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Recovery following clearing of an upper montane *Quercus* forest in Costa Rica

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Abstract: Pattems in recovery following clearing of upper montane *Quercus* forests (2900 - 3000 m alt.) in the Costa Rican Cordillera de Talamanca have been studied and four different successional forest phases (pioneer, early successional, mid-successional, mature) have been distinguished. Arboreal species richness increases during succession being largest in the mid-successional forest phase. Woody Asteraceae dominate the early secondary phases, while Araliaceae, Lauraceae and to a lesser extent Myrsinaceae become prominent in later phases including the mature stage. *Quercus* recovers largely, being the dominant genus in mid-successional and mature forest. Young secondary phases are rich in rapid-growing light-demanding canopy species, while more developed multi-layered phases are dominated by a large number of shade-tolerant subcanopy species. In general, secondary succession may lead (within a period of approximately 35 years after clearing and abandonment) to an arboreal recovery of about 70 % of the original tree species composition in mature forest.

Key words: Costa Rica, disturbance, montane, *Quercus*, recovery, seccondary succession, tropical forest.

During the last few decades tropical montane forests have been cleared and degraded on a broad scale (Budowski 1968, Monasterio *et al.* 1987). Recovery after clearing of these forests is considerably slowed down by low temperatures due to the diurnal climate prevailing in the montane tropics. At present there is little knowledge about this process in the pluvial neotropical upper montane forest belt. Indeed, most studies on neotropical forest succession following clearing and abandonment have been conducted in lowland rain forest (*e.g.* Ewel 1980, Gómez-Pompa and Del Amo 1985, Purata 1986, Saldarriaga 1988, Toro and Saldarriaga 1990, Brown and Lugo 1990) or in mid-elevation cloud forests (*e.g.* Byer and Weaver 1977, Sugden *et al.* 1985).

To fill this gap, a study of the patterns in recovery after clearing of neotropical upper montane forest has recently been initiated in primary (mature) and secondary (recovering) *Quercus* forests. These high-elevation forests blanket large parts of the Atlantic and Pacific slopes of the western part of the Costa Rican Cordillera de Talamanca. They have been selected for the present study since different studies on their botany and ecology have become available during the last five years (*e.g.* Blaser 1987, Jiménez *et al.* 1988, Van Velzen and Wijtzes 1990, Kappelle 1992, Kappelle *et al.* 1989, 1991, 1992). On this occasion the preliminary results of this study are presented, thus offering a first outline of forest recovery in the Costa Rican upper montane vegetation belt.

MATERIAL AND METHODS

The study area is situated in the Cordillera de Talamanca, which is formed of intrusive, and Tertiary volcanic rocks, alternated with marine sediments (Weyl 1980, Castillo 1984, Kappelle *et al.* 1989). Pleistocene glaciations have left its traces such as fossil periglacial phenomena on the Cerro de la Muerte (3491 m alt.) at the nearby Buenavista massif (Hastenrath 1973). Soils sustaining montane *Quercus* forests are developed from volcanic

ashes, medium-textured, moderately fertile, very acid and excessively drained (Vásquez 1983, Van Uffelen 1991). Average annual temperature at the nearby town of Villa Mills (3000 m a.s.l.) is 10.9 °C, while average rainfall is 2812 mm (Instituto Meteorológico Nacional 1988). Diurnal mist during the afternoons is considerable (cloud forest), especially during the rainy season (May to November).

Sample sites are located in the highly deforested 62,000 ha Los Santos Forest Reserve in the western part of the Cordillera de Talamanca (9°35'40"N, 83°44'30"W). This protected area created in 1975 (Meza and Bonilla 1990) serves since 1982 as a buffer zone to the 612,570 ha UNESCO-declared Amistad Biosphere Reserve (Reserva de la Biósfera de la Amistad 1990). Clearing of upper montane oak forest stands occured frequently during the last five decades generating a highly heterogeneous pattern of vegetation types. Today, within the borders of the Los Santos Forest Reserve between elevations of 2400 and 3200 m tracts of pristine upper montane *Chusquea - Quercus* forests form a mosaic with patches of secondary vegetation of different ages, including grasslands, shrublands and forests (Kappelle *et al.* 1989, Van Velzen and Wijtzes 1990). The best example of such a vegetational mosaic is found in the upper part of the Río Savegre watershed in the vicinity of Jaboncillos and San Gerardo de Dota (Copey District, Dota Canton, San José Province).

Recovery following clearing of upper montane *Quercus* forest was studied here. Therefore, forest patches with similar topographic, geomorphologic, edaphic, climatic and anthropogenic characteristics were selected. Patches were randomly chosen on south-facing Pacific slopes of 20 to 35 degrees at about 2900 to 3000 m altitude. They had topsoils (0-25 cm) mainly containing darkbrown organic matter with dispersed charcoal fragments giving rise to a very high root density, and subsoils (25-100 cm) showing (pale) yellowish-brown clay material with orange-brown mottling caused by small weathered stone fragments (2-5 cm diam.), sometimes layered in an iron pan bed. Here, during one wk in the early dry season of 1991 - 1992 minimum temperatures fluctuated between 5 and 7 °C and maximum temperatures between 15 and 23 °C. The average annual temperature as measured at 60 cm soil depth oscillated between 9.8 and 11.2 °C, a range very similar to the value at the above-mentioned Villa Mills station. Before abandonment and recovery, all secondary forest patches selected had been used for dairy cattle grazing during a period of 5 to 10 yr following clearing and burning. In order to avoid significant differences in propagule input (primary species invasion) from nearby mature forest, sites sustaining secondary forest were selected within a range of 200 to 400 m distance to primary forest.

Three subsequent recovering forest phases of different ages since abandonment as well as a mature forest phase for reference purposes were examined. Sixteen 0.05 ha forest plots were distributed over *a.* primary (mature) forest, and secondary (recovering) forests of approximately *b.* 8-12 yr (pioneer), *c.* 20-22 yr (early successional), and *d.* 30-35 yr (mid-successional) since abandonment. Late successional forest (40-80 yr of recovery following clearing) could not be sampled, because it was absent in the study area: deforestation started only in the 1950's after the construction of the Intermerican Highway to San Isidro del General. In each present forest phase four plots were established and marked on recent and past aerial photographs in order to check former land cover and use. Personal observations on land use history were confirmed by oral information from local farmers (E. Ceciliano and M. Navarro, pers. com.).

In each plot trees $\geq$ 3 cm dbh were sampled, recorded, identified, and when necessary plant material was collected and subsequently examined and deposited at the Costa Rican National Herbarium (CR). Aerial crown cover values were estimated for all tree species separately, following basic phytosociological procedures (Mueller-Dombois and Ellenberg 1974, Braun-Blanquet 1979). For each species crown cover values estimated in four plots belonging to one phase were averaged and used for a preliminary phytosociological analysis (Table 1). Considering dominance - based on average aerial crown cover percentages - an ecological optimum at a certain moment in the successional sere could be distinguished for every species. Thus, tree species could be divided into four main ecological species groups: I. pioneer trees, II. early secondary trees, III. late secondary trees, and IV. primary trees. According to the vegetation layer preference of each species

TABLE 1

List of 50 tree species present in four successional forest phases of the Costa Rican upper montane Quercus *forest ecosystem*

Families (N=29)	Species (N=50)	Aerial crown cover (%) PF	ES	MS	MF	Layer Prefer.
Pioneer tree species (9)						
ASTERACEAE	*Senecio copeyensis* Greenm.	1				C
PAPAVERACEAE	*Bocconia frutescens* L.	1	1			C
ASTERACEAE	*Senecio multivenius* Benth.	<1	<1			C
SAURAUIACEAE	*Saurauia veraguasensis* Seemann	<1	<1			C
GARRYACEAE	*Garrya laurifolia* Hartweg ex Benth. ssp. *quichensis* (Smith) Dahl.	<1	<1			C
ASTERACEAE	*Ageratina subcordata* (Benth.) R. King & H. Robinson	6	1	<1		C
ASTERACEAE	*Verbesina oerstediana* Benth.	10	3	1		C
POLYGALACEAE	*Monnina xalapensis* Kunth	2	1	<1		C
FLACOURTIACEAE	*Abatia parviflora* Ruíz López & Pavón	5	4	<1		C
Early secondary tree species (10)						
SYMPLOCACEAE	*Symplocos irazuensis* Cuf.		<1			C
LOGANIACEAE	*Buddleja nitida* Benth.		22	<1		C
ESCALLONIACEAE	*Escallonia myrtilloides* L.f. var. *patens* (Ruiz & Pavon) Sleumer		3	<1		C
MELASTOMATACEAE	*Miconia schnelli* Wurd.		1	<1		S
ONAGRACEAE	*Fuchsia arborescens* Sims.	1	4	2		C
CHLORANTHACEAE	*Hedyosmum mexicanum* Cordemoy	<1	1	<1		S
SYMPLOCACEAE	*Symplocos serrulata* Kunth	<1	<1	<1		S
AQUIFOLIACEAE	*Ilex discolor* Standley var. *lamprophylla* (Standley) Edwin	<1		<1		S
CORNACEAE	*Cornus disciflora* Mociño & Sessé	1	13	3	<1	C
ARALIACEAE	*Oreopanax xalapense* (Kunth) Decne. & Planchon	2	7	1	1	C
Late secondary tree species (9)						
LAURACEAE	*Ocotea calophylla* Mez			<1		S
MYRSINACEAE	*Ardisia* aff. *nigropunctata*			<1		S
LAURACEAE	*Persea vesticula* Standley & Steyerm.			<1		S
MYRSINACEAE	*Ardisia glandulosomarginata* Oersted			1		S
RUTACEAE	*Zanthoxylum melanostictum* Schldl. & Cham.		<1	1		S
ERICACEAE	*Comarostaphylis arbutoides* Lindley ssp. *arbutoides* Lindley	<1	<1	1		S
MYRTACEAE	*Myrcianthes fragrans* var. *hispidula* McVaugh	<1	<1	1		S
CAPRIFOLIACEAE	*Viburnum costaricanum* (Oersted) Hemsley	<1	5	3	4	S
MYRSINACEAE	*Myrsine coriacea* (Sw.) R. Br. ex Roemer & Schultes	<1	2	3	1	S
Primary tree species (22)						
MELASTOMATACEAE	*Miconia tonduzii* Cogn.				2	S
ARALIACEAE	*Oreopanax nubigenus* Standley				2	S
ROSACEAE	*Prunus annularis* Koehne				2	S
CLUSIACEAE	*Clusia palmana* Standley				<1	S
CLUSIACEAE	*Clusia rotundata* Standley				<1	S
SYMPLOCACEAE	*Symplocos austinsmithii* Standley				<1	S
MYRSINACEAE	*Ardisia costaricensis* Lundell			<1	7	S
ARALIACEAE	*Schefflera pittieri* (Marchal) Frodin			<1	2	C
LAURACEAE	*Nectandra salicina* Allen			<1	<1	S
LAURACEAE	*Ocotea pittieri* (Mez) Van der Werff			<1	<1	S
RHAMNACEAE	*Rhamnus oreodendron* L.O. Williams			<1	<1	S
WINTERACEAE	*Drimys granadensis* L.f.			<1	<1	S
FAGACEAE	*Quercus copeyensis* Com. Mueller	1	1	44	80	C
FAGACEAE	*Quercus costaricensis* Liebm.	1	1	4	26	C
STYRACACEAE	*Styrax argenteus* Presl	<1	<1	3	15	S
CUNONIACEAE	*Weinmannia pinnata* L.	<1	13	4	15	C
THEACEAE	*Cleyera theaeoides* (Sw.) Choisy	3	3	6	11	S
ERICACEAE	*Vaccinium consanguineum* Klotzsch	<1	1	1	11	S
AQUIFOLIACEAE	*Ilex pallida* Standley	<1	<1	<1	3	S
MYRSINACEAE	*Myrsine pellucidopunctata* Oersted	<1	<1	1	2	S
ARALIACEAE	*Oreopanax capitatus* (Jacq.) Decne. & Planchon	<1	<1	<1	1	S
RUTACEAE	*Zanthoxylum scheryi* Lundell	<1	<1	1	1	S

Note: Each species is assigned to one out of four ecological species groups (**bold**), according to their dominance based on aerial crown cover. Average species cover percentages in 0.05 ha forest plots are presented for each successional phase (PF pioneer, ES early successional, MS mid-successional, MF mature). Cover percentages less than 1% are represented by a '<1' sign. Data on layer preference of each species is given (C canopy, S subcanopy).

they could be subdivided into: A. canopy trees; and B. subcanopy trees. Diagrams showing distribution patterns of species groups could be made for all four forest phases, and for the *Quercus* forest ecosystem as a whole. The forest phases - each with a different set of characteristic tree species - could be described and compared in order to discover general trends in upper montane *Quercus* forest recovery.

RESULTS AND DISCUSSION

Fifty tree species in 29 families with individuals ≥ 3 cm dbh have been recorded in four different successional phases (pioneer, early and mid-successional, and mature) of Costa Rican upper montane *Quercus* forest (Table 1). Each phase is characterized by a different set of pioneer, secondary and primary, canopy and subcanopy tree species, which appear at different moments during the process of recovery. A schematic vegetation profile representing this successional sere on basis of its principal tree species is shown in Fig. 1. Below, a brief description of each phase is given on basis of its tree composition.

The pioneer forest phase: The pioneer forest phase, which has been recovering after abandonment about 10 yrs ago, is made up of 29 tree species, half of which are canopy species. This phase is characterized by rapid-growing, large-leaved pioneer trees with a low wood density, such as *Senecio copeyensis* and *Bocconia frutescens*. Four out of nine pioneer trees belong to the composite family: *Ageratina subcordata, Senecio copeyensis, S. multivenius* and *Verbesina oerstediana*. These species dominate this phase, together with *Abatia parviflora, Cleyera theaeoides, Monnina xalapensis* and *Oreopanax xalapense*.

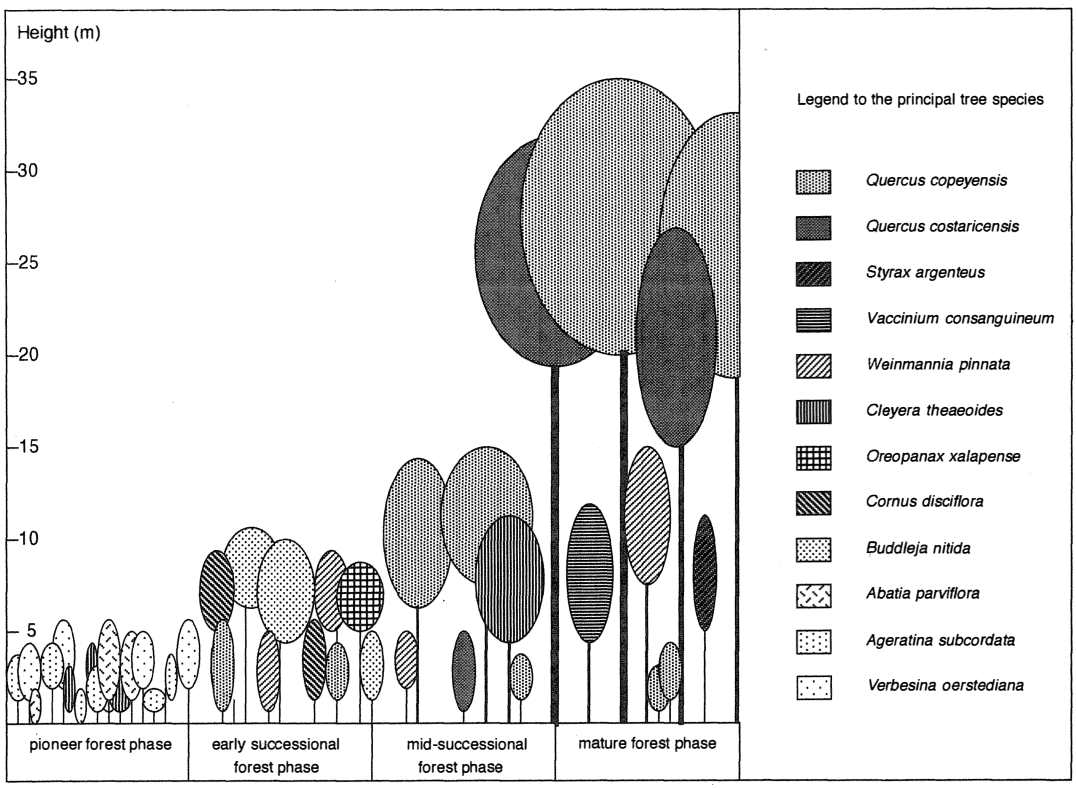

Fig. 1. Schematic vegetation profile representing the successional sere in a Costa Rican upper montane *Quercus* forest ecosystem.

The latter, an araliaceous species with short-lived compound palmate leaves looks very similar to species of the genus *Cecropia*, abundant in lowland successional forest, and may occupy its niche in high-altitude environments. Other, less common canopy species include *Cornus disciflora, Fuchsia arborescens, Garrya laurifolia* ssp. *quichensis* - a species well-known from above-situated subalpine dwarf forests -, *Saurauia veraguasensis*, and occasionally *Quercus copeyensis, Q. costaricensis* and *Weinmannia pinnata*. During this phase many late secondary and primary subcanopy trees are already present in low numbers but do not reach their mature state. Among them are *Comarostaphylis arbutoides* ssp. *arbutoides, Hedyosmum mexicanum, Ilex discolor* var. *lamprophylla, I. pallida, Myrcianthes fragrans* var. *hispidula, Myrsine coriacea, M. pellucidopunctata, Oreopanax capitatus, Styrax argenteus, Symplocos serrulata, Vaccinium consanguineum, Viburnum costaricanum* and *Zanthoxylum scheryi.*

The early successional forest phase: The successional phase representing early secondary forest of about 20 yr old since abandonment contains 32 tree species and is dominated by *Buddleja nitida, Cornus disciflora, Weinmannia pinnata* and *Oreopanax xalapense* canopy trees. Large-leaved pioneering *Senecio copeyensis* has disappeared totally. *Abatia parviflora* and *Verbesina oerstediana* individuals are still numerous, but loose some of the vigor they had in the former phase. The same may be true for *Bocconia frutescens, Garrya laurifolia* ssp. *quichensis, Saurauia veraguasensis*, and *Senecio multivenius*. Canopy trees like *Fuchsia arborescens*, on the contrary, get prominent. Several other species, such as *Escallonia myrtillioides* var. *patens, Miconia schnellii, Symplocos irazuensis* and *Zanthoxylum melanostictum* occur for the first time. Many other species that were already present in the pioneer forest phase continue their life-cycle, although they display low aerial crown cover percentages, as do *Ageratina subcordata, Comarostaphylis arbutoides* ssp. *arbutoides, Hedyosmum mexicanum, Ilex pallida, Monnina xalapensis, Myrcianthes fragrans* var. *hispidula, Myrsine coriacea, M. pellucidopunctata, Oreopanax capitatus, Quercus copeyensis, Q. costaricensis, Styrax argenteus, Symplocos serrulata, Vaccinium consanguineum, Viburnum costaricanum* and *Zanthoxylum scheryi.*

The mid-successional forest phase: The third distinguished phase comprises secondary forest of 30 to 35 yrs old. The association of many pioneer and secondary trees together with a large array of primary species makes it by far the most tree species-rich stage: 38 tree species (76 % of the total number of species found) inhabit the four 0.05 ha plots of mid-successional forest. This phase is dominated almost exclusively by 10 to 15 m tall *Quercus copeyensis* trees, accompanied by the less-dominant canopy species *Q. costaricensis* and *Weinmannia pinnata*. Subcanopy trees and treelets belonging to the species *Myrsine coriacea, Viburnum costaricanum, Comarostaphylis arbutoides* var. *arbutoides, Myrcianthes fragrans* var. *hispidula* and *Zanthoxylum melanostictum* seem to have their ecological optimum in this phase. However, it is believed, that *C. arbutoides, M. fragrans*, and *Z. melanostictum* get their maximum aerial crown cover in mature forest, although they have not been recorded in the primary forest plots. In the relatively darker parts of the subcanopy - below rather dense boles of *Quercus* trees - many 4 to 8 m high individuals are found belonging to *Cleyera theaeoides, Ilex pallida, Myrsine pellucidopuctata, Oreopanax capitatus, Styrax argenteus, Vaccinium consanguineum* and *Zanthoxylum scheryi*. Several species found in this phase occur for the first time during succession, but still with low aerial crown cover percentages. They belong mainly to either the Myrsinaceae (*Ardisia costaricensis, A. glandulosomarginata* and *A.* aff. *nigropunctata*) or the Lauraceae (*Nectandra salicina, Ocotea calophylla, O. pittieri* and *Persea vesticula*). Other newly appearing trees include *Drimys granadensis, Rhamnus oreodendron*, and *Schefflera pittieri*. Although present with less individuals and lower aerial crown cover values numerous pioneer and early-secondary species are still occupying small relatively open areas. Among them most prominent are *Cornus disciflora, Fuchsia arborescens, Verbesina oerstediana* and *Oreopanax xalapense.*

The mature forest phase: The mature or primary forest phase of the upper montane *Quercus* forest ecosystem is indeed dominated by *Quercus* spp. It resembles the *Quercus costaricensis - Quercus copeyensis* forest community earlier described by Kappelle *et al.* (1989) and consists of mature forest characterized by 30 to 40 m tall *Quercus* trees and dense stands of 5 m high *Chusquea* spp. bamboos. In four 0.05 ha plots together only 26 species were recorded, which is about a two-third of the number of tree species present in the late-secondary phase. This might be explained by the lack of a dozen of secondary species. Most conspicuous is the rather uniform canopy layer in comparison with the highly diverse subcanopy layer. About 60 to 95 % of the canopy aerial crown cover is made up of *Quercus* spp. with only few canopy individuals belonging to *Schefflera pittieri* and *Weinmannia pinnata*. In the 8 to 15 (20) m tall subcanopy, on the contrary, a series of shade-tolerant trees find their place. Species such as *Styrax argenteus, Cleyera theaeoides, Vaccinium consanguineum* and *Ardisia costaricensis* dominate this vegetation layer. Other less-abundant trees like *Ilex pallida, Myrsine pellucidopunctata* and *Oreopanax capitatus* - present from the beginning of succession - get their greatest dominance in this 'final' successional phase. Primary subcanopy species like *Ocotea pittieri* and *Rhamnus oreodendron* already present in late secondary forest become more prominent. In relatively recent tree fall gaps one may encounter *Oreopanax xalapense* and *Cornus disciflora*, two successional species well-known from the canopy of early and mid-successional forest phases. At the border of such gaps *Viburnum costaricanum* and *Myrsine coriacea* are common. Six species have been found only in mature forest, two of them belonging to the primary forest genus *Clusia*. The species *Prunus annularis*, which has an average 2 % aerial crown cover in the mature forest phase, might be considered as an indicator for undisturbed upper montane primary *Quercus* forest.

General patterns in arboreal recovery: Comparing the four forest phases one notes immediately the initial increase in the number of tree species during succession (Fig. 2), a phenomenon well-known from other tropical

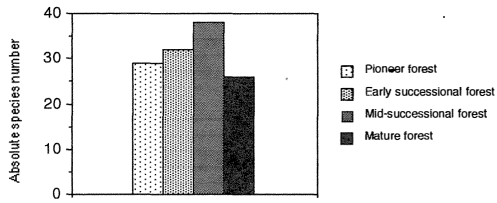

Fig. 2. Total numbers of tree species in four different successional phases of the Costa Rican upper montane Quercus forest ecosystem.

ecosystems (West *et al.* 1981, Gómez-Pompa and Del Amo 1985, Sugden *et al*, 1985, Brown and Lugo 1990). However, it is quite remarkable, that the lowest tree species richness is found in the mature forest phase. Other studies on forest recovery in both neotropical lowland and montane forest present it as the most species-rich phase (Purata 1986, Saldarriaga 1988, González-Espinosa *et al.* 1991). In the Mexican Chiapas highlands, for example, 40 yr old secondary *Pinus-Quercus* forests recovered just a 85 % of the species richness found in mature forest, including all vascular terrestrial plants (González-Espinosa *et al.* 1991). There are several possible causes that might explain why mid-successional forest in montane Costa Rica is richer in tree species than the mature forest. First, many primary tree species are already appearing in the shrub layer of pioneer and early successional forest (e.g. *Quercus* spp., *Styrax argenteus, Weinmannia pinnata, Cleyera theaeoides, Vaccinium consanguineum*), whereas numerous pioneer and early secondary species are absent in the mature forest phase (e.g. *Senecio* spp., *Bocconia frutescens, Verbesina oerstediana, Ageratina subcordata, Monnina xalapensis, Abatia parviflora*). Secondly, the area of mature forest sampled might be too small to include many 'late secondary species' (e.g. *Ardisa* spp., *Ocotea calophylla, Persea vesticula, Comarostaphylis arbutoides*), which are believed to be primary species, according to earlier studies (Kappelle *et al.* 1989). Third, it might be just a matter of chance, that many other primary species well-known from upper montane *Quercus* forests in the study area, such as *Myrsine pittieri, Magnolia* spp., and Podocarpaceae (Kappelle *et al.* 1989, 1991), have not been found in the mature forest studied. Finally, physical characteristics (light availability, soil properties) may differ over short topographic ranges locally favouring *Quercus* species.

Comparing the most species-rich families as occurring in the four different successional phases, the decline of Asteraceae species as secondary succession advances is evident (Fig. 3), an event also known from Mexican high-elevation pine-oak forest (González-Espinosa *et al.* 1991). Composite trees recorded result to be large-leaved, light-demanding pioneer and early-secondary species, which do not bear the shady conditions prevailing under large *Quercus* canopy structures in mid-successional and mature forest phases. Myrsinaceae, Araliaceae, and Lauraceae, on the other hand, get more prominent as secondary forests grow older, and numbers stabilize at the end of the successional pathway.

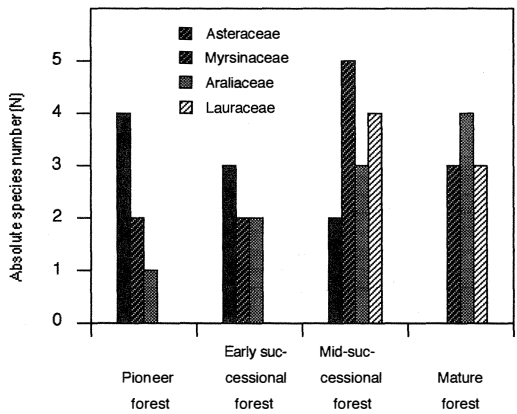

Fig. 3. Most species-rich tree families in absolute numbers for each of four different successional phases of the Costa Rican upper montane *Quercus* forest ecosystem.

When we have a look at the relative numbers of pioneer, early and late secondary, and primary species as distributed over the four forest phases (Fig. 4), one observes an expected decrease in pioneer species and an increase in primary species during succession. It is interesting to note, however, that not more than about 30 % of all tree species recorded in pioneer forest are true pioneer trees, while over 80% of the trees found in primary forest are true primary trees. Thus, pioneer forest - although dominated by pioneer trees, when considering aerial crown cover projections - is made up of a mixture of pioneer, secondary and primary species. The mature forest phase instead is almost entirely made up of primary species. Exceptions are the secondary tree species *Cornus disciflora, Oreopanax xalapense, Viburnum costaricanum* and *Myrsine coriacea*, which are present throughout succession, including the mature phase. On the whole, almost half of all recorded species (45 %) are primary species, while the other half is more or less equally distributed over the pioneer, early and late secondary species groups.

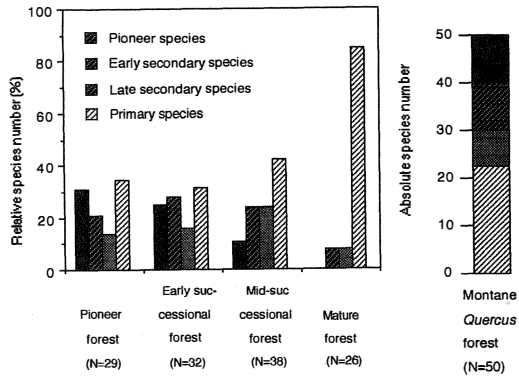

Fig. 4. Pioneer, early and late secondary, and primary tree species in relative numbers for each of four different successional phases of the Costa Rican upper montane *Quercus* forest ecosystem, and in absolute numbers for the ecosystem as a whole.

Finally, a distinction can be made between canopy and subcanopy species sets. In each forest phase a different canopy species / subcanopy species - ratio is displayed, showing a decrease in canopy species, and an increase in subcanopy species along the successional gradient (Fig. 5). Pioneer forest has equal numbers of canopy and subcanopy species, but mature forest has about 20 % canopy species and almost 80 % subcanopy species. This might be explained by the fact that canopy species diversity decreases largely during succession. In later forest phases the canopy gets monogenerically dominated: two species of *Quercus* reduce the light and space available to other species, which are finally outcompeted. Only *Schefflera pittieri* and *Weinmannia pinnata* may reach canopy heights and share the upper forest stratum with *Quercus* spp. The subcanopy, on the contrary, becomes better developed during succession, in later phases harbouring a large range of small trees and treelets with different ecological demands. Most of these subcanopy species appear to be primary species (Fig. 6), thus having their ecological optimum, *i.e.* their highest aerial crown cover percentages, in the mature forest phase (Table 1).

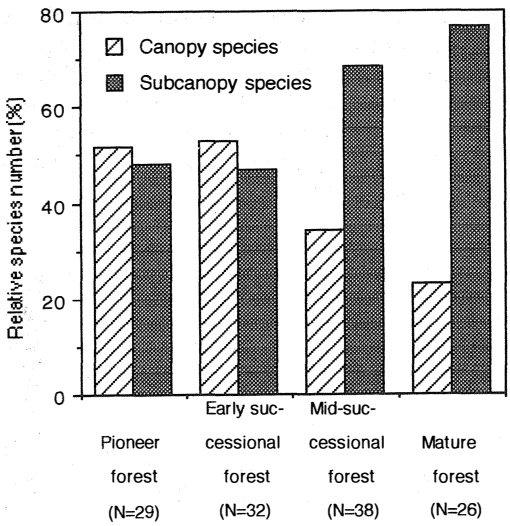

Fig. 5. Canopy and subcanopy tree species in relative numbers for each of four different successional phases of the Costa Rican upper montane *Quercus* forest ecosystem.

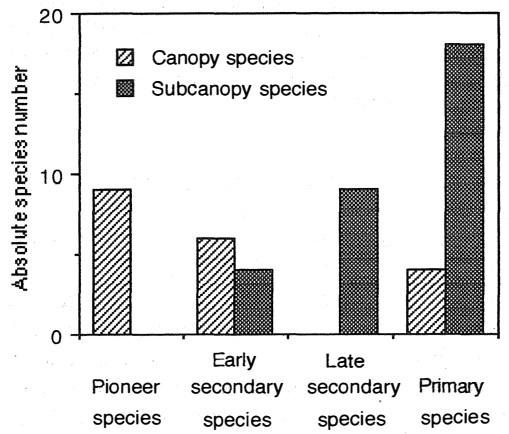

Fig. 6. Canopy and subcanopy tree species in absolute numbers distributed over pioneer, early and late secondary, and primary species of the Costa Rican upper montane *Quercus* forest econsystem.

Results of the recovery after clearing of Costa Rican upper montane *Quercus* forests show a hopeful successional process, where it concerns compositional recovery. Arboreal recuperation in forests, which developed after having been cleared and abandoned 30 to 35 yr ago, reaches a 70 % of the primary tree species composition in mature forest. By that time a dozen of pioneer and early secondary canopy trees are almost completely replaced by primary *Quercus* trees, offering shade to numerous subcanopy elements, such as lauraceous species. Although primary forest was expected to be richest in tree species, later secondary forest phases were more diverse, combining species from different stages. Overall, compositional recovery tends to develop at a faster rate than earlier authors expected. Ewel (1980), for instance, found very little forest recovery in the first yr following clearing of an oak-dominated forest at nearby Ojo de Agua (2900 m alt.). He stated that the regrowth of such a high-elevation tropical forest is so slow that it may never reestablish after clearing. The present study, on the other hand, shows that a complete recovery of the arboreal compostion in Costa Rican montane oak forests may be possible. However, the vertical forest structure may restore itself at a much slower pace than the mere tree species composition treated here (Kappelle *et al.* in prep.).

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RESUMEN

Se han estudiado los patrones de la recuperación después de la tala de los bosques montano-altos de *Quercus* en la Cordillera de Talamanca, Costa Rica, distinguiéndose cuatro fases sucesionales (pionera, sucesional temprana, sucesional intermedia, madura). La riqueza de especies arbóreas aumenta durante la sucesión siendo más grande en la fase intermedia. Las asteráceas leñosas dominan las fases secundarias tempranas, mientras que las araliáceas, las lauráceas y en menor parte las mirsináceas suelen ser importantes en las fases tardías, incluyendo la fase madura. El género *Quercus* (roble, encino) se recupera muy bien, dominando el bosque secundario tardío y maduro. Las fases jóvenes son ricas en especies heliófitas de

crecimiento rápido en el dosel, mientras que las fases más desarrolladas están dominadas por un gran número de especies del subdosel tolerantes a la sombra. En general, la sucesión secundaria puede llegar - dentro de un período de aproximadamente 35 años después de la tala y el abandono - a una recuperación arbórea de un 70 % de la composición original de especies de árboles en el bosque maduro.

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