand diversification. In Puerto Rico, for example, Lugo (1992) found that the species richness of 50-year-old plantations of mahogany (*Swietenia macrophylla*) was comparable to that of equal-aged natural forest. Others have reported similar findings with a broad array of tropical plantation species (see papers in Parrotta & Turnbull 1997). The plantation tree co-opts resources that would have been used by life forms of smaller stature, typically grasses or vines. Once the trees achieve significant height they are less-effective inhibitors of new colonists than were the ground-covering plants that preceded them.

Sometimes it is the vine itself that is the product, not the problem. Commercially important vines are found in a number of families (e.g. rattan, *Arecaceae*; vanilla, *Orchidaceae*; black pepper, *Piperaceae*; wicker for basketry, *Araceae*). In these cases it is the supporting plant that must be chosen carefully, with



particular attention paid to climbability (trellis diameter, bark traits, strength) and density of shade.

## Conclusions

Whether the consequence of completely passive acts, such as the senescent palm frond crashing to the forest floor, or highly evolved mechanisms, such as a chemical signal transmitted from one species when damaged and received by an undamaged neighbour, interactions among plants are an important part of the intriguing diversity that characterizes tropical ecosystems. A common suite of essential resources leads to a range of processes when species share habitat. These can extend from competitive exclusion of one or more species to the complementary sharing of the available resources in ways that enhance total resource use and productivity.

Complementary sharing can occur qualitatively, spatially or temporally, and of these three possibilities it is the third – temporal partitioning – that is perhaps most intriguing and most often overlooked. Species' roles in a community change with time such that today's dominant might become tomorrow's victim of competition. Resource capture is a function, in part, of plant size, and as size increases with age the plant's impact on ecosystem processes is likely to increase. It is this change with time that is often overlooked, yet it is clearly important on various scales: the past, because plants formerly present leave a biogeochemical or regeneration legacy; the present, as the dominance hierarchy among cohabiting plants shifts on the scale of years to decades; and the future, as shifting climates and human-mediated dispersal change both the abiotic and the biotic ground rules over large geographic scales.

Errors in selection of plant species, choice of habitats and trajectory of community development are commonly committed in the name of conservation biology, restoration ecology and agroforestry: use of a species that might have been predicted to fail (e.g. introduction of heliophytes into the shade of old-growth forests for conservation purposes); selection of habitats that require perpetual maintenance (e.g. fire exclusion in habitats surrounded by invasive grasses in attempts at restoration); inadequate attention to the consequences of well-intended introductions (e.g. use of invasive, alien nitrogen-fixing trees in sustainable agriculture) . . . the list could go on. By learning about the ways that species interact with one another and with their local habitats, and how they fit into longer-term objectives and larger spatial scales, scientists should be able to improve the success rate of resource managers. We need to move forward from the current, and lamentably costly, situation, which consists of tackling each problem as if it were a unique case. Understanding nature's mix of species and the mechanisms involved in its maintenance is the key to our quest for generalization.

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