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Secondary Succession Under a Slash-and-burn Regime in a Tropical Montane Cloud Forest: Soil and Vegetation Characteristics

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Successional forest stand dominated by *Pinus Chiapensis*; Sierra Norte, Oaxaca, Mexico.

Tropical montane cloud forest (TMCF) areas in southern Mexico are commonly used for growing maize and companion crops under slash-and-burn agriculture. As a result, the landscape is being transformed into a mosaic of crop fields, secondary forest and primary forests. Despite being a widespread process, very little is known about forest regeneration in TMCF areas. This chapter describes secondary succession in the TMCF of El Rincón Alto, Oaxaca, Mexico, with particular reference to soil and vegetation characteristics, taking advantage of successional chronosequences spanning a century of forest development. Cultivation practices cause severe losses of soil and carbon; the original vegetation and soil organic horizons vanish. Such effects are reversed, in part, during earlier stages of secondary succession. Soil layers, including those with organic horizons, begin to accumulate. Epiphytes, low-stature plants and shrubs begin to colonize very early during succession. Species richness of shrubs, geophytes and low stature plants peak within the first 15 years after abandonment. The largest recorded decline in concentration of soil cations, and the highest annual rates of soil carbon sequestration also characterize this period. A pine-dominated community characterizes the first 10–75 years. Early successional species do not prosper under this forest canopy and an emergent stratum of broadleaf trees eventually replaces the former pine forest. Colonization of trees, lianas and climbing plants exceed local extinction rates during the first century of forest development. The dominant groups of terrestrial and epiphytic plants are trees and liverworts, respectively, during all studied stages of forest development. Self-thinning of the first colonizing trees took place between 45 and 75 years after abandonment and coincided with a second increase in abundance of shrubs and other low-stature plants, but tree basal area did not decline significantly. Species of terrestrial plants typical of early stages are rare or absent in late successional stages. Thus, disturbances generated by autogenic processes such as natural tree-fall are different from allogenic disturbances such as fires and landslides. Soil becomes increasingly acidic and infertile during forest development, a problem that is aggravated by the presence of soluble aluminium. Such acidity fosters mineral hydrolysis, releasing cations to the soil. Soil N/P ratios steadily decrease during forest development. We conclude that environmental changes derived from slash-and-burn processes increase landscape and species diversity under the long fallow regimes observed.

Introduction

Disruption of the original forests of the world by anthropogenic disturbances is becoming increasingly common and widespread. Of these, deforestation, which refers to the complete elimination of the original vegetation cover, is one of the most frequent sources of disturbance in forests. If the disturbance that destroyed the original vegetation ceases, the ecosystem may undergo a series of changes involving the colonization of a diverse suite of organisms, which, in turn, are replaced by others. This process is referred to as secondary succession. Short-term microclimatic and soil changes are inherent features of secondary succession and may critically affect the outcome of succession (Huston and Smith, 1987; Glenn-Lewin and van der Maarel, 1992).

One of the ecosystems most affected by deforestation is tropical montane cloud forest (TMCFs) (Aldrich and Hostettler, 2000; Chapter 2). A persistent, frequent or seasonal cloud cover at vegetation level characterizes this ecosystem. Compared to lowland tropical rainforests, TMCFs usually occur at higher elevations, the stature of trees is lower and epiphytes are more common (Hamilton *et al.*, 1995). TMCFs are among the most endangered ecosystems in the world

owing to land clearing mostly for agriculture or cattle raising (Churchill *et al.*, 1995; Webster, 1995; Rzedowski, 1996; Bruijnzeel and Hamilton, 2000).

Understanding the underlying process of secondary succession in TMCF areas is critical for several reasons. First, owing to the high rates of deforestation and other types of forest disturbance, most of the forest remnants are becoming secondary. Second, in many tropical areas of the world, including TMCF areas, land is managed under the slash-and-burn rotation system, in which the location of the cultivated area is changed in a regular sequence, thus generating fallow periods (Manshard, 1974). Such periods enable the forest to regenerate to an extent dependent on a range of factors, not all of which have been completely characterized. Secondary succession is therefore a key process in landscapes subjected to shifting cultivation. The search for improved methods of land management requires a deeper understanding of successional processes following forest clearance. Third, ecological restoration is becoming increasingly important given the urgent need to rehabilitate areas of degraded forestlands for conservation purposes and for improved provision of ecosystem services. Secondary succession is the natural and cheapest way to regenerate natural ecosystems. Developing forest regeneration practices requires an understanding of how forests regenerate naturally after anthropogenic disturbance. Restoration and conservation in TMCF areas are particularly important because these ecosystems play a key role in environmental services such as carbon sequestering and water provision (Doumenge *et al.*, 1995), and their disruption may aggravate environmental problems such as global warming (Aldrich and Hostettler, 2000). Moreover, TMCFs are among the richest forests in terms of biodiversity and are characterized by high numbers of endemic species (Rzedowski, 1991; Webster, 1995). Deforestation therefore causes significant losses of biodiversity in TMCF areas. Finally, one of the most important topics of research in ecology is elucidating the factors that drive the dynamics of communities and thus influence species diversity and abundance. The study of secondary succession can be a useful tool for understanding such factors as the entire process involves species replacement. It is still little known to what extent the species assemblage in a community is driven by the characteristics of the species, relating to their niches or functional roles, or by factors such as chance and random dispersal (Hubbell, 2001).

Ideally, the study of secondary succession would involve following an ecosystem over long periods of time after the disturbance that destroyed the original vegetation. However, because of the long time scales involved, this approach is impractical in most cases. For this reason, modelling approaches are widely used to explore successional processes in forests (see Chapters 9–11). Alternatively, the chronosequence approach or space-by-time substitution can be used to study succession, in which neighbouring stands with different ages after disturbance are compared under the assumption that the observed between-stand differences can be attributed to age after abandonment (see Glenn-Lewin and van der Maarel, 1992; Foster and Tilman, 2000). Of course, time is not the only factor that may change the characteristics of such stands. Local environmental variation may have a profound influence

on plant community structure and composition (e.g. del Castillo, 1999). It is therefore necessary to estimate the magnitude of the effect of time after disturbance relative to other local factors that may also influence the characteristics of forest stands. This can be achieved by studying several chronosequences composed of similar stages in the same area. In this way, conventional analysis of variance techniques can be used to assess the relative importance of within-age to between-age changes in the properties analysed (e.g. Bautista-Cruz and del Castillo, 2005). Despite the advantages of this approach, relatively few studies of multiple successional chronosequences have been undertaken in forest ecosystems, and we are aware of no such prior investigation performed within TMCFs.

This chapter compiles results from a recent study of secondary succession performed in El Rincón Alto, Oaxaca, Mexico, involving assessments of soil characteristics, terrestrial vegetation and epiphytes, in an area originally occupied by TMCFs, used for maize cropping, and later abandoned. This study was based on analyses of three chronosequences sharing similar ages after disturbance, located within the same area. Such replicates allow the relative effect of time after abandonment on the ecosystem changes studied to be evaluated. This information is used to describe general patterns of change in soil and vegetation during secondary succession and their ecological and conservational implications.

The Study Site

The study area is located in the Sierra Madre de Oaxaca Mountain Range, and is part of El Rincón Alto region in Oaxaca state, southern Mexico, at 1850 ± 150 m altitude, where TMCF is the primary vegetation. Topography is usually steep (15–64%). The climate is temperate-humid to subhumid (Comisión Nacional para el Conocimiento y uso de la Biodiversidad, 1998). The average annual temperature ranges between 20 and 22°C. The average annual precipitation at the nearest meteorological station (c.16 km from the study site) is 1719 mm/year, with a rainy season in summer and a dry season in winter (Instituto Nacional de Estadística, Geografía e Informática, 1999). The soil lies on a bedrock of schist from Mesozoic (Consejo de Recursos Minerales, 1996).

Secondary Succession and the Slash-and-burn System of Management

Understanding the process of secondary succession in humid montane areas of Mexico can only be fully accomplished by considering the systems of land management in these areas. Maize cropping ('milpa') in association with companion crops, such as squash and beans, is the main system of land management, used by all ethnic regions of Sierra Madre de Oaxaca, including the Zapotec to which El Rincón Alto belongs (Boege, 1988). Maize is grown under

the slash-and-burn method of cultivation. First, an area of the forest is cleared by tree felling, drying of the plant material and burning of the material. Maize is cultivated for several years, after which time cultivation moves to another piece of land. In the previously cultivated land, a fallow period commences, allowing the development of secondary vegetation. The length of the fallow period varies widely from one region to another, and tends to decline as human population size increases. At the study site, however, at least three social factors have allowed the recovery of secondary forest for periods of time sometimes longer than a century, by reducing anthropogenic pressures on the land in certain portions of the Sierra. First, low population densities and emigration rates are common in these areas (Instituto Nacional de Estadística, Geografía e Informática, 2003). Second, entire towns were displaced, reducing the pressure on the land adjacent to the former locations of the towns (López-Chavez, 1953). Finally, shifts in the economic activities of the landholders have resulted in former maizefields at higher altitudes being permanently or semi-permanently abandoned for 60 years or more. In particular, the introduction of coffee plantations at lower altitudes in the Sierra reduced pressure in areas above 1500 m, many of which were used for growing maize. Moreover, certain municipalities, such as that of San Juan Juquila Vijanos, have agreed to leave untouched portions of their forest as a natural reserve, which is secured to avoid furtive exploitation. As a result, the landscape is a mosaic of maizefields, secondary forests of different ages after abandonment, and primary forests.

Three chronosequences were selected for study: Tanetze, Juquila and Yotao. Each chronosequence consisted of a series of stands of different ages after abandonment with the same climate and parent material, and similar topography. The approximate ages were 0, '15, '45, '75 and >100 years after abandonment (Fig. 7.1). These age estimates were based on: (i) the estimated age of the shade-intolerant pioneer tree *Pinus chiapensis*, obtained from ring counts using increment borers; (ii) the floristic composition and vegetation structure of the stands, in particular the abundance and size of tree species typical of primary TMCFs (see below); and (iii) the opinion of the local people regarding the age rank of the stands. The age of *P. chiapensis* gives only an approximate estimate of the time after abandonment, as establishment of this species usually does not take place immediately after abandonment. These three procedures gave the same rank category to each of the studied stands (for details, see Bautista-Cruz and del Castillo, 2005).

Changes in flora

During the Maize (*Zea mays*) cropping phase, bracken ferns (*Pteridium* spp.) are the most common weeds. Herbaceous or shrubby weeds of the Asteraceae, Melastomataceae, Phytolacaceae, Poaceae, Rubiaceae and Smilacaceae families are also present. Cultivation at the study site is typically short-lived, lasting 3–5 years. Grasses, shrubs and forbs prosper during the first few years after abandonment, but are eventually shaded out by short-lived light-demanding pioneer species, which dominate the first stages of succession.

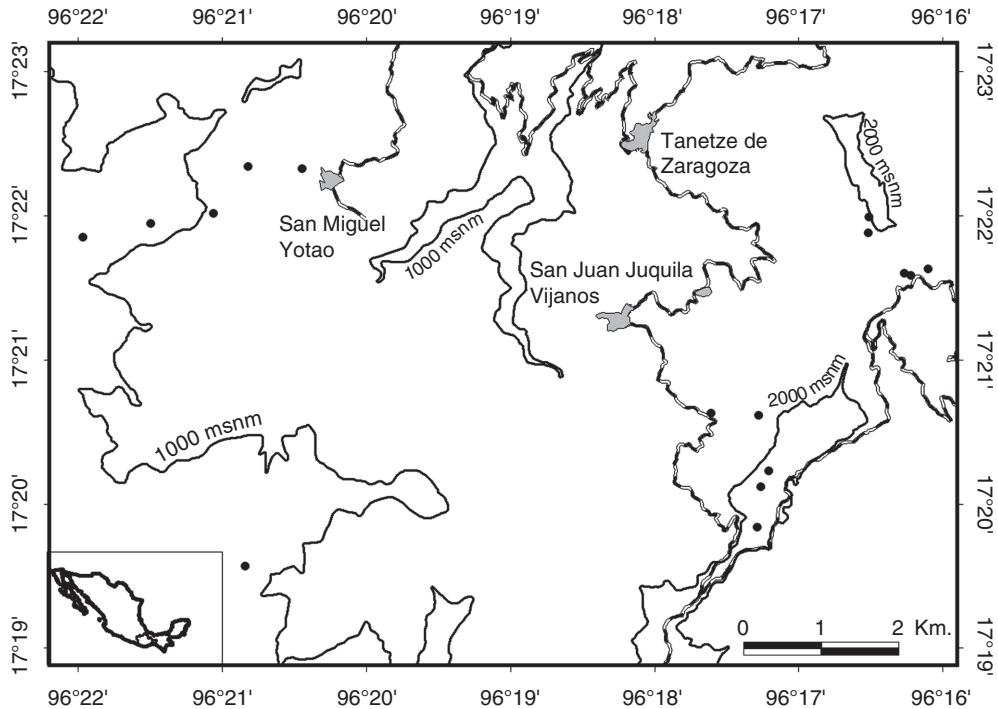


Fig. 7.1. Map of El Rincón and the study sites used for successional studies (from Cordova and del Castillo, 2001).

Ferns such as *Pteridium* spp., *Gleichenia palmata*, *Gleichenia bancroftii* and *Odontosoria schlechtendalii*, and shrubs such as *Tibouchina scabriuscula* are also common in recently disturbed places. Forest regeneration is accomplished not only by incoming propagules but also by plants with subterranean perennial tissues that have persisted during the cultivation phase. Bracken ferns are one of the best examples, as they persist as rhizomes even when their aerial parts are removed during weeding activities. This fern is also the first to be noticed in recently burned forests (R.F. del Castillo, CIIDIR Oaxaca Instituto Politécnico Nacional, Santa Cruz Xoxocotlán, Oaxaca, Mexico, personal observation).

The first forest to appear, approximately 10–15 years after abandonment, is dominated by *P. chiapensis*. Other important species are: *Clethra integerrima*, *Gaultheria acuminata*, *Liquidambar styraciflua*, the sweetgum and *Phyllonoma laticuspis*. Some young localized stands are dominated by sweetgum. The proximity of the trunks of this species leads to the suggestion that many of the plants of sweetgum observed in such stands are clonal. At '45 years *Bejaria mexicana*, *Clethra kenoyeri*, *P. laticuspis* and *Vaccinium leucanthum* are the most common species. After this stage, self-thinning takes place, and pine trees eventually are replaced by hardwoods. Thus, the previous species, together with *Persea americana*, *Quercus* spp., *Rapanea* spp. and *Ternstroemia hemsleyi* are common in forests of '75 years old. Old-growth forest 100 years old or

older also contains *Beilschmiedia ovalis*, *Freziera* sp., *Osmanthus americana* and *Quetzalia occidentalis* as common species (Blanco-Macías, 2001). In primary forest, *Billia hyppocastanea*, *Oreopanax flaccidus*, *Podocarpus matudae*, *Quercus* sp., *Quercus corrugata*, *Quercus salicifolia*, *Symplocos coccinea*, *Ternstroemia oocarpa* and the species observed in old-growth forest stands are among the most conspicuous species (Cordova and del Castillo, 2001) (Table 7.1). The original vegetation is an upper TMCF *sensu* Webster (1995). With the exception of few shrubs at early successional stages, the family Leguminosae was virtually absent in the TMCF areas studied. This is one of the most distinctive floristic differences with lowland tropical forest, where legumes are usually one of the richest families in terms of species numbers (Gentry, 1988).

Table 7.1. Common species of successional chronosequences in El Rincón Alto region in Oaxaca.

(a) Species typical of secondary forest, which are absent or rare in old-growth forest, but are among the most conspicuous and abundant in secondary forests:

Brunellia mexicana Standley
Kohleria deppeana (Schldl. and Cham.) Fritsch
Pinus chiapensis (Mart.) Andresen
Podochaenium pachyphyllum (Klatt) Jansen, Naudin
Tibouchina scabriuscula (Schltdl.) Cogn.
Rubus spp.

(b) Species typical of old-growth forest:

Bejaria laevis Benth.
Beilschmiedia ovalis (Blake) C. K. Allen
Begonia hydrocotylifolia Otto and Hook.
Billia hippocastanum Peyr.
Chamaedorea liebmannii Marttens, M.
Dendropanax populifolius (Marchal) A.C. Smith
Drimys granadensis A.C. Smith
Greigia sp.
Maianthemum paniculatum (Mart. and Gal.) La Frankie
Marattia weinmanniifolia Liebm.
Ocotea helicterifolia (Meissn.) Hemsley
Oreopanax xalapensis (Kunth) Decne. and Planchon
Osmanthus americana (L.) Benth. and Hook.
Parathesis tenuis Standley
Passiflora cooki Killip
Persea liebmannii Mez
Psychotria galeottiana (Mart.) Taylor and Lorence
Quetzalia occidentalis (Loes.) Lundell
Quercus leiophylla A. DC.
Quercus salicifolia Née
Styrax argenteus var. *ramirezii* (Greenm.) Gousolin
Symplocos pycnantha Hemsley
Ticodendron incognitum Gómez-Laurito and Gómez-P.
Weinmannia pinnata L.

Changes in terrestrial vegetation

Whereas many studies of succession in forests have focused on trees, there are reasons to consider all groups of terrestrial vascular plants as they have different functional roles and may influence each other during succession. Even in other better-studied systems such as temperate forests, the responses of other groups of plants are not very well understood (e.g. Gilliam *et al.*, 1995). In terms of their functioning roles in the ecosystem, some plant species may be effectively redundant (Wilson, 1999). However, this is not true for plant life forms, which may constitute natural associations that can be examined separately. If community dynamics is shaped by the functional role of species, then each life form should follow different patterns of change during succession that can be predicted in terms of their ecology. Otherwise, such changes should be random and independent of their life form. Classification of the plants on the basis of their functional role is not trivial, as many traits can potentially be considered (e.g. Díaz *et al.*, 1999). Following a system similar to that of Raunkiaer, but including growth habits as well, Blanco-Macías (2007) classified the vascular plants of successional forests at El Rincón as geophytes, shrubs, trees, lianas (including climbing plants) and 'low plants' (including herbs and other low-stature plants, such as trailing plants). Such a classification, though not ideal, has several advantages, as it considers the vertical structure of the community, in particular their relationship with light (see Whittaker, 1975). Height appears to be of chief importance in competition for light and for influencing succession (Huston and Smith, 1987). Plant height is also positively correlated with other important plant attributes such as seed size, which influence dispersal (Leishman *et al.*, 1995). Furthermore, this classification is easy to apply without an extensive knowledge of the biology of the species. Finally, several simple hypotheses can be constructed regarding the general trends of change in life form abundance with succession. By virtue of their low stature and short life cycles, low plants, in the first place, and geophytes in second should be more abundant at earlier stages of succession before taller plants shade out the forest floor, limiting the availability of space and light. Shrubs should follow, before trees reach their maximum height. Colonization by trees should be slower by virtue of their longer life cycles and their overall larger seed sizes, which might limit dispersal (see Leishman *et al.*, 1995). Therefore, trees should be more abundant and diverse at later successional stages. Similarly, lianas and climbing plants require support from other plants, and therefore should prevail at intermediate or late stages of succession.

Changes in vegetation during succession at El Rincon were studied by means of ten (nine in two sites) 2 × 50 m plots established for trees in Yotao, Tarantulas and Juquila chronosequences, which were used for sampling plants >3.5 cm diameter at breast height (dbh). Within each of these plots, two subplots of 2 × 2 m were randomly established in which all freestanding plants were identified, mostly to the species level, measured and mapped (Blanco-Macías, 2007).

Results indicate that the highest rate of increase in tree density takes place during the first 15 years of forest development. This rate decreases over the next 30 years in such a way that tree density peaks in stands of *c.*45 years age. After that time, self-thinning reduces tree density to approximately 30%, reaching a local minimum at *c.*75 years. A small increase in tree density is detected subsequently (Fig. 7.2). Despite the marked decline in density after 45 years, no equivalent decline was observed in basal area. Tree basal area, an estimate of tree biomass, increased during the first century of forest development, with the highest increase during the first 45 years (Fig. 7.2) (Blanco-Macías, 2001). Thus, these results are consistent with the logistic biomass accretion model in which biomass increases towards a maximum, at least regarding trees, which are by far the dominant group of plants in TMCF areas, and contrast with other models that predict a dramatic decrease in biomass associated with the thinning phase (Peet, 1992). A study performed on *P. chiapensis*, the dominant species at earlier stages of succession in the study area, shows evidence that the highest rate of mortality takes place among the slowest growing trees (del Castillo, 1996). Thus, the loss of biomass by mortality of trees during self-thinning appears not to be great and trees that survive self-thinning, which are probably the largest plants, are likely to have achieved higher growth rates following release of competition. Indeed, some evidence of release of resources is indicated by an increase in concentration of nutrient cations detected in soil after self-thinning in some of the chronosequences (Bautista-Cruz and del Castillo, 2005).

As predicted, the density of geophytes, shrubs and low plants increased at higher rates than that of trees during earlier stages of succession, showing

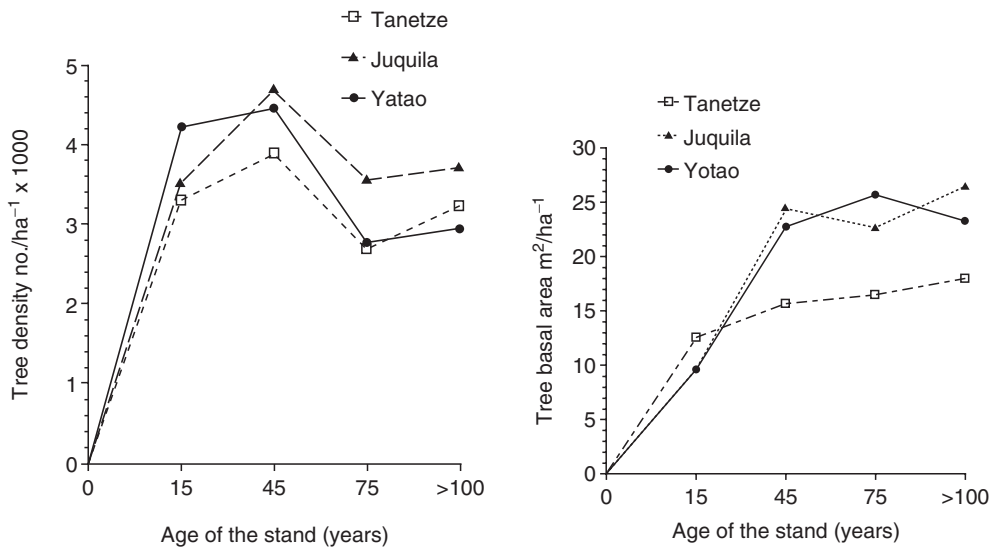


Fig. 7.2. Relationship between tree density (left) and tree basal area (right) with the approximate age of the stand after agricultural use in Tanetze, Juquila and Yotao chronosequences in el Rincón, Sierra Norte, Oaxaca (after Blanco Macías, 2001).

peaks in density during the first 15 years after abandonment, and a decline following this age reaching a minimum between 45 and 75 years (Blanco-Macías, 2007). Such a decline coincides with the period at which trees achieve their maximum density and basal area (Fig. 7.2). Thus it is likely that trees inhibited the development of low stature plants, probably by diminishing light availability, and reducing soil nutrients and water availability (see below).

From the first 15–45 years of stand development, *P. chiapensis* dominates, and the entire vegetation appears like a typical pine forest. However, shade-tolerant plants such as *B. ovalis*, *Freziera* sp., *Magnolia dealbata*, *O. americana*, *P. americana*, *Quercus* spp. and *Rapanea* spp. establish on the shaded floor of early successional forest and start growing, to create a stratum intermediate in height between that of pine trees that create the forest canopy, and that of shrubs and low-stature plants. Pine trees therefore appear to facilitate the establishment of shade-tolerant plants, but at the same time inhibit their own establishment and that of low-stature plants, *P. chiapensis* itself being shade-intolerant as a young plant (del Castillo, 1996). After a century of forest development, only a few large old pine trees remain, and the forest is dominated by broadleaf species of trees. Pine forests are therefore secondary at mid-elevation tropical montane and humid areas. The same conclusion was reached by Gonzalez-Espinosa and colleagues in Chiapas Highlands (González-Espinosa *et al.*, 1991; Ramírez-Marcial *et al.*, 2001).

A greenhouse study revealed that *P. chiapensis* is a slow-growing plant compared to angiosperm trees such as *Brunellia mexicana*, a species typical of early successional stages, and species such as *T. hemsleyi* and *Ilex pringle* of late successional stages (Hernández Pérez, 2001). Therefore these results do not support the predictions that plants at early stages of succession are relatively fast growing (Huston and Smith, 1987). Perhaps the success of *P. chiapensis* at early successional stages can be explained by its high seed input (Pérez-Ríos and del Castillo, in preparation), and the ability of the seeds to establish successfully on recently created open areas (R.F. del Castillo, in preparation).

Gaps in the forest canopy are created by natural tree-falls. However, compared to lowland tropical forest (Martínez-Ramos, 1985), we do not have evidence that gaps opened in secondary forest in TMCF areas can be colonized by pioneer trees typical of secondary forest. As mentioned above, such species are virtually absent in old-growth and primary forests. Gaps are rapidly covered by grasses and ferns, and the shrubs and low-stature plants that have already established expand their canopies, rapidly shading such gaps at ground level. Earlier colonist plants such as *P. chiapensis* rapidly become locally extinct due to their inability to establish successfully in the forest, even in natural gaps. An ongoing study of *P. chiapensis* demography has shown that although seedlings of this species can establish during the first years after the gap was created, eventually all seedlings die, presumably by shading and competition with faster-growing grasses and other low-stature plants (R.F. del Castillo, in preparation). Without severe disturbance, for instance fires or landslides, early successional species are virtually absent in primary and old-growth forest. This kind of pattern is not compatible with

models of forest dynamics such as the shifting-mosaic steady state (see Urban and Shugart, 1992). This model envisioned the forest as a mosaic in which individual patches of the forest are in different stages of succession at any given time by virtue of gap formation. In the TMCFs studied, gap colonization appears to be a different process to the succession that follows the anthropogenic disturbance that destroyed the original vegetation. In other words, no pine forest patches are located within old-growth forest by virtue of tree-fall gap formation. Autogenic processes, such as natural tree falls, appear to generate different patterns of regeneration than allogenic process such as fire or landslides in TMCF areas.

As seen in Fig. 7.3, the patterns of change in species richness during succession obtained from Colwell *et al.*'s (2004) rarefaction method show that each plant group follows different trends of change during the first century of forest development. Trees were, by far, the group with the highest species richness at all successional stages analysed. As predicted, tree species richness increased steadily during the first century of forest regeneration. By contrast, low-stature plants such as geophytes, shrubs and low plants exhibited a peak in species richness during the first 15 years after abandonment, followed by a later decline, displaying a small increase coincident with self-thinning, following a similar trend to that observed for stem density (Blanco-Macías, 2007). As expected, lianas and climbing plants followed a similar pattern to that of trees, which provide support to them. Overall, these results suggest that the rates of colonization of trees, lianas and climbing plants exceed the rates of local extinction during the first century of forest development, whereas colo-

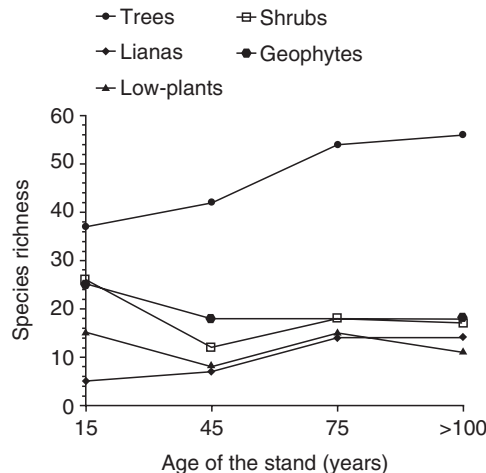


Fig. 7.3. Changes in species richness, obtained from Colwell *et al.*'s (2004) rarefaction method, during secondary succession in TMCFs. Different growth forms are illustrated, namely trees, shrubs, lianas, geophytes and low plants, during the first century of forest development in el Rincón Alto, Sierra Madre de Oaxaca, southern Mexico (from Blanco Macías, 2007).

nization rates of geophytes, shrubs and low plants exceed local extinction rates mostly during the first 15 years of forest development.

Changes in abundance of epiphytes

The changes in cover of six groups of epiphytes, micro-lichens, macro-lichens, liverworts, mosses, vascular plants and microscopic epiphytes (i.e. unidentified microscopic plants including protonema, green algae and cyanobacteria) were studied in the three chronosequences described above and in an adjacent primary forest. The epiphyte cover area was estimated in four 100 cm² grids at four height levels, 0–10, 50–60, 100–110 and 150–160 cm from the base of the trunk of the host plants, in 24 tree trunks in each stage and chronosequence (Cordova and del Castillo, 2001). The relationship of the age of the stand with total epiphyte cover followed a sigmoid pattern, with the highest rates of increase between 15 and 45 years after abandonment (Fig. 7.4). The patterns of colonization during succession were different for all groups studied. The group to colonize the trunks most rapidly were leafy liverworts (order Jungermanniales), which were the dominant epiphytes at all the seral stages studied. Mosses displayed the second highest rates of colonization and were also second in terms of cover at all stages. Vascular plants were the slowest group to colonize tree trunks. Of these, ferns colonized first, and orchids and bromeliads were the latest to colonize. In contrast, the absolute cover of micro- and macro-lichens were not significantly affected by the age

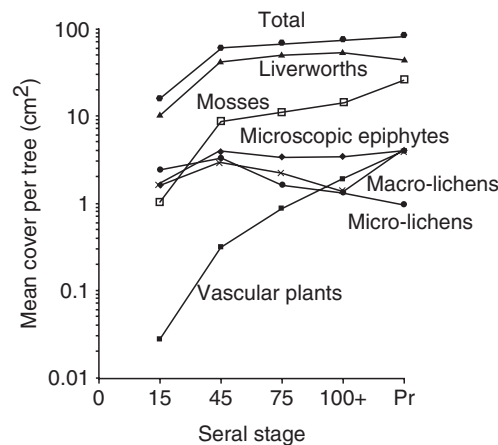


Fig. 7.4. Relationship between the absolute cover of total epiphytes, liverworts, mosses, macro lichens, micro lichens, vascular plants and microscopic epiphytes in four 1 dm² plots per tree, examined on the lower portion of the host tree with the approximate age of the stand after agricultural use in El Rincón, Sierra Norte, Oaxaca, Mexico. Average cover was examined in 72 trees in each seral stage of three chronosequences and 24 trees from an adjacent primary forest (Pr) (modified from Córdoba and del Castillo, 2001).

of the stand. However, the relative cover of micro-lichens on tree trunks decreased with stand age, following an opposite trend to vascular plants. Epiphyte cover was negatively related to the diameter of the host trunk in all stands except in the primary forest, suggesting that colonization is not limited by space during the earlier stages of succession, probably because the increase in diameter of the tree trunks takes place at higher rates than the capability of epiphytes to colonize them. The colonization of trunks by epiphytes may take 100 years or more to achieve the values observed in primary forest (Cordova and del Castillo, 2001).

Soil processes during secondary succession

Slash-and-burn imposes severe changes to the soil system in TMCF areas of southern Mexico, affecting soil genesis and mineralization (Bautista-Cruz *et al.*, 2005). Indeed, during the cultivation stage, the O, A and B horizons of the soil are lost by erosion. Soil losses are probably fostered by heavy rains and steep slopes, typical of TMCF areas, in conjunction with the lack of any practice of soil retention and the sparse vegetation cover of cornfields. As a result, soil rejuvenates and the pedogenic processes appear to reinitiate, forming entisols in the cornfields. After the cultivation period, secondary succession promotes soil evolution, in particular the rapid formation of a B horizon and the development of an O horizon. Therefore, all the studied profiles of soils from forest stands were classified as inceptisols (Bautista-Cruz *et al.*, 2005).

The most dramatic changes in soil properties usually took place during the first 15 years of abandonment after agricultural use. These include the highest drop in the soil concentrations of exchangeable K, Mg and Ca (Fig. 7.5).

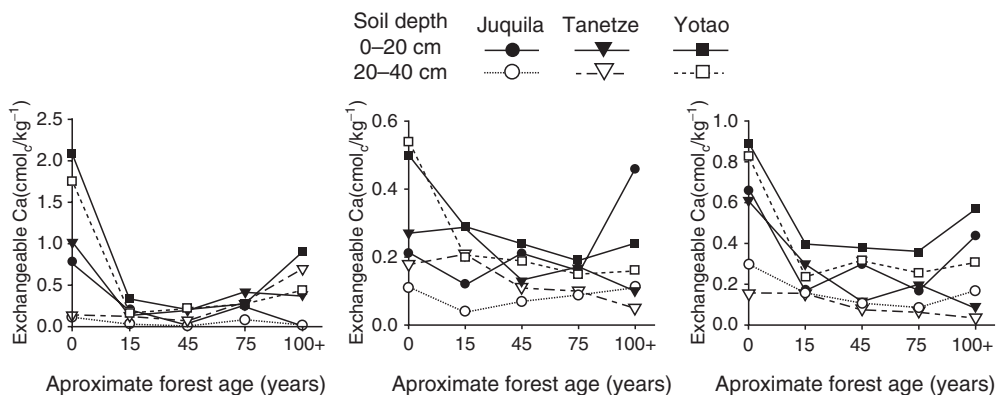


Fig. 7.5. Patterns of response to the age of the stand (mean values) for exchangeable calcium, potassium and magnesium at 0–20 and 20–40 cm soil depths in three chronosequences in a tropical montane cloud forest area in El Rincón, Oaxaca, Mexico (from Bautista-Cruz and del Castillo, 2005). (Reproduced with permission from Soil Science Society of America, 677 S. Segoe Rd, Madison, Wisconsin 53711, USA.)

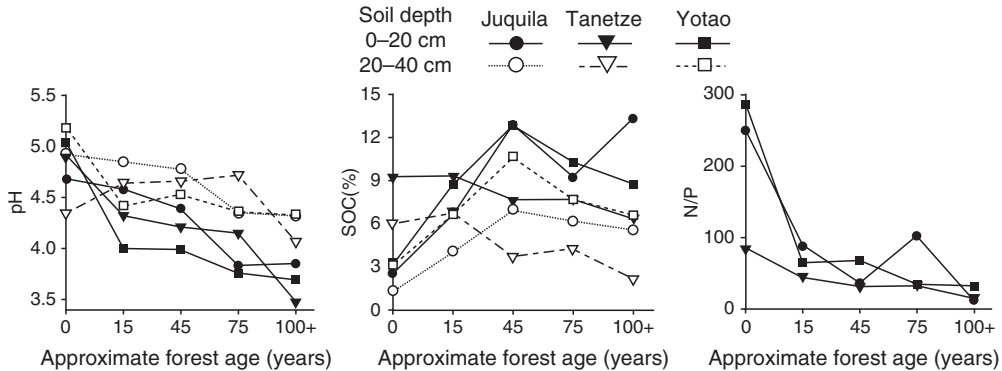


Fig. 7.6. Patterns of response to the age of the stand (mean values) for soil organic matter, in three chronosequences in a tropical montane cloud forest area in El Rincón, Oaxaca, Mexico (from Bautista-Cruz and del Castillo, 2005). (Reproduced with permission from Soil Science Society of America, 677 S. Segoe Rd, Madison, Wisconsin 53711, USA.)

This result can be explained in part by the rapid growth of the vegetation in that time interval, and the increase in soil acidity. Soil organic matter (SOM) accumulated at higher rates than it decomposed (Fig. 7.6). Stands of 45 years or younger had only undecomposed and partially decomposed SOM. By contrast, stands of 75 years or older had undecomposed, partially decomposed and highly decomposed SOM. In the old-growth forests, SOM was strongly humified, and appears to have been relocated to give rise to a Bh horizon (Bautista-Cruz *et al.*, 2005).

Forest soils in TMCF areas appear to be important reservoirs of carbon. Significant amounts of carbon are expected to be released to the atmosphere during forest clearing and subsequent cultivation in TMCF areas, since after that phase virtually all of the original vegetation has disappeared together with the organic layers of the soil. In general, when soil is brought under cultivation, most of the organic matter is oxidized to CO_2 (Schlesinger, 1997). Secondary succession in TMCF areas reverses part of the effects responsible for soil organic carbon losses that occurred when the land was converted to agricultural fields. The highest rates of soil carbon sequestration per year took place during the first 15 years after abandonment in the three studied chronosequences ($429 \text{ gC/m}^2/\text{year}$ at 0–20 cm; and $168 \text{ gC/m}^2/\text{year}$ at 20–40 cm soil depth; such rates decrease afterwards and may vary from one site to another (Bautista-Cruz and del Castillo, 2005). The rates of carbon accumulation in soil detected during the first 15 years after abandonment exceed the long-term mean rate observed in forest establishment after agricultural use ($33.8 \text{ gC/m}^2/\text{year}$) (Post and Kwon, 2000), and are comparable to those reported for young soils in tropical volcanic islands (Schlesinger *et al.*, 1998). Other indications of the retention of carbon during secondary succession is the thickness of the litter layer, which increases steadily during the first century of forest development, reaching 10–30 cm in old-growth

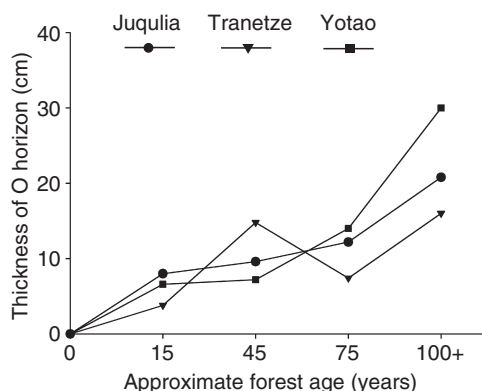


Fig. 7.7. Patterns of response to the age of the stand (mean values) for the thickness of the O horizon in three chronosequences in a tropical montane cloud forest area in El Rincón, Oaxaca, Mexico (from Bautista-Cruz and del Castillo, 2005). The x axis indicates approximate forest age in years. (Reproduced with permission from Soil Science Society of America, 677 S. Segoe Rd, Madison, Wisconsin 55711, USA.)

forest (Bautista-Cruz and del Castillo, 2005) (Fig. 7.7), and the increase in tree basal area described before (Fig. 7.2). These results are evidence of the importance of secondary forests in TMCF areas for providing environmental services, in particular carbon sequestration.

Soil pH decreases significantly as forest ages (Bautista-Cruz and del Castillo, 2005) (Fig. 7.6). Indeed, soils of old growth forests are very acidic, with soil pHs (1:2 soil:water) as low as 3.2. Acidification, in turn, appears to affect many ecosystem processes. Primary and secondary minerals are hydrolysed. In particular, muscovite, the dominant mineral of the coarse fraction of the soil, and chlorite, from the fine fraction, decreased with the age of the stand (Bautista-Cruz *et al.*, 2005). In turn, the release of potassium and other nutrient cations from such a process may help to replace part of the ions immobilized by plants and SOM, or lost by leaching. Nevertheless, the availability of nutrient cations in soil decreases as the forests age (Bautista-Cruz and del Castillo, 2005).

There is little cation exchange capability to buffer the soil solution, which together with the continuous supply of acidic litter by the vegetation makes the soil progressively acidic. Other processes that need to be studied may also contribute to enhance soil acidity. Nitrification may play a key role in the H⁺ budget, driving soil pH to very low levels and reducing soil fertility (Robertson, 1989). Moreover, processes such as denitrification and nitrification have been shown to change dramatically during secondary succession in other tropical ecosystems (Robertson and Tiedje, 1988). As a consequence of low pH, exchangeable aluminium was high in soils of TMCF areas (Bautista-Cruz and del Castillo, 2005). These results contrast with those found by other studies on secondary succession, indicating that succession improves soil conditions (see Peet, 1992). Plants, particularly those of late successional stands in TMCF areas, are expected to be adapted to conditions

of low soil fertility and to cope with problems of aluminium toxicity. Soil fertility appears to be one of the limiting factors in tropical ecosystems. For instance, above-ground net primary productivity in trees has been shown to be positively correlated to soil fertility in a Peruvian tropical rainforest (Cook *et al.*, 2005). In the TMCF area studied, the stands with the lowest basal area for a given forest age were those with the lowest levels of soil fertility (Bautista-Cruz and del Castillo, 2005). Species richness, on the other hand, generally increases with soil fertility in tropical plant communities (Gentry, 1988). In contrast, in TMCF areas studied, species richness increased in older stands, which tend to be less fertile. Caution should be taken when trying to make generalizations about soil fertility and species richness.

Phosphorous levels were very low in all stands, something typical of many forests soils (Waring and Schlesinger, 1985). However, the N/P ratio increases significantly with the age of the stand (Fig. 7.6). The opposite trend was expected, as P tends to become largely bound to SOM or secondary minerals, and N fixation is expected to increase during the course of succession, owing to colonization of nitrogen-fixing organisms (see Walker and Syers, 1976; Huston and Smith, 1987; Aerts, and Chapin, 2000). The absence of species of Leguminosae (notable for their symbiotic relationship with nitrogen-fixing bacteria) in most of TMCF areas studied perhaps helps to explain this pattern. The steady increase in N/P during succession in TMCF areas of southern Mexico points to the need of further studies on the dynamics of N and P, and highlights the need for caution when making generalizations about nutrient dynamic trends in secondary succession in forest areas (Bautista-Cruz and del Castillo, 2005).

Discussion

The levels of disturbance inflicted by the slash-and-burn method of cultivation in TMCF areas of southern Mexico can contribute to enhance biodiversity at least at landscape and species levels. However, this type of land use results in dramatic environmental changes. The soil environment, for instance, differs greatly in crop fields by displaying lower acidity than old-growth forests, a higher exchangeable nutrient cation content and by being poorly developed. Forest soils, by contrast, are well-developed, particularly at later successional stages, and have a very low content of exchangeable nutrient cations, high soluble aluminium content and low N/P ratios. On the other hand, an open area of agricultural fields lacking the shading of trees and shrubs contrasts sharply with the dense stands of trees in 45-year-old forests, and with forests older than 75 years after self thinning. Therefore it is not surprising that certain species prosper primarily at earlier successional stages, whereas others do so at late successional stages.

Conservation of biodiversity is an urgent environmental priority (e.g. Lubchenco *et al.*, 1991). Therefore, an understanding of the processes influencing diversity is of critical importance. Connell (1978) and Huston (1979) in their classic papers hypothesized that intermediate levels of disturbance may

enhance biodiversity by generating a state of non-equilibrium, where competitive exclusion is prevented. This study suggests that one of the sources of disturbance that can enhance diversity is slash-and-burn agricultural practices. In agreement with the Connell–Huston hypothesis, the relationship between slash-and-burn disturbance and diversity may be non-linear, with diversity displaying maximum values at intermediate intensities of disturbance. A landscape composed exclusively of old-growth forest, that is in the absence of slash-and-burn practices or other sources of disturbance, does not sustain most of the common species of young secondary forests. But, at the other extreme, a landscape with high deforestation rates such as that observed in the Chiapas highlands (Chapter 2) would result in many species being threatened with extinction, including even some typical of earlier successional stages. Both extremes are likely to generate lower environmental variation than a landscape composed of a mixture of forests of different ages and croplands. Thus, a maximum diversity is likely to be achieved in situations in which slash-and-burn is neither very frequent nor very uncommon in both time and space. Spatial heterogeneity is one of the factors that may permit the coexistence of a high number of species (Tilman, 1982). A moderate slash-and-burn practice is a source of disturbance that can prevent a reduction of diversity by generating such spatial heterogeneity in TMCF areas.

Succession seems to depend also on the proximity of source pools of colonists (Cook *et al.*, 2005). The landscape studied consists of a series of adjacent forest fragments and croplands. Therefore the close proximity of sources of old-growth forest in all chronosequences studied may help explain the relatively rapid replacement of pine forest by hardwoods and the excess of tree colonization over tree local extinction during the first century of forest development. The role of distance to source pools in the outcome of succession has been studied in other humid forest areas of Latin America (see Chapter 2), suggesting that extension and proximity of disturbed lands to seed sources is important for forest regeneration. Indeed, many species typical of old-growth forest have large seed sizes and appear to have restricted seed dispersal capabilities, in contrast to early successional species (Pérez Ríos and del Castillo, in preparation).

Changes of diversity and abundance in life forms during the course of secondary succession in TMCF areas appear not to be driven by chance but to follow predictable patterns related to environmental changes. Trees, lianas, climbing plants, epiphytic liverworts and vascular epiphytes prosper better at later successional stages, whereas low-stature plants, such as herbs and geophytes, are more abundant and diverse at earlier stages of forest development. These results highlight the importance of the functional role of species in the successional process, and does not support the hypothesis that all plant species or growth forms have the same probability of succeeding at any successional stage. These results clearly point to the need to analyse each functional group separately. The classification of plants in terms of the position of their reproductive organs and growth habits has enough discriminatory power to allow consistent patterns to be identified during secondary succession in TMCF areas.

Secondary forests in TMCF areas appear to be important as both reservoirs of species diversity and as suppliers of ecosystem functions. As mentioned above, secondary forests harbour the highest species richness in some groups of plants. High species diversity in early successional stands has been detected in other forest ecosystems such as temperate forests (e.g. Peet, 1978) and in secondary succession areas of former TMCFs (e.g. Romero-Romero *et al.*, 2000). In the absence of disturbance, many species typical of secondary forest will go extinct. Disturbances might also enhance genetic diversity by allowing shifts in selection regimes (Namkoong and Koshy, 2000).

However, slash-and-burn causes important changes to the soil. Fire, which is used to clear forest areas prior to crop cultivation, plays a major role in making available soil nutrients for plants by releasing nutrients from biomass and SOM, and reducing the levels of aluminium toxicity by increasing soil pH. In the long run, slash-and-burn prepares the land for the colonization of pines, since pine forests, being a transient successional stage, readily colonize recently abandoned crop fields. Adjacent old-growth forest, on the other hand, may be important for supplying a source of colonists to the developing pine forest, thereby facilitating the transition from pine forest to broadleaf forest. It remains to be explored what are the regeneration capabilities of a primary TMCF in the absence of nearby secondary forest, or what would be the outcome of early forests dominated by pine in the absence of nearby primary or old-growth forests as seed suppliers. This point is relevant, as most species of early secondary stages appear not to persist in old-growth forest or established secondary forest; nor do late successional species appear to be good colonizers as they establish only under a forest canopy. Thus, the close conjunction of agricultural activities, as a major source of disturbance, together with adjacent secondary forests and old-growth forests, appear to contribute to the maintenance of biodiversity at the landscape level.

Old-growth forests are important suppliers of environmental services, such as operating as a carbon sink, both in terms of tree biomass and soil organic matter. The soil acidity they generate appears to be important for rock weathering, helping to replenish to the soil some of the nutrients immobilized by plant biomass or SOM, or lost by leaching or run-off. Moreover, old-growth forests harbour the highest abundance of epiphytes, and probably other groups of organisms, such as large mammals. The role of old-growth forest in trapping cloud water is expected to be higher than that of young forests, which in general give the impression of being drier habitats. However, the microclimatic changes associated with succession in TMCF have not yet been studied in detail.

The rate of successional change in TMCF areas cleared for maize cropping and later abandoned generally declines with time. The first 15 years of forest re-growth shows the greatest change in several of the characteristics analysed. These include the highest rates of epiphyte colonization on lower tree trunks, the highest rates of colonization of herbs, shrubs and geophytes, the highest decrease in soil contents of exchangeable nutrient cations such as K, Mg and Ca. Also, the rate of C sequestration in soil peaks within this time period. The

rapid growth of virtually all plants forms during early stages of succession may explain such results. The decline in rates of successional change with age has been detected in other studies (Foster and Tilman, 2000, and references therein), and suggests that opportunities for colonization are greater than local extinction probabilities for most groups of plants at early succession stages. The highest rates of colonization involve high demands for soil nutrients, thus explaining the highest decline in nutrients detected. Such a decline coupled with the shading at floor level may rapidly shift the balance of colonization and local extinction in favour of the latter for low stature-plants after 15 years of forest development, once trees overtop other life forms. In contrast, tree species richness steadily increases during the first hundred years of forest development, suggesting that colonization opportunities continue to be available for trees, perhaps facilitated by the proximity of sources of colonists, as explained above. Trees also have, on average, deeper roots than shrubs and other low stature plants, thus permitting greater volumes of soil to be explored for nutrient uptake. Trees also create suitable habitats for epiphyte and liana colonization, a clear example of facilitation *sensu* Connell and Slatyer (1977). Indeed, liana success appears to be controlled by the availability of large trees in other tropical ecosystems (Phillips *et al.*, 2005). Similar trends have been observed in lowland tropical forest, in which a decrease in herbaceous vines was accompanied by increases in shrubs and trees, and epiphytes underwent a dramatic surge in abundance (Guariguata and Ostertag, 2001). Lianas influence the outcome of succession by altering differentially the survival rate of trees in other tropical forests (Pérez-Salicrup, 2001), a relationship that needs to be explored in TMCF areas.

Self-thinning at *c.*45–75 years after abandonment appears to be an important landmark for certain processes that show a shift in trend during this stage. For instance, the density of geophytes, low plants, herbs and shrubs decreased from 15 to 45 years, but increased after 45 years. After the end of self-thinning, that is *c.*75 years after abandonment, nutrient cation concentrations in the soil show a slight increase. As suggested before, such changes may reflect changes in the availability of resources.

Conclusions

Moderate slash-and-burn practices in former TMCF areas may create habitat heterogeneity at the landscape scale, which, in turn, can enhance plant species richness.

The cultivation phase of slash-and-burn agriculture imposes severe losses of soil and carbon. Soil rejuvenates, and organic horizons are lost. Soil pH and cation exchange capacity rises. The original vegetation practically disappears.

Secondary succession reverses, in part at least, the effects of the cultivation phase. Soil carbon is sequestered at high rates during the early stages, and soil layers accumulate. Vegetation starts to regenerate first as shrubs and forbs and other low stature plants, then as a pine-dominated forest, and,

finally, as a hardwood forest. Epiphytes start to colonize the trees very early during succession, but the process may take more than a century to reach the values of cover observed in primary forests.

Old-growth forests do not contain some of those species common in early successional stages. The process of gap formation in such forest is not comparable to forest regeneration following the cultivation phase of the slash-and-burn. Therefore, the persistence of species typical of early secondary forest appears to depend entirely on periodic allogenic disturbances. These species, however, are key to the process of secondary succession as they are the first to colonize abandoned areas.

In contrast to other successional processes in humid forest areas, soil becomes progressively acidic, infertile and toxic as a result of high soluble aluminium concentrations, and the N/P ratio steadily decreases during the first century of forest development. Legumes are virtually absent in all successional stages. The increase in soil acidity allows the weathering of the parent material, hydrolyzing primary and secondary minerals and releasing base cations to the soil. Slash-and-burn reverses such trends: soil pH and cation exchange capacity rises and consequently soluble aluminium levels drop.

Periodic disturbances such as those of moderate slash-and-burn create open areas for secondary forest to develop, allowing the persistence of pioneer species in the landscape. Forest development, however, depends on source pools of old-growth forest, as species typical of early successional stages cannot succeed under their own canopy. Thus, periodic moderate disturbances produce a landscape with a mixture of crop fields, early secondary forest and old-growth forest, and appear to maintain stability, resilience and species richness at the landscape scale.

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