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Successional age and forest structure in a Costa Rican upper montane *Quercus* forest

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ABSTRACT. Changes in structure of a Costa Rican upper montane *Quercus* forest were studied in twelve 0.1 ha plots along a chronosequence including 8- to 20-year-old Early Secondary Forest (ESF), 25- to 32-year-old Late Secondary Forest (LSF) and mature Primary Forest (PF). In 1.2 ha 2854 stems ≥ 3.0 cm dbh belonging to 42 tree species were recorded. Tree species richness per 0.1 ha ranged from 15 to 30. Diversity indices did not change significantly during succession. Stem density did not differ significantly among successional phases, while basal area was significantly higher in PF than in ESF and LSF. Maximum canopy height and basal area increased linearly during the first three decades of recovery. Height and dbh showed a significant, logarithmic regression for all forest phases. A period of 84 y was estimated as the theoretically minimum time needed for structural recovery. The maximum canopy height and basal area recovered two to five times slower in upper montane than in lower montane or lowland Neotropical forests.

KEY WORDS: chronosequence, Costa Rica, disturbance, dynamics, forest structure, *Quercus*, recovery, regeneration, secondary succession, tropical montane forest.

INTRODUCTION

During the last three decades, human impact on tropical montane forests has increased at an alarming rate (Monasterio *et al.* 1987). Forest clearing and subsequent land degradation have become major threats to complex ecosystems inhabiting the tropical uplands (e.g. Budowski 1968, González-Espinosa *et al.* 1991). Ewel (1980) recognized that the rate of regrowth following clearing in the upper montane tropics is slowed down considerably by diurnal low temperatures. Yet, little is known about the patterns and processes of recovery following clearing in these fragile high-altitude ecosystems. At present most studies on Neotropical forest succession and recovery after human impact have been

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conducted in lowland rainforest (Ewel 1980, Gómez-Pompa & Vázquez-Yanes 1981, Purata 1986, Saldarriaga *et al.* 1988, Toro & Saldarriaga 1990; see also Brown & Lugo 1990) or in mid-elevation cloud forests (e.g. Byer & Weaver 1977, Sugden *et al.* 1985, van Valkenburg & Ketner 1994).

To fill this gap the recovery and resilience of a Costa Rican upper montane *Quercus* forest at c. 3000 m altitude was studied by a chronosequence covering the last 30 y of secondary succession after clearing, burning, grazing and subsequent abandonment. The present paper deals especially with patterns of forest structure recovery in differently aged secondary oak forests in comparison to the structural status of undisturbed mature primary oak forest. Patches of secondary and primary forest were selected in the south-western part of the Cordillera de Talamanca, because various studies on Costa Rican montane oak forest ecology and management are carried out there and thus offer an excellent background setting for this study (e.g. Blaser 1987, Jiménez *et al.* 1988, Kappelle *et al.* 1989, 1991, 1992, 1995).

STUDY SITE

The study site is in the upper part of the Río Savegre watershed on the Pacific slope of the Costa Rican Cordillera de Talamanca (9° 35' 40" N, 83° 44' 30" W). It is located near Jaboncillo de Dota (2800–3000 m altitude) within the limits of the highly deforested 62,000 ha Los Santos Forest Reserve (Meza & Bonilla 1990). At present this protected area serves as a buffer zone to the 612,570 ha Amistad Biosphere Reserve, a World Heritage Site (Kappelle & Juárez 1994, 1995, Whitmore 1990).

The Cordillera de Talamanca is formed of intrusive, and Tertiary volcanic rocks, alternated with marine sediments (Weyl 1980). Pleistocene glaciations have left their traces such as fossil periglacial phenomena on the Cerro de la Muerte (3491 m alt.) at the near-by Buenavista massif (Hastenrath 1973). Slopes are mainly convex, moderately steep to very steep (20 to 35 degrees). Soils are principally derived from volcanic ashes originating from the Cordillera Central. Kennis & de Vries (1993) following van Uffelen (1991) classified soils at Jaboncillo de Dota as Humic [Mollic or Umbric] Andosols according to FAO (1988) and as (Histic) Hapludands according to the USDA System (Soil Survey Staff 1975). In general these montane oak forest soils are brown-yellowish coloured, rich in organic matter (>15 cm of litter and humus), medium-textured, moderately fertile and excessively drained (van Uffelen 1991, Vásquez 1983). As in many tropical areas, they are relatively acid (pH in H₂O at 15 cm soil depth: 4.5–5.5). C/N ratios for litter and humus range from 10 to 35, and A-, B- and C-horizons from 10 to 20 (Kennis & de Vries 1993).

The average annual temperature at 15 km E of the study site at the town of Villa Mills (3000 m alt.) is 10.9°C, while the average rainfall is 2812 mm (Instituto Meteorológico Nacional 1988). January is the coldest month with an average temperature of 10°C. Frost may occur during clear nights with

temperatures down to 3°C below zero. Diurnal mist during the afternoons is considerable (cloud forest), especially during the rainy season (May to November). According to van Dunné (1993) the average temperature near the forest floor in a primary oak forest at Jaboncillo de Dota was 14°C during five days in the dry season (20–24 February 1992) and 12°C during five days in the wet season (20–24 August 1992). For the same periods this author mentions an average relative humidity of 68% in the dry season and of 86% in the wet season, respectively.

Originally the upper Río Savegre watershed has been totally covered with tropical evergreen (upper) montane oak-dominated rainforest (Holdridge *et al.* 1971, Kappelle *et al.* 1989). However, since the construction of the Interamerican Highway in the 1940s, clearing of mature montane forest stands has occurred frequently, generating a highly heterogeneous pattern of vegetation types. Today tracts of pristine *Chusquea-Quercus* forests form a mosaic with pasturelands, orchards and patches of differently aged secondary vegetation, including abandoned grassland, shrubland and successional forest communities (Kappelle *et al.* 1989, 1994).

METHODS

Site selection and data collection

With the help of a baseline study on plant communities in montane secondary vegetation at the study site (Kappelle *et al.* 1994) and recent detailed aerial photographs (scale *c.* 1:15,000) twelve 0.1 ha plots (25 m × 40 m) were selected in differently-aged secondary and primary oak forest patches between 2900 and 3000 m alt. Sample size was in accordance with studies in comparable tropical regions (Kuzee *et al.* 1994, Young 1993). A minimum edge of 5 m width was maintained around secondary forest plots and a 10 m wide edge around primary forest plots. Successional age of secondary forests was estimated on basis of oral information from local farmers and landowners. The reliability of this information was corroborated through interviewing local residents independently and cross-checking the data gathered (Kappelle & Juárez 1995).

An earlier forest classification study (Kappelle *et al.* 1995) using multivariate data on the composition of the terrestrial vascular flora learned that three seral stages (successional forest phases) could easily be distinguished: an early secondary forest (ESF) with recovery ages of 8 to 20 y since abandonment, a late secondary forest (LSF) with recovery ages of 25 to 32 y since abandonment and a mature primary forest (PF) of unknown age (probably >*c.* 150 y since the formation of the last large natural tree fall gaps). Verbal information on former and today's land use practices at and near each plot was gathered on-site from local farmers. Topographic data were collected in all plots, while additional abiotic data were gathered in a selected series of plots, each representing a different forest phase.

For the present study tree layers were sampled by identifying all tree stems with a diameter at breast height (dbh) ≥ 3.0 cm. For each tree dbh was measured and crown top height estimated or measured using a Haga altimeter. Stems originating from one root system such as sprouts or reiterations from a single tree stump branching near the forest floor, as in the case of multiple-stemmed trees, were considered as separate individuals in accordance with Cailleux (1980). In each forest phase one illustrative plot was randomly selected by lot for a more in-depth study of structural and positioned variables of each tree individual (crown top height, crown base height, first ramification height, two perpendicular crown diameters at peripheral height and horizontal crown position coordinates).

Data analysis and interpretation

Species identification and nomenclature followed the *Flora of Costa Rica* (Standley 1937–1938), the *Flora Costaricensis* (Burger 1971–1993), the *Flora of Panamá* (Woodson & Schery 1943–1980) and older works cited therein. Voucher specimens were deposited at the herbaria of the Museo Nacional de Costa Rica (CR) and the Utrecht University (U).

On the basis of earlier work (Kappelle 1993, Kappelle *et al.* 1995) replicate plots of 0.1 ha were classified into a set of early secondary forest stands (ESF, $n = 5$), a set of late secondary forest stands (LSF, $n = 4$) and a set of primary forest stands (PF, $n = 3$). For each 0.1 ha plot numbers of tree species (i.e. species richness), genera and families were established. Next, tree species diversity was found by calculating two alpha diversity indices following Whittaker (1975) and Magurran (1988): Shannon–Wiener's index and the reciprocal of Simpson's index.

Following Synnott (1979) and Lamprecht (1986) stem density (number of stems ha^{-1}) and relative abundance as well as basal areas ($\text{m}^2 \text{ha}^{-1}$) and relative dominance were calculated for each tree species in each plot (stems ≥ 3.0 cm dbh). Relative frequencies of species and derived importance value indices were not estimated for each successional forest phase as the number of plots per phase varied too much and values would be unreliable. In order to determine the size–class distributions of stems in different forest phases the following six stem diameter classes (dbh) were distinguished: (I) $3 \leq \text{dbh} < 5$ cm, (II) $5 \leq \text{dbh} < 10$ cm, (III) $10 \leq \text{dbh} < 20$ cm, (IV) $20 \leq \text{dbh} < 40$ cm, (V) $40 \leq \text{dbh} < 80$ cm and (VI) $\text{dbh} \geq 80$ cm. Frequency distributions of size classes were drawn for all tree species.

Kruskal–Wallis ANOVA tests were used to compared diversity indices, density and basal area among three successional forest phases. Student's *t*-tests were applied to compare differences in basal area between primary and secondary forest phases.

To find patterns of growth the relationship between height and dbh was assessed for each illustrative plot. The minimum time needed for the recovery

of the forest structure was estimated using regression analysis of the relationships among maximum canopy height, basal area and age of the successional forest plots. Confidence intervals for regression coefficients were calculated in accordance with Zar (1984).

RESULTS

Species diversity, floristic composition and stratification

In the sampled forest area of 1.2 ha (12 plots of 0.1 ha each) a total of 42 tree species was found distributed over 35 genera and 29 families. Tree species richness ranged from 15 to 30 species per 0.1 ha in ESF, 18 to 24 species in LSF and 18 to 21 species in PF (Table 1). The Shannon–Wiener diversity index (H') ranged from 2.90 to 3.90 for 0.1 ha plots. Shannon–Wiener values were very similar among successional forest phases (Kruskal–Wallis ANOVA, $P = 0.45$). A similar trend was seen in the reciprocal of Simpson's index ($1/D$), which ranged from 3.88 to 9.62 (Kruskal–Wallis ANOVA among phases, $P = 0.23$).

The maximum height of the closed canopy ranged from 5 to 14 m in ESF, from 11 to 18 in LSF and from 35 to 40 m in PF (Table 1). In the absence of emergents there were two clear tree layers in PF: (i) a uniform canopy layer

Table 1. Some structure and diversity parameters for three different successional phases of upper montane *Quercus* forest in the Costa Rican Cordillera de Talamanca. Data are presented as means per 0.1 ha (plot area) ± 1 SE.

Successional forest phase	Early secondary forest (n = 5)	Late secondary forest (n = 4)	Primary forest (n = 3)
Age (y) ^a	8–20	25–32	— — —
Max. canopy height (m)	10.0 $\pm$ 1.1	15.5 $\pm$ 1.6	36.0 $\pm$ 1.0
Number of stems per 0.1 ha by diameter classes			
I ≥ 3 –5 cm dbh	118.6 $\pm$ 8.4	108.3 $\pm$ 14.3	68.0 $\pm$ 6.8
II ≥ 5 –10 cm dbh	96.8 $\pm$ 23.6	97.5 $\pm$ 6.4	56.3 $\pm$ 5.2
III ≥ 10 –20 cm dbh	26.2 $\pm$ 11.1	53.8 $\pm$ 12.2	33.0 $\pm$ 3.5
IV ≥ 20 –40 cm dbh	1.8 $\pm$ 1.1	9.0 $\pm$ 4.1	17.7 $\pm$ 2.3
V ≥ 40 –80 cm dbh	—	—	10.0 $\pm$ 2.0
VI ≥ 80 cm dbh	—	—	2.7 $\pm$ 0.3
Total (≥ 3 cm dbh)	243.4 $\pm$ 32.0	268.5 $\pm$ 27.2	187.7 $\pm$ 4.7
Stems ≥ 10 cm dbh (%)	10.0 $\pm$ 3.4	22.8 $\pm$ 4.3	34.0 $\pm$ 4.0
Number of species ^b	21.0 $\pm$ 2.5	20.3 $\pm$ 1.3	19.7 $\pm$ 0.9
Number of genera	19.6 $\pm$ 2.2	18.0 $\pm$ 1.0	16.7 $\pm$ 0.9
Number of families	18.2 $\pm$ 2.1	16.5 $\pm$ 0.9	14.3 $\pm$ 0.7
Shannon–Wiener's H'	3.39 $\pm$ 0.16	3.14 $\pm$ 0.14	3.31 $\pm$ 0.09
Simpson's reciprocal $1/D$	7.37 $\pm$ 0.88	5.39 $\pm$ 1.06	6.33 $\pm$ 0.90

^a Age of secondary forests in years since abandonment; — — — unknown.

^b Tree species with stems ≥ 3 cm dbh.

Table 2. Density^a and basal area of 42 tree species with stems ≥ 3 cm dbh in three different successional phases of upper montane *Quercus* forest in the Costa Rican Cordillera de Talamanca. Plot size was 0.1 ha. Species are ranked by basal area values from high levels during early succession to high values during late succession. Data are presented as means $\pm$ SE.^b A single dash (—) means zero abundance.

Successional forest phase	Age (y) ^c	Density (number of stems ha ⁻¹)			Basal area (m ² ha ⁻¹)		
		Early secondary forest (n = 5)	Late secondary forest (n = 4)	Primary forest (n = 3)	Early secondary forest (n = 5)	Late secondary forest (n = 4)	Primary forest (n = 3)
		8–20	25–32	— — —	8–20	25–32	— — —
Species	Family ^d						
<i>Bocconia frutescens</i> L.	PAP	78.0 $\pm$ 25.0	—	—	0.36 $\pm$ 0.19	—	—
<i>Senecio copeyensis</i> Greenm.	AST	12.0 $\pm$ 7.4	—	—	0.10 $\pm$ 0.08	—	—
<i>Senecio multiviridis</i> Benth.	AST	46.0 $\pm$ 26.9	22.5 $\pm$ 22.5	—	0.09 $\pm$ 0.05	—	—
<i>Saurauia veraguasensis</i> Seemann	SRA	4.0 $\pm$ 4.0	—	—	0.01 $\pm$ 0.01	—	—
<i>Symplocos serrulata</i> Kunth	SYM	4.0 $\pm$ 2.5	—	—	0.01 $\pm$ 0.01	—	—
<i>Buddleja nitida</i> Benth.	LOG	144.0 $\pm$ 51.2	47.5 $\pm$ 31.5	—	1.47 $\pm$ 0.89	0.22 $\pm$ 0.19	—
<i>Fuchsia arborescens</i> Sims.	ONA	256.0 $\pm$ 104.3	30.0 $\pm$ 14.7	—	0.94 $\pm$ 0.37	0.05 $\pm$ 0.03	—
<i>Abatia parviflora</i> Ruiz López & Pavón	FLC	216.0 $\pm$ 93.5	17.5 $\pm$ 17.5	—	0.93 $\pm$ 0.40	0.06 $\pm$ 0.06	—
<i>Verbesina verstediana</i> Benth.	AST	304.0 $\pm$ 125.3	7.5 $\pm$ 4.8	—	0.75 $\pm$ 0.29	0.02 $\pm$ 0.01	—
<i>Monnina crepinii</i> Chodat	PGL	188.0 $\pm$ 93.1	10.0 $\pm$ 7.1	—	0.43 $\pm$ 0.16	0.01 $\pm$ 0.01	—
<i>Cornus disciflora</i> Mocino & Sessé	COR	174.0 $\pm$ 83.0	57.5 $\pm$ 13.1	3.3 $\pm$ 3.3	0.65 $\pm$ 0.42	0.14 $\pm$ 0.05	—
<i>Ilex discolor</i> Standley	AQF	16.0 $\pm$ 8.1	12.5 $\pm$ 12.5	—	0.04 $\pm$ 0.01	0.01 $\pm$ 0.02	—
<i>Miconia schnellii</i> Wurd.	MLS	12.0 $\pm$ 7.4	7.5 $\pm$ 4.8	—	0.03 $\pm$ 0.02	0.01 $\pm$ 0.01	—
<i>Myrcianthes fragrans</i> McVaugh	MRT	6.0 $\pm$ 6.0	10.0 $\pm$ 10.0	—	0.02 $\pm$ 0.02	0.01 $\pm$ 0.01	—
<i>Hedyosmum mexicanum</i> Cordenoy	CLR	2.0 $\pm$ 2.0	10.0 $\pm$ 10.0	—	0.07 $\pm$ 0.07	0.09 $\pm$ 0.09	—
<i>Garrya laurifolia</i> Hartweg ex Benth.	GAR	6.0 $\pm$ 6.0	22.5 $\pm$ 19.3	—	0.01 $\pm$ 0.01	0.02 $\pm$ 0.02	—
<i>Escallonia myrtilloides</i> L.f.	ESC	6.0 $\pm$ 4.0	32.5 $\pm$ 23.6	—	0.01 $\pm$ 0.01	0.08 $\pm$ 0.06	—

<i>Solanum storkii</i> Morton & Standley	SOL	36.0 ± 18.3	7.5 ± 4.8	—	0.06 ± 0.03	0.10 ± 0.10	—
<i>Conarostaphylis arbutoides</i> Lindley	ERI	4.0 ± 2.5	142.5 ± 53.4	—	0.01 ± 0.01	0.42 ± 0.16	—
<i>Viburnum costaricanum</i> (Oersted) Hemsl.	CPR	152.0 ± 81.8	155.0 ± 56.4	66.7 ± 14.5	0.70 ± 0.40	0.37 ± 0.10	0.20 ± 0.07
<i>Oreopanax xalapense</i> (Kunth) Decne. & Pl.	ARL	44.0 ± 16.3	22.5 ± 6.3	13.3 ± 8.8	0.23 ± 0.16	0.16 ± 0.08	0.11 ± 0.05
<i>Ocotea pitieri</i> (Mez) Van der Werff	LAU	16.0 ± 16.0	2.5 ± 2.5	13.3 ± 3.3	0.06 ± 0.06	0.01 ± 0.01	0.04 ± 0.03
<i>Myrsine coriacea</i> (Sw.) R. Br. ex R. & Sch.	MRS	46.0 ± 24.4	157.5 ± 60.6	33.3 ± 24.0	0.13 ± 0.07	0.31 ± 0.12	0.09 ± 0.07
<i>Zanthoxylum scheryi</i> Lundell	RUT	6.0 ± 4.0	35.0 ± 13.2	60.0 ± 15.3	0.01 ± 0.01	0.18 ± 0.14	0.11 ± 0.03
<i>Quercus copeyensis</i> Corn. Mueller	FAG	216.0 ± 145.1	912.5 ± 351.8	640.0 ± 101.2	1.20 ± 0.99	8.93 ± 4.02	37.14 ± 4.74
<i>Quercus costaricensis</i> Liebmann	FAG	34.0 ± 22.7	287.5 ± 191.0	50.0 ± 35.1	0.08 ± 0.05	4.60 ± 2.79	9.69 ± 6.64
<i>Weinmannia pinnata</i> L.	CUN	186.0 ± 92.1	220.0 ± 57.9	156.7 ± 23.3	0.88 ± 0.55	0.78 ± 0.24	5.77 ± 0.16
<i>Syrax argenteus</i> Presl.	STY	48.0 ± 38.3	75.0 ± 24.0	203.3 ± 23.3	0.12 ± 0.10	0.18 ± 0.05	1.54 ± 0.27
<i>Cleyera theaeoides</i> (Sw.) Choisy	TEA	88.0 ± 40.8	212.5 ± 46.3	96.7 ± 29.1	0.18 ± 0.13	0.52 ± 0.13	1.35 ± 0.30
<i>Vaccinium consanguineum</i> Klotzsch	ERI	30.0 ± 11.0	22.5 ± 16.0	53.3 ± 14.5	0.06 ± 0.03	0.04 ± 0.03	0.96 ± 0.28
<i>Ardisia costaricensis</i> Lundell	MRS	8.0 ± 8.0	40.0 ± 33.7	196.7 ± 26.0	0.02 ± 0.02	0.06 ± 0.05	0.59 ± 0.09
<i>Myrsine pelucidopunctata</i> Oersted	MRS	12.0 ± 5.8	60.0 ± 16.3	53.3 ± 8.8	0.02 ± 0.01	0.07 ± 0.02	0.55 ± 0.13
<i>Magnolia sororum</i> Seibert	MAG	4.0 ± 4.0	—	3.3 ± 3.3	0.01 ± 0.01	—	0.53 ± 0.53
<i>Perea vestitula</i> Standley & Sreyermark	LAU	—	10.0 ± 10.0	6.7 ± 6.7	—	0.05 ± 0.05	0.03 ± 0.03
<i>Oreopanax capitatus</i> (Jacq.) Decne. & Pl.	ARL	—	10.0 ± 10.0	13.1 ± 3.3	—	0.03 ± 0.03	0.03 ± 0.02
<i>Ilex pallida</i> Standley	AQF	2.0 ± 2.0	32.5 ± 16.0	56.7 ± 8.8	—	0.08 ± 0.06	0.24 ± 0.08
<i>Symphlocos austinsmithii</i> Standley	SYM	2.0 ± 2.0	12.5 ± 12.5	60.0 ± 45.8	—	0.02 ± 0.02	0.83 ± 0.51
<i>Ocotea mollicella</i> (Blake) Van der Werff	LAU	—	—	13.3 ± 8.8	—	—	0.03 ± 0.03
<i>Miconia tonduzii</i> Cogn.	MLS	18.0 ± 18.0	—	13.3 ± 3.3	—	—	0.03 ± 0.01
<i>Drinys grandensis</i> L.f.	WIN	—	—	6.7 ± 6.7	—	—	0.04 ± 0.04
<i>Rhamnus orodendron</i> L.O. Williams	RHM	8.0 ± 8.0	—	36.7 ± 23.3	—	—	0.08 ± 0.05
<i>Schleffera rodriguesiana</i> Frodin	ARL	—	2.5 ± 2.5	26.7 ± 6.7	—	—	0.31 ± 0.27
Total		2434.0 ± 320.0	2685.0 ± 271.7	1876.7 ± 47.0	9.77 ± 3.14	17.42 ± 3.44	60.69 ± 2.23

^a Density is equal to tenfold the absolute abundance for a certain species in a 0.1 ha plot.

^b Values indicated with ‘—’ indicate the species’ absence in that particular phase.

^c Age of secondary forests in years since abandonment.

^d Families are given as mnemonic three-letter acronyms following Weber (1982).

between 15 and 40 m height and dominated by *Quercus copeyensis* Corn. Mueller and *Q. costaricensis* Liebm., and (ii) a mixed subcanopy layer between 0 and 18 m with *Ardisia costaricensis* Lundell, *Cleyera theaeoides* (Sw.) Choisy, *Myrsine pellucidopunctata* Oersted, *Ocotea mollicella* (Blake) van der Werff, *Styrax argenteus* Presl. and *Vaccinium consanguineum* Klotzsch together with *Quercus* trees. *Weinmannia pinnata* L. and *Schefflera rodriguesiana* Frodin did occur in both tree layers. On the contrary, in ESF and LSF a clear differentiation in two tree layers had not yet appeared. ESF was characterized by dominant species such as *Abatia parviflora* Ruiz López & Pavón, *Fuchsia arborescens* Sims., *Monnina crepinii* Chodat and *Verbesina oerstediana* Benth. In their shade grew seedlings and saplings of *Quercus* species. LSF was even more complex as numerous species appeared with similar abundances. Here, *Buddleja nitida* Benth., *Cornus disciflora* Mociño & Sessé, *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult., *Oreopanax xalapensis* (Kunth) Decne. & Planch. and *Viburnum costaricanum* (Oersted) Hemsl. became prominent, while typical pioneer species such as the large-leaved *Bocconia frutescens* L., *Saurauia veraguasensis* Seemann, *Senecio copeyensis* Greenm. and *S. multivenius* Benth. gave way to large numbers of *Quercus copeyensis* and *Q. costaricensis* with heights >15 m. These were apparently the trees that could initiate the development of a new canopy layer, leaving behind the taller successional species that enter their senescent phase.

Forest structure

A total of 2854 stems ≥ 3.0 cm dbh were counted, identified and measured in a forest area of 1.2 ha. Numbers of stems decreased with increasing stem diameter in all successional forest phases (Table 1). The percentage of trees with stems ≥ 10.0 cm dbh increased from almost 3% in 8-year-old ESF to nearly 40% in undisturbed PF. Stem density ranged from 1670 stems ha^{-1} for 10-year-old ESF to 3270 stems ha^{-1} for 32-year-old LSF (Table 2). Stem density did not differ significantly among the three successional forest phases (Kruskal–Wallis ANOVA, $P = 0.14$). Basal area increased linearly with plot age for secondary forests and ranged from 4.46 $\text{m}^2 \text{ha}^{-1}$ in 8-year-old ESF to 64.69 $\text{m}^2 \text{ha}^{-1}$ in undisturbed PF (Table 2). Significant differences were found in basal area among the successional forest phases (Kruskal–Wallis ANOVA, $P = 0.024$). Indeed, basal areas were significantly higher in PF than in ESF or LSF (Student's *t*-tests: (i) for ESF and PF; $t = -11.25$, d.f. = 6, $P < 0.001$; and (ii) for LSF and PF: $t = -9.58$, d.f. = 5, $P < 0.001$).

Considering in detail the size–class distributions of stems for all tree species the following observations were made. First of all, the majority of the species shows a gradual change in forest structure and tree composition along the successional gradient (Figure 1). One notes the shift of smaller stems towards stems with larger dbh values within a species as forest recovery takes place. This is especially true for *Fuchsia arborescens* and *Abatia parviflora* in differently aged ESF plots, and for *Quercus copeyensis* in the change from LSF towards

PF. *Myrsine coriacea* was most abundant in LSF, but occurred in low numbers in PF, where it occupied relatively open sites such as older gaps. A similar strategy was found in *Cornus disciflora* and *Oreopanax xalapensis* (Kappelle 1993).

Concerning the relative abundance and dominance of each species, the following observations are made. While *Monnina crepinii* in ESF appeared equally abundant and dominant, *Verbesina oerstediana* was much more abundant than dominant (e.g. in plot 3). This is explained by the fact that *V. oerstediana* is found with many individuals, which have rather tiny stems. The opposite was seen in *Quercus costaricensis* in PF plot 10. Here, this oak species was much more dominant than abundant, since few stems were found, but these displayed exceptionally high dbh values responsible for a great basal area and high relative dominance. Another interesting feature is the heterogeneity of ESF (many species codominant) and the homogeneity of LSF and PF (few species codominant). This is a clear result of the growing importance of *Quercus* with increasing forest maturity. Which species of oak dominates at a certain site depends on local circumstances (e.g. nearness of seed sources, germination and growth at the most optimum time, edaphic circumstances). Thus, while most LSF plots were characterized by almost pure stands of *Quercus copeyensis*, plot 9 harboured a relatively large number of huge *Q. costaricensis* trees, which locally replaced the former.

Growth, recovery and resilience

An analysis of the relationship between $\log_e$ (ht) and $\log_e$ (dbh) showed significant simple regressions for stems ≥ 3.0 cm dbh in representative and illustrative plots of all three forest phases:

- (1) ESF plot 3: $\log_e$ (ht) = $0.87 + 0.48 \log_e$ (dbh)
($R^2 = 0.47$, $n = 176$ stems, $P < 0.0001$)
- (2) LSF plot 8: $\log_e$ (ht) = $1.09 + 0.51 \log_e$ (dbh)
($R^2 = 0.55$, $n = 140$ stems, $P < 0.0001$)
- (3) PF plot 10: $\log_e$ (ht) = $0.66 + 0.68 \log_e$ (dbh)
($R^2 = 0.83$, $n = 128$ stems, $P < 0.0001$)

with dbh in cm and ht (height) in m. Whereas the intercept coefficient fluctuated around $0.88 (\pm 0.22)$ as succession proceeded, the slope of the regression line rose slightly as a consequence of the increase in numbers of large oaks with time. At the same time the distribution of trees remained skewed to the right: most stems were short and thin in all forest phases. Furthermore, the regression coefficient became larger with increasing forest maturity.

An analysis of the relationships between $\log_e$ (maximum canopy height), $\log_e$ (basal area) and $\log_e$ (time of recovery) revealed significant simple regressions for the successional forest plots:

Figure 1. Changes in the distribution of the number of stems (Y-axis) per stem diameter class (X-axis) for 42 tree species found in 0.1 ha plots representing early secondary forest (ESF, $n = 5$), late secondary forest (LSF, $n = 4$) and primary forest (PF, $n = 3$) in the upper montane *Quercus* forest belt of the Costa Rican Cordillera de Talamanca.

- (4) All secondary plots: $\log_e(\text{ht}) = 1.33 + 0.40 \log_e(\text{age})$
 $(R^2 = 0.73, n = 9 \text{ plots}, P < 0.005)$
(confidence limits: $t_{95\%} = 2.37, b = 0.40,$
 $L_1 = 0.62, L_2 = 0.18)$
- (5) All secondary plots: $\log_e(\text{ba}) = 0.05 + 0.82 \log_e(\text{age})$
 $(R^2 = 0.71, n = 9 \text{ plots}, P < 0.005)$
(confidence limits: $t_{95\%} = 2.37, b = 0.82,$
 $L_1 = 0.36, L_2 = 1.29)$
- (6) All secondary plots: $\log_e(\text{ht}) = 1.38 + 0.46 \log_e(\text{ba})$
 $(R^2 = 0.91, n = 9 \text{ plots}, P < 0.0001)$
- (7) All plots: $\log_e(\text{ht}) = 1.11 + 0.58 \log_e(\text{ba})$
 $(R^2 = 0.95, n = 12 \text{ plots}, P < 0.0001)$

with ba (basal area) in $\text{m}^2 \text{ha}^{-1}$, ht (maximum canopy height) in m and age (time of recovery) in y. On the basis of regression equations (4) and (5) the theoretically minimum time needed for forest structure recovery was estimated: (i) by solving for X (age) where Y (maximum canopy height) is the mean PF maximum canopy height of 36 m, the minimum time required for a secondary forest to reach structural maturity is 87 y (regression equation (4)); whereas (ii): by solving for X (age) where Y (basal area) is the mean PF basal area of $60.3 \text{ m}^2 \text{ha}^{-1}$, the minimum time required for a secondary forest to reach structural maturity is 74 y (regression equation (5)). An average recovery period is thus 80 y. However, it has to be taken into account that R^2 ranges from 0.71 to 0.73 for both equations and that therefore c. 25–30% of the total variance of Y remains unexplained after these regressions. Moreover, although ‘structural maturity’ does mean that the physical dimensional parameters of the forest have reached values comparable to those found in primary forest, no dynamic equilibrium is created: changes in the tree population (e.g. through treefalls) will occur and gradually become less severe – a process that may take several tree generations.

DISCUSSION

Trends in forest recovery along the successional gradient

A study of the changes in the structure of a tropical upper montane oak forest following a large-scale disturbance by man showed that secondary succession in the area appeared to be a gradual, progressive process leading to a structurally more complex and mature forest phase with increasing time of recovery. Tree species diversity indices did not differ significantly among three successional forest phases (ESF, LSF and PF), whereas terrestrial vascular plant diversity in the area was significantly higher in ESF due to the downslope migration and invasion of numerous paramo herb species and subalpine shrub species into initial phases of succession (Islebe & Kappelle 1994, Kappelle *et al.* 1995).

The dominant genus *Quercus* displays a great recovery capacity, as many oaks with stems >3.0 cm dbh appear after human disturbance in ESF. From the moment of establishment oak stem numbers rapidly rise and increase throughout the first successional stages. After more than 30 to 35 y stem density levels off, while stem sizes continue to increase and reach their highest values at the end of the successional pathway, when forest maturity is reached. In this mature PF phase the distribution of the number of oak stems by dbh class is represented by a reversed J-shaped curve (see Figure 1 and Jiménez *et al.* 1988).

Stem number initially increases from *c.* 160–200 in ESF to *c.* 210–330 in LSF and later levels off towards the mature PF phase (*c.* 180–200 stems). This trend is explained by the natural thinning process which occurs in later phases due to increased competition. On the other hand, a gradual increase in basal area is evident for the shift from 8- to 32-year-old secondary forests and is caused by the recruitment of young oaks into the canopy of LSF.

Two more factors that influence the rate of forest recovery have to be considered: (i) the distance from a secondary forest to primary forest trees, and (ii) the former land use on the secondary forest site. Distance plays a particularly important role in secondary succession as primary forest vicinity accelerates the process of recovery, the speeding-up of succession (Geuze 1989, Guevara *et al.* 1986, Horn 1981, Purata 1986, Young 1993). To minimize the distance effect on the recovery rate we established secondary forest plots at a distance of 200 to 500 m from primary forest fragments. Although it was attempted to avoid differences in former land use among the plots, the intensity of burning after clearing seemed to have been much higher in 20-year-old ESF plot 2 than in any other secondary forest plot. This is expressed in the locally high abundance of *Buddleja nitida* in almost absolute absence of *Quercus*. The fact that oaks are suppressed here may be explained by the great damage the fire probably caused to the fine roots and associated mycorrhiza, without which a successful germination and growth of oaks is almost impossible (Chaverri & Rojas 1986).

Regression equations based on log-transformed data of maximum canopy height, basal area and successional age showed that tropical montane forest succession in the area is a recovery process similar to the growth process known of individual tropical montane tree species in the region (Jiménez 1984; cf. Ewel 1991, for other tropical regions). However, additional data on the structure of 1- to 8-year-old pioneer forest and of 40- to *c.* 100-year-old secondary forest are needed in order to make the presented estimations of the total recovery time more precise. Unfortunately, secondary forests >35 y old are not available in the study area as deforestation started only four decades ago. On the basis of our present calculations, a return to mature tropical montane oak forest in the area seems feasible, although the precise amount of time needed for complete forest recovery remains unknown.

As a final remark, it is suggested that the secondary succession discussed here does not conform well to an initial floristic composition model (*sensu* Egler 1954) as species composition, relative abundance and dominance in LSF and PF differ strongly from the initial composition in ESF. Reductionist models

including facilitation, tolerance and inhibition (*sensu* Connell & Slatyer 1977) are more likely to occur among individual species, but do not offer a satisfying answer to the complex question of forest recovery on the community level (cf. Finegan 1984). Yet, the establishment of several primary species is assumed to be favoured or at least tolerated by some early colonizers and inhibited by others. It is also believed that early (secondary) taxa alter the microenvironmental conditions and subsequently favour, allow, retard or prevent the establishment of following-up (primary) species. A study concerning the species' natural history (*sensu* Finegan 1984) – including attributes such as seed dispersion, shade-tolerance and longevity – may contribute to a clarification of this subject and help construct a realistic model for secondary succession in Costa Rica's montane oak forests.

Comparison with other tropical forests

The main structure and composition parameters of Costa Rican primary and secondary upper montane oak forests fall within the ranges known from other Neotropical forests (Table 3). Plot sizes in this study were comparable to sizes applied in other tropical regions (e.g. Kuzee *et al.* 1994, Saldarriaga *et al.* 1988, Uhl & Jordan 1984, Young 1993). Tree species richness in this study reached similar values as in subalpine Peru (Young 1993) and lower montane Costa Rica (Kuzee *et al.* 1994). Upper montane PF was about seven to eight times poorer in tree species than Mexican lowlands (Bongers *et al.* 1988) and the Colombian Chocó (Faber-Langendoen & Gentry 1991), while upper montane ESF and LSF were only two to three times poorer in trees than their even-aged lowland equivalents in Venezuela (Saldarriaga *et al.* 1988). This difference is due to the downslope invasion of supalpine species during early upper montane forest succession. Shannon–Wiener's diversity index decreased with increasing altitude (Table 3; see also Kappelle *et al.* 1995).

The steady rise in canopy height and basal area with successional age found in this study is the same for tropical forests in all elevational belts (Table 3 and Brown & Lugo 1990). Although the mean maximum canopy height in our PF is almost equal to the values for primary lowland rainforests (Bongers *et al.* 1988, Faber-Langendoen & Gentry 1991), the canopy of even-aged secondary forests is about one-fifth as tall as upper montane altitudes than in Venezuelan lowlands (Uhl & Jordan 1984). Furthermore, after a recovery period of *c.* 14–15 y lowland secondary forests have recovered a third of their original basal area (Saldarriaga *et al.* 1988), while upper montane secondary forests have recovered only a fifth to a sixth of their original basal area. Both trends (canopy height and basal area) support Ewel's (1980) statement on the decline in secondary forest growth rates with increasing altitude.

Densities in the PF plots are most similar to those for other primary upper montane *Quercus copeyensis* forests in Costa Rica. However, our mean PF density of 633 stems ha⁻¹ (stems ≥ 10 cm dbh) is *c.* 25% higher than that for the same size class in Jiménez *et al.*'s (1988) oak forest. This is probably explained by

Table 3. Comparison of structure and diversity characteristics of some primary and secondary forests in different Neotropical upland and lowland regions.

Forest phase	Country	Age ^a (y)	Plot Size (ha)	Mean Altitude (m)	Species Richness	Shannon wiener H'	Maximum canopy height (m)	Stem density (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Minimum dbh (cm) measured	Source
<i>Tropical subalpine forest</i>											
Primary	Peru	M	0.10	3400	9	—	7	1600	22.2	≥2.5	Young (1993)
<i>Tropical upper montane forest</i>											
Primary	Ecuador	M	1.00	3280	32	—	—	1058	25.7	≥5.0	Valencia & Jørgensen (1992)
Primary ^b	Colombia	M	0.80	2850	33	—	30	509	27.9	≥5.0	Bazuin <i>et al.</i> (1993)
Primary ^c	Costa Rica	M	8.00	2700	—	—	56	695	52.9	≥5.0	Blaser (1987)
Primary ^c	Costa Rica	M	—	2560	—	—	—	505	48.9	≥10.0	Jiménez <i>et al.</i> (1988)
Primary ^c	Costa Rica	M	0.10	2975	20	3.31	36	1877	60.3	≥3.0	This study (mean PF)
Secondary	Costa Rica	15	0.10	2975	21	3.39	10	2434	9.8	≥3.0	This study (mean ESF)
Secondary ^c	Costa Rica	30	0.10	2975	20	3.14	16	2685	17.4	≥3.0	This study (mean LSF)
<i>Tropical lower montane forest</i>											
Primary	Costa Rica	M	0.18	1050	105	4.06	21	3320	62.8	≥2.0	Kuzee <i>et al.</i> (1994)
Secondary	Costa Rica	11	0.19	1030	54	2.84	16	3392	24.6	≥2.0	Kuzee <i>et al.</i> (1994)
Secondary	Costa Rica	35	0.10	950	69	3.51	16	3850	37.5	≥2.0	Kuzee <i>et al.</i> (1994)
<i>Transition from lower montane to lowland forest</i>											
Primary	Puerto Rico	M	0.40	725	40 ^d	—	20	1850	40.0	≥4.1	Weaver & Murphy (1990)
Secondary	Puerto Rico	15–30	0.20	550	19	—	19	2436	28.0	≥4.0	Lugo (1992) (Cubuy site)
<i>Tropical lowland forest</i>											
Primary	Colombia	M	0.10	50	166	6.70	35	3483	28.9	>2.5	Faber-Langendoen & Gentry (1991)
Primary	Mexico	M	1.00	340	142	4.65	35	2976	38.1	≥1.0	Bongers <i>et al.</i> (1988)
Primary	Venezuela	M	0.09	119	66	5.45	35	4378	35.6	≥1.0	Saldarriaga <i>et al.</i> (1988)
Secondary	Venezuela	5	0.09	119	56	4.60	14	7800	8.9	≥1.0	Uhl & Jordan (1984)
Secondary	Venezuela	14	0.09	119	56	4.63	—	5244	11.1	≥1.0	Saldarriaga <i>et al.</i> (1988)
Secondary	Venezuela	30	0.09	119	77	5.18	—	6989	11.7	≥1.0	Saldarriaga <i>et al.</i> (1988)
Secondary	Venezuela	80	0.09	119	79	5.02	—	3933	23.2	≥1.0	Saldarriaga <i>et al.</i> (1988)

^a M = mature forest.^b Forest dominated by *Quercus humboldtii*.^c Forest dominated by *Quercus copeyensis*.^d Forty species in 1.0 ha.

the locally high level of natural regeneration in our PF plots, expressed in the fairly large amount of trees in the smaller stem diameter classes. This implies that relatively small (0.1 ha) areas of primary forest are possibly not representative for the whole forest region. This assumption is further supported by the much lower basal area values (48–53 m² ha⁻¹) found in large-sized study plots by both Blaser (1987) and Jiménez *et al.* (1988) for stems ≥ 5 cm dbh and stems ≥ 10 cm dbh, respectively. These authors counted between 450 and 550 stems ha⁻¹, a range also found for Andean *Quercus humboldtii* Bonpland forests in Colombia (Bazuin *et al.* 1993). On the other hand, with a basal area of 27.9 m² ha⁻¹ for stems > 5 cm the Colombian oak forests obviously lack the pure stands of giant oaks, often with dbh > 100 cm, which are so typical of the Costa Rican upper montane forests.

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