

Effects of Fire on Rainforest Regeneration in the Amazon Basin

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In the rainforests of the Amazon, fire is used extensively to create pastures following timber extraction and to establish farms following deforestation. Fire is the principal tool for removing slash after the forest has been cut and dried. Without fires, removing slash would be both impractical and uneconomical. With fire, vast areas of slash can be eliminated in a few days with minimal effort, after the forest has been felled.

Natural fires in primary rainforest of the Amazon appear to be rare today, except in seasonal localities on the edge of the Basin that experience an extended dry season (Uhl, Kaufman, and Cummings 1988) or during extremely severe El Niño droughts. The presence of charcoal in soil cores in many Amazonian localities (Sanford et al. 1985; Saldarriaga and West 1986; Bassini and Becker 1990) reflects drier conditions in the geological past, perhaps mega El Niño events (Absy 1982; Markgraf and Bradbury 1982; Meggers 1994a, 1994b) or anthropogenic burning by Native Americans in pre-Columbian times. Where evidence for fire exists, the fire return intervals appear to be on the order of 400–1,000 years, longer than the life expectancy of most trees (but see Chambers, Higuchi, and Schimel [1998]

and Chapter 7 for very old trees). In more recent history, it is doubtful that today's intact rainforests have been subjected to frequent fires (Kaufman and Uhl 1990). In fact, rainforest trees do not exhibit adaptations to fire as do trees in areas known to burn naturally (Williamson, Schatz, et al. 1986; Kaufman and Uhl 1990; Rebertus, Williamson, and Platt 1993).

In primary forest of the wet tropics the moisture content of the forest litter's fine fuels generally remains above the level below which combustion can be maintained (Kaufman and Uhl 1990). This "moisture of extinction," derived for temperate hardwoods as 25 percent (Albini 1976), is assumed to apply to tropical hardwood forests as well (Kaufman and Uhl 1990). Furthermore, woody fuel is almost always above its "fuel ignition threshold" of 15 percent (Kaufman and Uhl 1990). However, after the rainforest is cut, the tropical sun in the Amazon can dry the slash before it is burned. A general rule of thumb is that after ten consecutive days of sunshine without rain and cloud cover, the moisture content of the slash drops and the litter becomes combustible (Uhl and Kaufman 1990). The ignition source is always anthropogenic.

Where the rainforest has been disturbed

by selective timber extraction or by edge effects around forest fragments, humidity is reduced and sufficient fuel may be present to allow fires to penetrate the forest without clear-cutting (Uhl 1987; Kaufman 1991; Nepstad, Veríssimo, et al. 1999). Fire frequently spreads through secondary forest and selectively cut forest without penetrating primary forest (Kaufman and Uhl 1990). The differential susceptibility to fire is especially evident during the El Niño Southern Oscillation (ENSO)-related drought of 1982–83 in Borneo, where fires spread rapidly through secondary and high-graded rainforests but burned little primary rainforest (Leighton and Wiraman 1986; Woods 1989). Preliminary data suggest similar differences between primary and secondary Amazonian forests in the 1997–98 drought (Hammond and Steege 1998).

Responses of Rainforest Trees to Fire

In ecosystems where fires occur naturally, there are three basic mechanisms for genetic survival of woody plants (Carpenter and Recher 1979; Williamson, Schatz, et al. 1986; Rebertus, Williamson, and Platt 1993). Where fire intensity is low (surface fires), fire frequency is high (many times in the lifetime of a tree) and fires are relatively periodic (low variance about the mean frequency), trees often survive fires by having thick bark to protect the lateral cambium and trunks tall enough that apical buds survive above the heat (table 25.1). This “adult stem lives” strategy, which is common among tree species of the *cerrado* (woody savannah) vegetation in Brazil (Coutinho 1990) and the sub-tropical savannas of the United States (Rebertus, Williamson, and Platt 1993), is unknown among Amazon rainforest trees. In the rainforest many trees have long boles, but they lack thick bark. Uhl and Kaufmann (1990) measured bark

thickness in trees in undisturbed rainforest in the eastern Amazon and estimated that 98 percent of all stems greater than 1 cm DBH would be killed in the event of a surface fire.

Beyond the absence of thick bark, there are no rainforest trees known to exhibit the temporal survival mode of the “adult dies” strategy (table 25.1), in which fire kills the adult trees but breaks the dormancy of seeds stored in the soil or in serotinous fruits or cones on the tree, as is the case for some North American pines (Richardson 1988), Australian *Eucalyptus* (Gill 1981), chaparral shrubs (Horton and Kraebel 1955), Mediterranean shrubs (Le Houreau 1973), Australian shrubs (Lamont and Barker 1988), and tropical montane shrubs (Williamson, Schatz, et al. 1986). With seeds tolerant of fires and seed dormancy broken by fire, this mode of genetic survival often results in a cohort that germinates, grows, and reproduces the next generation of seeds that remain dormant until the next fire. However, most species of old-growth rainforests do not share these key adaptations; to the contrary, their seeds are not dormant (Garwood 1989, Thompson 1992), and even when buried in the soil they seem to be particularly susceptible to fire (Brinkmann and Vieira 1971).

Where fires are intense, but infrequent and aperiodic (table 25.1), woody plants exhibit a “resprout” strategy of which the key adaptations are subterranean buds at the base of the stem or on lateral roots and a highly distorted root:shoot ratio (below-ground:above-ground distribution of biomass). Among fire-adapted resprouters, these root:shoot ratios are distorted as high as 6:1 in favor of roots and may reach 10:1, even in controlled circumstances where the above-ground tissue is protected from fires (Rebertus, Williamson, and Moser 1989). Most fire-adapted resprouters can be burned in successive years, losing only a fraction of

TABLE 25.1. Responses of Adult Trees to Natural Fires, Their Mode of Genetic Survival and Their Key Adaptations for Survival, All Associated with Fire Regimes Varying in Frequency, Intensity, and Periodicity

Adult plant response	Survival mode	Key adaptations for survival	Fire regime		
			Frequency	Intensity	Period
Adult stem lives	Spatial, above ground	Thick bark Tall bole	high	low	high
Adult dies	Temporal Fire-tolerant seeds	Fire-dormant seeds	low	high	high
Adult resprouts	Spatial, below ground	Subterranean buds High roots:shoot ratio	high	high	low

their biomass in each fire; for example, a resprouter losing 10 percent in five successive fires would retain 59 percent (0.90^5) of its biomass, even assuming no gain from growth between fires. The evolutionary cost of maintaining such a high proportion of biomass underground is, of course, slow growth. Annual biomass accumulation in classical resprouting species may be less than 20 percent even in the first few years of growth, a time when many woody plants double in size annually.

At first appearance some rainforest trees might be expected to resprout after fires because they have demonstrated abilities to resprout along the main stem when it is broken in treefalls (Putz and Brokaw 1989), snapped by hurricanes (Vandermeer et al. 1995), cut (Hartshorn 1989; Gorchov et al. 1993), or uprooted (Negrelle 1995). Even so, few of them have dormant buds or regenerative capacity underground where it would be protected from fire. Consequently, burning that girdles trees close to the ground causes higher mortality than cutting or snapping, which occurs higher on the stem well above the root collar. Kaufman (1991) reported that prescribed fire at two selectively logged forests in the state of Pará, Brazil, killed 94 percent of the tree crowns and 66 percent of the individuals.

The fate of rainforest individuals that re-

sprout after fire—for example, the 34 percent of individuals showing basal or epicormic sprouting (along the main stem) in the study cited above (Kaufman 1991)—is fairly predictable in anthropogenic systems. Successive fires in pastures exhaust the reserves of resprouting plants and cause death before the pasture is abandoned (five to fifteen years after clear-cutting) for most species because rainforest trees do not maintain a large portion of their biomass underground. Where pastures are managed less intensively by burning every two or three years, resprouting rainforest trees with subterranean buds may survive as new shoots. Stems resprouting on slash-and-burn agricultural sites often face only one fire but successive weedings that exhaust their reserves as well. For example, Uhl (1987) reported the density of woody resprouts dropped from $0.43/\text{m}^2$ six months after an initial slash-and-burn prior to weeding and then dropped to $0.07/\text{m}^2$ after several weedings.

Responses of Rainforest Pioneers to Fire

Species in the two main genera of pioneers of the Brazilian Amazon (Albuquerque 1980), *Vismia* and *Cecropia*, appear sensitive to hot surface fires, with most individuals suffering crown mortality. For example,

80 km north of Manaus around the Colosso Reserves (1202 and 1104; see fig. 4.1, table 4.3, and plate 1) of the BDFFP, following a fire in 6 yr old second growth we surveyed trees with a DBH of 5 cm or more in 5 ha and noted 100 percent mortality in *C. purpurascens* and *C. sciadophylla* and 99 percent mortality in *V. cayennensis*, *V. guianensis*, and *V. japurensis*. Individual stems sometimes survived the fire in incompletely burned patches such as low pockets and some protected slopes.

Although *Cecropia* and *Vismia* spp. share sensitivity to fire, they differ in their ability to resprout. *Cecropia* species appear able to resprout only epicormically but not from the stem base, nor from lateral roots. In general, cut *Cecropia* trees resprout, but surface fires kill the epicormic buds and the tree. While there may be variation in sensitivity to fire among the 100 species of *Cecropia* (Berg 1978; Gentry 1993), none have been recorded with subterranean buds that would allow the trees to regenerate following fires. Therefore, most *Cecropia* individuals are killed in surface fires, and certainly all are eliminated where repeated burning occurs, as in heavily used pastures. Kaufman (1991) reported mortality of 85 percent in *Cecropia* individuals in fires that were ignited in secondary forests without clear-cutting fires that were of lower intensity than those that follow clear-cutting.

In contrast, of the thirty *Vismia* species in the Neotropics (Ewan 1962; Gentry 1993), the few that have been investigated appear capable of resprouting from the base of the stem (Uhl 1987; Dias-Filho 1990), and some species resprout as well from lateral roots (Williamson, Mesquita, et al. 1998). For example, along a four-year-old road cut, adjacent to the BDFFP primary forest at Reserve Km 41, 75 percent of the adult stems of *Vismia cayennensis* were ramets—stems connected to other adjacent stems via lateral

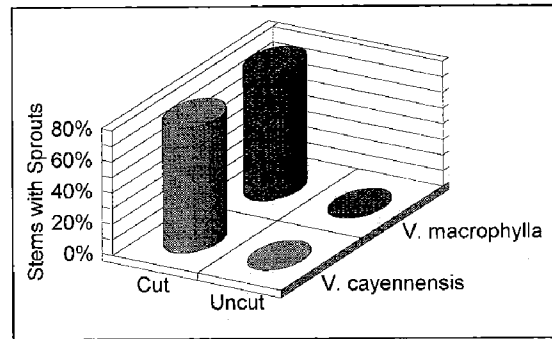


Fig. 25.1. Percentage of stems that produced lateral, basal, or epicormic resprouts for stems that were cut and those that were uncut for *Vismia cayennensis* and *V. macrophylla*.

roots (table 25.2). However, another species, *V. japurensis*, did not show lateral root connections between adjacent adult stems, although this species does resprout basally when the main stem is cut or burned. In a nearby forest light gap a small sample of the same species exhibited no lateral root connections between adjacent adults (table 25.2).

In the primary forest, *Vismia* species are present as pioneers in light gaps, often co-occurring with *Cecropia* species, although their leaves are inconspicuous and their presence has been overlooked (Lucas et al. 1998). *Vismia* is not clonal in these forest openings, perhaps because the stems are never cut or burned. In fact, *Vismia* in forest lightgaps rarely exhibits even basal sprouts. To test the resprouting ability of *Vismia* in the primary forest at Km 41 we cut stems at heights of 5 to 150 cm above the base and compared their responses to those of uncut stems one month later. Cut stems showed basal, lateral, or epicormic sprouts in 80 percent of the cases for both *V. cayennensis* and *V. macrophylla*, whereas uncut stems never produced a resprout (fig. 25.1). For both species, half the stems producing sprouts included lateral root sprouts, up to 50 cm away from the main stem. Some stems produced lateral, basal, and epicormic sprouts,

TABLE 25.2. Percentage of Stems that Were Ramets for Two *Vismia* Species

Species	Percent ramets (n)	
	Along road cut	Forest lightgap
<i>Vismia cayennensis</i> (12)	75% (12)	0%
<i>Vismia japurensis</i>	0% (27)	0% (4)

Notes: Ramets are stems connected to adjacent stems via lateral roots. Stems were sampled along a road cut and in an adjacent forest lightgap, 80 km north of Manaus. Total number of stems sampled is shown in parentheses (n).

although higher-cut stems produced more epicormic sprouts and fewer basal and lateral sprouts. Thus, *Vismia* in the primary forest has the capacity to resprout, although, as far as we know, resprouting has no role in its natural regeneration and may simply be derived phylogenetically. Root sprouting occurs in other Guttiferae genera, such as *Garcinia* and *Mammea*, as well as in the closely related African genus *Psorosperum*, which readily resprouts after fires (P. F. Stevens, pers. comm.).

In contrast to the lack of resprouts by *Vismia* species in forest light gaps, the fire and disturbance associated with pastures seem to stimulate massive resprouting. Following a pasture burn in October 1997 at the BDFFP's Colosso site, we carefully excavated all young shoots 1.0 cm or more in height along a 5 m transect from the base of stem-killed *Vismia* spp. adults in mid-December 1997 to determine whether the

shoots were basal resprouts from a previously existing stem, lateral resprouts from existing lateral roots, or newly germinated seedlings. The density of shoots varied by two orders of magnitude, from 125/m² for *V. cayennensis* to 16/m² for *V. guianensis* to 1.3/m² for *V. japurensis* (table 25.3). For *V. cayennensis* and *V. guianensis*, more than 99 percent of the shoots in the total area sampled (10 m²) were lateral resprouts, but *V. japurensis* produced as many basal sprouts as lateral sprouts (table 25.3).

Whereas *Vismia* spp.'s ability to resprout suggests adaptation to fire or disturbance, its root:shoot ratio is not one of a fire-adapted resprouter (see table 25.1). Root:shoot ratios of young *Vismia guianensis* seedlings were 1:2, a normal ratio for non-fire-adapted tree seedlings (Uhl 1987; Dias-Filho 1995). Under an annual burning regime, a seedling which would lose two-thirds of its biomass to fire would then have to triple in biomass, a growth increment of 200 percent, simply to regain its previous size. Such recovery is not impossible (Uhl 1987) but is unlikely on a sustained basis of annual burning, assuming that each year involves additional mortality risk from fire and reduced nutrient levels. However, in pastures under moderate use that are burned irregularly (for example, every second or third year), seedlings have ample time to recover and grow between fires. Pastures under light and moderate use frequently contain *Vismia* spp. clones, whereas heavily used pastures are often

TABLE 25.3. Number of Basal Sprouts, Lateral Sprouts, and Seedlings Two Months After a Pasture Fire

Species and tree number	Basal sprouts	Lateral sprouts	Seedlings
<i>Vismia cayennensis</i>	6	1,238	6
<i>Vismia guianensis</i>	0	154	2
<i>Vismia japurensis</i> #1	12	0	0
<i>Vismia japurensis</i> #2	2	17	0
<i>Vismia japurensis</i> #3	4	5	0

Note: Trees measured along a 5 m transect (10m²) from the base of stem-killed *Vismia* species.

void of *Vismia* spp. (Uhl, Buschbacher, and Serrão 1988; Nepstad, Uhl, et al. 1996).

The differential resprouting capacity of *Vismia* spp. and cecropia has led to the perception by some authors that *Vismia* species “thrive” on intensively managed land (Lucas et al. 1998). Actually *Vismia* spp., rather than thriving, are, at best, surviving relative to *Cecropia* spp., because both genera, along with other woody plants from the rainforest, are eliminated by repeated annual fires if the period of use is long enough (Fearnside 1990c; Nepstad, Uhl, and Serrão 1990). Thus, pastures subjected to heavy use, such as eight to ten years of frequent burning, as well as some weeding and mechanical scraping or discing, are nearly free of arboreal vegetation, *Vismia* spp. notwithstanding (Uhl, Buschbacher, and Serrão 1988; Nepstad, Uhl, and Serrão 1990).

There are no data on how many successive fires *Vismia* species can tolerate, but obviously many pastures are abandoned before all *Vismia* spp. individuals are eliminated. Throughout Amazonas, pastures abandoned after six to twelve years of moderate use (without mechanized disturbance or herbicides) have patches of *Vismia* clones (Uhl, Buschbacher, and Serrão 1988; Saldarriaga and Uhl 1991; Williamson, Mesquita, et al. 1998), leading to the misconception that *Vismia* spp. may be “fire-adapted.” Indeed, *Vismia* spp.’s apparent “success” in pastures results from pastures being degraded and abandoned faster than *Vismia* spp. are eliminated.

As active pastures age, they degrade through soil compaction, nutrient depletion, and invasion by weeds—all factors that contribute to the demise of arboreal vegetation. However, we believe that fire is the ultimate culprit and that cecropia, as well as other genera, are absent from pastures where they otherwise could readily flourish (Pereira and Uhl 1998). To test whether cecropia could

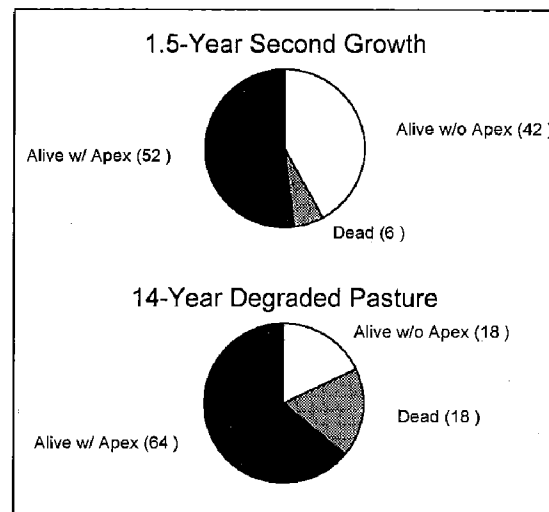


Fig. 25.2. Percentage of transplanted *Cecropia sciadophylla* that after two months were (1) alive with apical bud intact, (2) alive without the apex, or (3) dead, for two habitats, 1.5-year-old second growth and 14-year-old degraded pasture.

survive soil conditions in a moderately used pasture, we transplanted *C. sciadophylla* saplings, 1 to 3 m tall, from an area of 1.5 yr old second growth into a 7.5 yr old pasture where cecropia had been eliminated. For comparison, control saplings were dug up in the 1.5 yr old second growth and transplanted back into it. After two months the saplings were classified as alive with the apical bud intact, alive by epicormic or basal sprouting after death of the apical bud, or dead. The large apical bud, important in cecropia’s rapid growth, wilts when the saplings are transplanted. The bud’s survival is a measure of the sapling’s subsequent recovery. There were no significant differences in the responses of the transplanted cecropia saplings between the pasture and the second growth (fig. 25.2, Chi-square test of independence, 3×2 , $P = 0.06$).

To test the impact of fire on *C. sciadophylla*, the same pasture was burned two months after the saplings were transplanted, with the result that ten of the eighteen cecropia saplings that had survived the trans-

plant were killed. The fire, early in the dry season, was very light and resulted in an incomplete burn of the grass but still killed 55 percent of the cecropia saplings.

Another fact pointing to the importance of fire in the elimination of cecropia is the occasional cecropia individual in moderately and intensively used pastures. On close inspection, these individuals are invariably associated with rocky outcrops where grass will not grow or moist low pockets where fires are extinguished. These edaphic refugia are regular features of moderately used pastures, although they rarely fall within study plots that are usually located within the main extent of the grassland (Nepstad, Uhl, et al. 1996).

Dominated by woody vegetation, these edaphic pockets and other "tree islands" (*sensu* Nepstad, Uhl, et al. 1996) may play a crucial role as perches or feeding roosts for birds and bats that otherwise might not venture far into abandoned pastures (Guevara, Purata, and van der Maarel 1986; Gorchoy et al. 1993; Vieira, Uhl, and Nepstad 1994; Miritti 1998). The vertebrates, of course, are illustrious dispersal agents of seeds of second-growth trees, especially cecropia and *Vismia* spp. (Vázquez-Yanes et al. 1975; Fleming and Heithaus 1981; Estrada, Coates-Estrada, and Vázquez-Yanes et al. 1984; Gorchoy et al. 1993). Their importance cannot be overestimated because bird- and bat-dispersed trees make up about 80 percent of natural second growth in the Amazon rainforest (Charles-Dominique 1986).

Seed rain, via dispersers, may be crucial in the colonization of abandoned pastures because dormant seeds in the soil will have already germinated after successive years of exposure to full sunlight (Nepstad, Uhl, et al. 1996; Chapter 24). Of course, most of these seedlings will have perished if the pastures have suffered annual burns. If so, re-

cruitment of seedlings following the third or fourth fire may be limited to the annual seed input via the seed rain from the adjacent forest. Disperser movements into pastures will have a dramatic effect on the rate of recovery of woody vegetation (Charles-Dominique 1986; Gorchoy et al. 1993), and tree islands will have a dramatic effect on disperser movements.

Alternative Successional Sequences for the Central Amazon

The pattern of succession on abandoned agricultural land of terra firme in the central Amazon will depend on the history of land use (see Chapter 25). Where the forest is clear-cut and abandoned with little management for agriculture, pasture, or timber extraction, a high density of second-growth species, dominated by cecropia but including *Vismia* and *Bellucia* species, will regenerate from the forest seed bank to combine with a diverse recruitment of stump sprouts of primary forest species (Williamson, Schatz, et al. 1998). The forest will recover rapidly and maintain much of its vegetative species richness throughout the period of regeneration, as if a hurricane had simply snapped most of the trees (e.g., Vandermeer et al. 1995). However, clearing of old-growth forest is almost always followed by anthropogenic fire.

Where land management is very intensive and includes the use of fire, dormant seeds will be exhausted from the seed bank, and stump sprouts from most primary forest trees will be killed. Even a single fire to clear the slash will eliminate most primary forest sprouts and their nondormant seeds (Brinkman and Vieira 1971; Garwood 1989). The dormant portion of the seed bank is somewhat more resilient, as the seeds are drier and deeper in the soil where they are better protected from the heat of the fire. The

demise of the dormant seeds is brought about by the post-clearing exposure to full sunlight, which stimulates germination (Schafer and Chilcote 1970; Dias-Filho 1998) followed by subsequent fires that kill the emerging seedlings. Only such resprouting genera as *Vismia* will be maintained. Moderately used pastures after five to ten years of biennial burning contain an ample supply of resprouts of *Vismia* spp. The second-growth forests that dominate abandoned pastures are almost exclusively *Vismia* spp. and *Bellucia* spp. (Saldarriaga and Uhl 1991; Williamson, Mesquita, et al. 1998; Chapter 24). The latter genus is not an active resprouter but rapidly colonizes the clones of *Vismia* spp. sprouts, as seeds of both genera are dispersed by bats (Saldarriaga and Uhl 1991). *Bellucia* spp. gain some protection from fire by casting deep shade that hinders grass growth, thereby leaving the area around its trunk free of fine fuel from grasses. Presumably, fires burn cooler near *Bellucia* spp. trunks. For example, the primary forest at the Colosso Reserves of BDFFP was clear-cut in 1980 for pasture, used moderately for several years, and then abandoned in 1989. By 1997 it produced a second-growth forest dominated 92 percent by *Vismia* and *Bellucia* species (fig. 25.3). For trees larger than 5 cm DBH, we encountered only nine species outside these two dominant genera, in 676 m².

There is one report that the *Vismia-Bellucia* canopy and the historical conditions that created it may impede succession relative to the cecropia-dominated canopy and the conditions that created it; plant species richness recruited under cecropia canopies after nearly a decade was double that under *Vismia* canopies (Williamson, Mesquita, et al. 1998). *Vismia* species are extremely persistent as well, in other parts of the Amazon Basin (Saldarriaga 1985; Saldarriaga and Uhl 1991; Williamson, Mesquita,

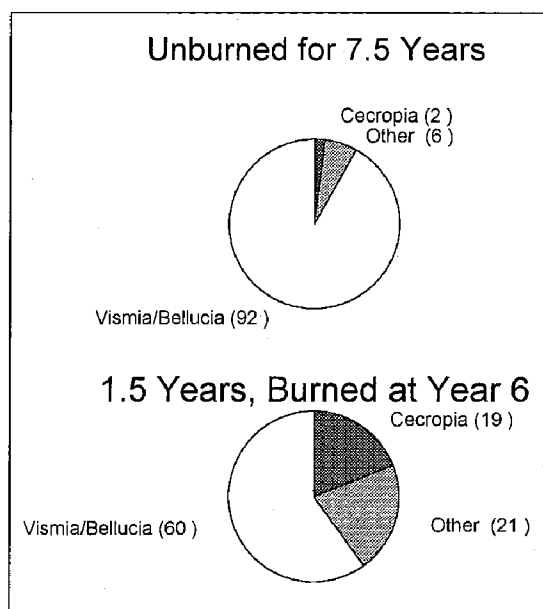


Fig. 25.3. Relative density in percent of *Cecropia* versus *Vismia* and *Bellucia* versus other genera in second growth derived from pasture abandoned for 7.5 years. In plots unburned for the entire 7.5 years, relative density is based on stems at least 5 cm DBH. In plots burned after 6 years, relative density in the 1.5-year-old regrowth is based on stems at least 1.5 m tall.

et al. 1998), and in French Guiana cecropia litter has been shown to be more effective than *Vismia* spp. litter in restoring soil conditions that facilitate the return of the mature forest species (Maury-Lechon 1991). If *Vismia* spp. and *Bellucia* spp. inhibit succession relative to cecropia, then land management of abandoned pastures may harbor some surprising techniques to diversify the pioneer community (see also Chapter 24).

Using Fire to Increase Biodiversity of Abandoned Pastures

A portion of the *Vismia-Bellucia* dominated pasture at the Colosso Reserves was burned at the end of 1995 with some interesting results. The fire killed nearly all the above-ground stems, although some stems re-

sprouted from the base. However, resprouting was much more frequent by smaller individuals than by larger individuals, so the pre-fire dominant individuals were either killed by the fire or resprouted from their smaller lateral roots. This pattern of decreased probability of resprouting by larger individuals following crown death is common among fire-adapted resprouters (Rebertus, Williamson, and Moser 1989), although it has never been examined in rainforest trees. With the prior canopy stems dead, resprouts were small and unable to completely dominate the recovery, so many seeds germinated from the then 6 yr old seed bank to provide a more diverse community of pioneers. Some of these pioneers may have entered from seed rain after the fire, and we do not know the relative contributions of resprouts, the 6 yr old seed bank, and the post-fire seed rain, but the density of seedlings early after the fire is indicative of a significant contribution by the seed bank. A comparison of the 7.5 yr old pioneer community (larger than 5 cm DBH) to the 1.5 yr old pioneer community (stems taller than 1.5 m) indicated a dramatic increase in *Cecropia* individuals and other non-*Vismia*, non-*Bellucia* pioneer genera (e.g., *Solanum*, *Trema*, *Laetia*, *Goupia*, *Miconia*). On average, dominance of *Vismia* spp. and *Bellucia* spp. dropped from 92 percent to 60 percent as a result of the fire (fig. 25.3).

The result that burning a young *Vismia-Bellucia* stand increased species richness is somewhat counterintuitive because annual or biennial fires were the cause of the loss of diversity when the forest was cleared. Time since abandonment and the last fire, in this case six years, had two important effects. First, with time, the stand developed a canopy that probably increased visitation by forest birds and bats dispersing seeds (e.g., Chapter 20), thereby restoring a diverse soil seed bank. Second, the dominant trees be-

came large enough that they were unable to produce large resprouts following crown death in the fire, thereby leaving regeneration to the seed bank and resprouts of smaller individuals.

Whether that diversity will be maintained through the early years of succession remains unknown. It is notable that some of the new pioneer genera (*Cecropia*, *Solanum*, *Trema*) were among the tallest saplings in the study plots, so they are not likely to be suppressed by *Vismia* and *Bellucia* species. It is also unknown whether the net gain in biodiversity will compensate for the lost time—for example, ten years into the future will today's *Vismia-Bellucia* dominated stand at age 17.5 yr still be less diverse than today's burned stand at age 11.5?

Conservation Lessons

1. Clear-cutting of the rainforest, followed by moderate and heavy use as pasture, will leave a depauperate woody flora with few resprouts from the original forest and a seed bank exhausted of forest species; succession to a primary forest will be very slow and perhaps diverted unless steps are taken to increase the diversity of the pioneer and early secondary species. How this enrichment is attempted will vary among sites, land use histories, and status of other forests in the surrounding landscape.
2. Increasing the number of woody trees, which provide perch sites or feeding roosts, prior to abandonment or in the first one to two years of succession may have a dramatic effect of increasing the rate of seed rain from forest trees and the rate of forest regeneration.
3. Artificial seeding of diversifying pioneer genera (*Cecropia*, *Trema*, *Solanum*, *Stryphnodendron*, etc.) will facilitate succes-

- sion, although care must be taken to create favorable conditions for seed germination and seedling establishment; for example, seeding at the beginning of the rainy season following the last dry season fire when graminoid cover is reduced (Miriti 1998).
4. The two options above require land owners or land managers to have the foresight to take action around the time that land is abandoned and to have the necessity, perhaps by law (Uhl, Barreto, et al. 1998), to implement steps to facilitate forest regeneration. Where three to ten years have elapsed following abandonment and the regeneration is completely dominated by *Vismia* and *Bellucia*, another option may be necessary to foster biodiversity.
 5. Prescribed burning may produce a more diverse flora, but only under certain conditions. The fire must be intense enough to kill most of the dominant canopy trees, *Vismia* and *Bellucia*, but not sufficiently intense to kill seeds in the seed bank and most surface roots. The fire must be prescribed for small to medium parcels so that other remaining wooded parcels can maintain the community of seed dispersers. And finally, the fire can be controlled to preclude damage to adjacent secondary forests and edges of primary forests.
 6. Where fire is applied outside the above conditions, it will have a negative effect of setting succession back in the burned

plot if the seed bank is destroyed or of reducing the diversity of the landscape if the fire permeates adjacent, mature forests. We are reluctant to recommend the use of prescribed burns because fire, improperly applied, is extremely destructive. However, the apparent alternative of cutting the existing dominant trees will impede, not facilitate, succession as they will resprout with a fury only to yield the same *Vismia-Bellucia* community. Certainly more experimental research into prescribed fire is essential before any broad scale application is implemented.

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