Regeneration dynamics in canopy gaps of a montane forest of Chiloe Island, Chile

Dinámica de regeneración en claros de un bosque montano en la Isla de Chiloé, Chile

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ABSTRACT

We test the hypothesis that in forests characterized by disturbances which generate small-sized gaps, the canopy tends to a compositional equilibrium where the shade-tolerant trees remain the dominants. In a mid-elevation primary rain forest, Chiloé Island, Chile, we evaluated seed and seedling abundance at species level, in gaps of the forest. Then, we applied transition probabilities based on seedling/sapling abundances to test if the expected stationary specific composition of the canopy is correlated with the present canopy of the forest. Our results suggest that the observed canopy and subcanopy of this forest-type tends to be in a compositional equilibrium. Finally, we discuss the probable mechanisms responsible for this pattern.

Key words: compositional equilibrium, disturbance, succession, transition probabilities.

RESUMEN

En este trabajo ponemos a prueba la hipótesis que indica que en bosques caracterizados por perturbaciones que generan claros de pequeño tamaño, el dosel tiende a un equilibrio composicional, con las especies tolerantes a la sombra como las dominantes. En un bosque montano de la Isla de Chiloé (Chile), evaluamos la abundancia de plántulas y plantas juveniles a nivel de especie, en el interior de claros encontrados en el bosque. A través de probabilidades de transición nosotros pusimos a prueba si la composición específica esperada en el estado de equilibrio, se correlaciona con la composición específica observada en el dosel del bosque. Nuestros resultados sugieren que el dosel y el subdosel de este tipo de bosque tiende a estar en un equilibrio conposicional.

Palabras clave: equilibrio composicional, perturbación, sucesión, probabilidades de transición.

INTRODUCTION

In forests, disturbance (sensu Sousa 1984) often create gaps in the canopy, releasing resources which are exploited by colonizing species that eventually arrive to the area (Brokaw 1985, White & Pickett 1985, Runkle 1985). Depending on the spatial extent of the disturbance, canopy gaps may be classified in two groups representing the end points of a continuum: (i) very large gaps, resulting from the destruction of canopy trees as a result of unfrequent but severe disturbance (a volcanic eruption, hurricane, fire or landslide; Veblen 1985a), and (ii) small gaps resulting from the fall of one or a few trees by senescence, windthrow, or snow accumulation on tree tops (Brokaw 1985, Runkle 1985).

A central problem of forest dynamics is to understand the importance of large versus small gaps for the regeneration of forest trees (Veblen 1985a, Brokaw 1985, Denslow 1987, Spies & Franklin 1989). If small gaps are characteristic of a disturbance regime, then shade-tolerant tree species (sensu Brokaw 1985) will tend to occupy these gaps and eventually to dominate the canopy of the forest (Denslow 1980, Barden 1981). The canopy of this forest may remain in a compositional equilibrium, unless a large, catastrophic disturbance opens the canopy and allows the colonization by light-demanding species (Veblen 1985b). Alternatively, if

large-scale disturbances are frequent, the successional pathway will be different, and canopy composition will be less predictable from seedlings and saplings growing within large gaps (White et al. 1985).

Markovian chains may help us unravel the relevance of small gaps in forest succession (Veblen 1985a). Such models assume constant transition probabilities P_{ij}, which depend only on the present state and not on any previous state of the forest (Facelli & Pickett 1990). Values of P_{ij} give us an estimate of the probability that an individual of species i, found in a particular gap in the forest, will replace the fallen gap-maker of species j, in the canopy of that forest. The transition probability matrix allows us to predict the expected steady state composition of the system. Succession studies that use markovian matrices have recently been questioned (Veblen 1992). The basic assumptions of this model: (i) transition probabilities are constant over time and (ii) transition probabilities only depend on the preceding state of succession, are not supported by reality (Facelly & Pickett 1990). Therefore, an attempt to predict the future canopy composition of forests based only on transition probabilities will be just a theoretical exercise, unless we use this steady-state as a reference point to be compared with the observed canopy composition of the forest (Veblen 1992). In this way, we may pose the question of whether or not the dynamics inside gaps are predictable.

In this study, we examined a temperate rain forest on the east flank of the coastal range of Chiloé Island (42° 30' S), in southern Chile. Tree-fall gaps have been shown to be the most important component of this forest disturbance regime (Armesto & Fuentes 1988). Previous observations (Armesto & Figueroa 1987) suggest that in these forests the shade-tolerant trees tend to persist as dominants in the canopy and in the subcanopy. In this study, we tested this hypothesis by using the theoretical and methodological framework outlined above. Specifically, we compared the specific composition of seedlings and juveniles occupying tree-fall gaps, with the specific composition of adult trees in the canopy and subcanopy. Moreover, we simulated forest dynamic based on transition probabilities, using a Markovian matrix model, and finally we compared the simulated (expected) versus the observed forest composition.

METHODS

Study area

The forest studied is a remnant of primary rain forest, located between 350 and 450 m altitude on the coastal range of Isla Grande de Chiloé (42° 30' S). Species in the canopy are broad-leaved, evergreen trees and are profusely covered with woody vines and epiphytic ferns. The forest floor is covered with a dense carpet of mosses. The climate is temperate with a marked oceanic influence. Rainfall averages between 2000 and 3000 mm/yr, with more than one third of the total falling during the warm season (December-March). Minimum temperatures during winter are 2 to 3° C, and in summer, 5° to 10° C. Light snowfall is not uncommon during winter. The disturbance regime of the forest (snow storms) generates gaps which vary in size from 28 to 972 m^2 (mean size = 197 m^2; n = 37; Armesto & Fuentes 1988). The great majority of the gaps (89%) range from 100 to 300 m^2 (Armesto & Fuentes 1988) and the most important gap-makers were the Myrtaceous trees *Amomyrtus luma* (Mol) Legr. et Kausel and *Laureliopsis philipiana* (Looser) Schodde. Gaps in the Chiloé forest are according to Veblen (1989), small-sized (< 100 to 1000 m^2).

Tree abundance

We measured the abundance of canopy and subcanopy trees (> 10 cm dbh) along seven transects, 200 m long, NE to NW exposure, 5° and 20° slope, using the point-centered quarter method (Mueller-Dombois & Ellemberg 1974). We counted and identified the four nearest trees to each reference point, 20 m apart from each other along the transect. All trees recorded were either the canopy or the subcanopy, or were emergent. These values were used to estimate the relative frequency of species in the forest. The sampling covered an area of approximately 2.5 ha of forest.

Gaps and regeneration

For the gaps encountered along the transect lines or within 10 m, the gap-maker, that is the largest fallen tree, was identified at species level. We evaluated the abundance of tree seedlings (< 10 cm tall) and juveniles (> 10 cm tall) inside the gaps.

Seedlings were counted along a 2 m-wide transect following one of the main axes of the light gap. Juveniles were counted over the entire gap area. A gap consisted of a canopy openning with at least one fallen tree, and visible light directly above the center. Juveniles had heights up to 20 m, that is 10 or more metres below the top of the canopy. A total of 37 tree-fall gaps were sampled in the study site. The seedling and juvenile specific ranking found inside gaps was correlated with the observed ranking of adult trees of the forest.

Markovian matrix model

In order to evaluate transition probabilities, we assumed that the seedlings/juveniles that grow in gaps are the best candidates to replace the gap-maker in the canopy. We defined P_{ij} as the probability that species i will replace a gap-maker belonging to species j. Transition probabilities were estimated in two ways:

a) Mode 1: P_{ij} was estimated as the relative proportion of seedlings of species i present in gaps produced the species j (gap-maker).

b) Mode 2: same as mode 1, but using juveniles rather than seedlings to estimate P_{ij}.

These transition probabilities were used to construct two corresponding matrices. For tree species which were well represented in the canopy of the forest, but that did not form gaps, we assumed the existence of an hipothetical gap with equidistributed transition probabilities of seedlings and juveniles inside that gap. Multiplying a vector of initial species abundance by the transition probability matrix, we generated the species abundance vector of the next generation. To simulate long-term forest dynamics, the two transition matrices were used to predict the

specific composition of the forest, after the stationary state was reached. For both modes, the stationary state was reached after 100 iterations. No corrections for longevity were performed since the maximum age attainable by these species is unknown.

RESULTS

Canopy structure

A total of 264 adult trees were counted and identified in the seven transects. The most abundant species in the canopy were *Laureliopsis philipiana* and *Amomyrtus luma*; in the subcanopy, *Myrceugenia ovata* (H. et A.) Berg, *M. planipes* (H. et A.) Berg, were the most abundant (Table 1). Rare species (< 5% frequency) included *Drimys winteri* J.R. et G Forster, *Amomyrtus meli* (Phil.) Legr. et Kausel, *Nothofagus dombeyi* (Mirbel) Oersted, *Embothrium coccineum* J. R. et G. Forster, and *Raphithamnus spinosus* (A.L. Juss.) Mold. (Table 1).

Seedlings, juveniles and gap attributes

We found 2836 seedlings and 484 juveniles distributed in 37 gaps originated by *L. philipiana* (9), *A. luma* (17) *M. planipes* (1), *D. winteri* (6), *A. meli* (1) and *E. coccineum* (3). The most important gap-makers were *A. luma*, *L. philipiana and D. winteri*. We did not find gaps formed by *M. ovata*, one of the most important subcanopy trees (Table 1). However, seedlings and saplings of this species were abundant in gaps (Table 2 and 3). One small gap generated by a fallen branch of *M. planipes* had no saplings (Table 3). About 29% of the total area (2.5 ha) was estimated to correspond to canopy gaps, being their density near 14.8 gaps/ha. The areal extent of the gaps created by the different tree species was: *L. philipiana*, 2522 m²; *A. luma*, 2735 m², *M. planipes*, 141 m²; *D. winteri*, 1037 m²; *A. meli*, 145 m²; *E. coccineum*, 670 m².

Seedlings and juveniles of *A. luma* were the most abundant individuals in gaps (Table 2 and 3). There were no seedlings and saplings of *N. dombeyi* or *R. spinosus*, although they were represented to some extent in the

canopy of the forest (Table 1). The gaps we studied contained *A. meli* seedlings (Table 2) but no juveniles (Table 3).

The rank of species as seedlings was positively and significantly correlated with their rank as juveniles (Spearman, one-tailed test, $r = 0.75$, $P \ll 0.001$). Moreover, the rank of a species in the canopy, was positively and significantly correlated with its rank among seedlings (Spearman, one-tailed test, $r = 0.96$, $P \ll 0.01$) or juveniles (Spearman, one-tailed test, $r = 0.85$, $P \ll 0.005$).

Simulation

The transition matrix based on seedling and juveniles abundances inside gaps (Table 4 and 5) allowed us to predict the rank of a tree

TABLE 1

Abundance of the main canopy and subcanopy tree species observed in a mid-elevation montane forest in Chiloé Island, counted along seven transects of 200 m each. Figures represent the number of trees along the transects

Abundancia de las especies arbóreas de dosel y subdosel más importantes en un bosque de media altura, Isla de Chiloé, evaluada a lo largo de siete transectas de 200 m cada una. Se muestra la cantidad de árboles a lo largo de las transectas

| Species | TRANSECTS | | | | | | | | |
	1	2	3	4	5	6	7	Total	(%)
Laureliopsis philippiana	17	11	10	14	5	11	16	84	31.8
Amomyrtus luma	11	13	15	10	5	13	15	82	31.1
Myrceugenia ovata	1	4	7	4	13	5	7	41	15.5
Myrceugenia planipes	11	1	4	12	1	5	2	36	13.6
Drimys winteri	0	7	4	0	0	0	0	11	4.2
Amomyrtus meli	0	0	0	0	5	0	0	5	1.9
Nothofagus dombeyi	0	3	0	0	0	0	0	3	1.1
Embothrium coccineum	0	1	0	0	0	0	0	1	0.4
Raphithamnus spinosus	0	0	0	0	1	0	0	1	0.4
TOTAL	40	40	40	40	30	34	40	264	100

TABLE 2

Seedling abundance in canopy gaps in a mid-elevation montane forest, Chiloé Island. *L.p.* = *Laureliopsis philippiana*; *A.l.* = *Amomyrtus luma*; *M.o.* = *Myrceugenia ovata*; *M.p.* = *Myrceugenia planipes*; *D.w.* = *Drimys winteri*; *A.m.* = *Amomyrtus meli*; *E.c.* = *Embothrium coccineum*

Abundancia de plántulas en claros en un bosque de media elevación, Isla de Chiloé. *L.p.* = *Laureliopsis philippiana*; *A.l.* = *Amomyrtus luma*; *M.o.* = *Myrceugenia ovata*; *M.p.* = *Myrceugenia planipes*; *D.w.* = *Drimys winteri*; *A.m.* = *Amomyrtus meli*; *E.c.* = *Embothrium coccineum*

| Seedlings | CTR | | | | | | GAP-MAKER | |
	L.p.	*A.l.*	*M.p.*	*D.w.*	*A.m.*	*E.c.*	Total	(%)
L.p.	58	124	5	32	1	1	221	7.8
A.l.	439	680	6	156	4	16	1301	45.9
M.o.	150	353	0	31	7	35	460	16.2
M.p.	148	275	5	27	3	2	576	20.3
D.w.	26	96	0	126	0	8	256	9.0
A.m.	1	6	0	0	14	0	21	0.7
E.c.	0	1	0	0	0	0	1	0.04
Total	822	1535	16	382	29	62	2836	
Gap area (m²)	2522	2735	141	1037	145	670	7250	
Seedling Density (ind. x m⁻²)	0.33	0.56	0.11	0.37	0.20	0.09	0.39	

TABLE 3

Juvenile tree abundance in canopy gaps in a mid-elevation montane forest, Chiloé Island.
Abreviations of species names are the same as indicated in Table 2

Abundancia de árboles juveniles en claros de un bosque montano de media altura, Isla de Chiloé.
Las abreviaciones de los nombres de las especies son las mismas indicadas para la Tabla 2

| Saplings | GAP-MAKER | | | | | | | |
	L.p.	A.l.	M.p.	D.w.	A.m.	E.c.	Total	(%)
L.p.	15	35	0	17	0	11	78	16.1
A.l.	17	34	0	12	5	99	167	34.5
M.o.	18	59	0	5	3	9	94	19.4
M.p.	7	16	0	5	1	26	55	11.4
D.w.	6	56	0	10	0	17	89	18.4
A.m.	0	0	0	0	0	0	0	0.0
E.c.	0	0	0	1	0	0	1	0.2
Total	63	200	0	50	9	162	484	
Gaps area (m²)	2522	2735	141	1037	145	670	7250	
Sapling Density (ind. x m⁻²)	0.02	0.07	0	0.05	0.03	0.24	0.07	

TABLE 4

Transition probabilities estimated from seedling numbers oberved in canopy gaps of a
mid-elevation montane forest, Chiloé Island. The gap-maker is defined as the largest fallen tree
of the gap. Abreviations of species names are the same as indicated in Table 1.$^{(*)}$: an hipothetical
gap generated by M. ovata, with equidistributed transition probabilities

Probabilidades de transición estimadas a partir del número de plántulas observadas en claros de un bosque montano
de media altura, Isla de Chiloé. El árbol generador del claro es definido como el árbol caído de mayor altura dentro del claro.
Las abreviaciones de los nombres de las especies son las mismas que las indicadas en la Tabla 1. $^{(*)}$: un claro hipotético
generado por la caída de un árbol de M. ovata, cuyas probabilidades de transición están equidistribuidas.

| Successor | GAP-MAKER | | | | | | |
	L.p.	A.l.	M.o.*	M.p.	D.w.	A.m.	E.c.
L.p	0.071	0.080	0.142	0.312	0.084	0.034	0.016
A.l.	0.534	0.443	0.142	0.375	0.408	0.138	0.258
M.o.	0.182	0.230	0.143	0.000	0.081	0.241	0.565
M.p.	0.180	0.177	0.142	0.313	0.071	0.103	0.032
D.w.	0.031	0.062	0.142	0.000	0.330	0.000	0.129
A.m.	0.001	0.004	0.142	0.000	0.000	0.483	0.000
E.c.	0.000	0.0006	0.142	0.000	0.000	0.000	0.000

species in the canopy once a steady state (evaluated in terms of specific composition) was reached. The predicted species ranks calculated from seedling- and sapling-based matrices were positively correlated with the present canopy composition (Spearman, one-tailed test, r = 0.75, P < 0.05 for seedlings; Spearman, one-tailed test, r = 0.892, P < 0.05 for saplings; Table 6). In other words, the model predicts that the species which are most important in the forest canopy today, will continue to dominate the future canopy of the forest and will tend to maintain similar ranks.

DISCUSSION

Our results support the hipothesis advanced by Armesto and Figueroa (1987). That is, under the present scenario, primary mid-elevation montane forests of Isla Chiloé

TABLE 5

Transition probabilities estimated from juvenile numbers observed in canopy gaps of mid-elevation montane forest, Chiloé Island. (*): an hypothetical gap of *M. ovata* with equidistributed transition probabilities;(**): as there were no sapling in this gap-type, we used the transition probabilities estimated from seedlings (see Table 4). Abreviations of species names indicated in Table 1

Probabilidades de transición estimadas a partir de individuos juveniles observados en claros de un bosque montano de media altura, Isla de Chiloé. (*): un claro hipotético de *M. ovata*, con probabilidades de transición equidistribuidas; (**): debido a que no se encontraron juveniles en este tipo de claro, usamos las probabilidades de transición estimadas a partir de las plántulas encontradas en los claros (ver Tabla 4). Las abreviaturas de los nombres de las especies son indicadas en la Tabla 1

Successor	GAP-MAKER						
	L.p.	*A.l.*	*M.o.**	*M.p.***	*D.w.*	*A.m.*	*E.c.*
L.p.	0.238	0.175	0.142	0.312	0.340	0.000	0.072
A.l.	0.270	0.170	0.142	0.375	0.240	0.556	0.611
M.o.	0.286	0.295	0.143	0.000	0.100	0.333	0.056
M.p.	0.111	0.080	0.142	0.313	0.100	0.111	0.160
D.w.	0.095	0.280	0.142	0.000	0.200	0.000	0.105
A.m.	0.000	0.000	0.142	0.000	0.000	0.000	0.000
E.c.	0.000	0.000	0.142	0.000	0.020	0.000	0.000

TABLE 6

Observed and expected relative frequency of seven tree species of a mid-elevation montane forest, Chiloé Island. Mode 1: transition probabilities were estimated from seedling observed in gaps. Mode 2: transition probabilities were estimated from juveniles observed in gaps

Frecuencias relativas observadas y esperadas en un bosque montano de media altura, Isla de Chiloé. Modo 1: las probabilidades de transición fueron estimadas a partir de las plántulas observadas en los claros. Modo 2: las probabilidades de transición fueron estimadas a partir de las plantas juveniles observadas en los claros

	Relative frequency (%)			
	Observed		Predicted	
Species	N°	(%)	Mode 1	Mode 2
Laureliopsis philipiana	84	(32.3)	12.8	21.8
Amomyrtus luma	82	(31.6)	37.2	24.9
Myrceugenia ovata	41	(15.8)	16.5	18.9
Myrceugenia planipes	36	(13.8)	18.2	13.7
Drimys winteri	11	(4.2)	8.0	15.1
Amomyrtus meli	5	(1.9)	4.9	2.7
Embothrium coccineum	1	(0.4)	2.4	3.0
Total	260	(100)	100.0	100.0

are in or near a compositional equilibrium: shade-tolerant, late successional tree species are able to reproduce in the forest and subsequently to persist indefinitely in the canopy. Moreover, the positive and significant correlation between the ranking of species as seedling and/or juveniles and as adults, suggests that the knowledge of regeneration processes which occur in the gaps is sufficient to explain the present structure of the canopy and subcanopy.

Veblen (1985b) used transition probabilities, based on gap juveniles trees (> 2 m tall). He was unable to predict the present canopy structure of a lowland forest of Chiloé. He concluded that because of the abundance of medium to large gaps generated by windtrhrows, the pioneers such as *Eucryphia cordifolia* Cav. and *Weinmannia trichosperma* Cav. may regenerate successfully and become abundant (Armesto & Fuentes 1988). Veblen (1985b) inferred that large-scale disturbances, therefore large gaps, must be frequent in the history of lowland forests in Chiloé. Our results, that is the simulations based on transition probabilities estimated from juveniles trees (those comparable with Veblen's results), show exactly the opposite: we predicted the canopy structure of the forest of study (Table 6). The absence of *E. cordifolia* and *W. trichosperma* and the paucity of other light-demanding species *(Drymis winteri, Nothofagus dombeyi)* in the canopy (Table 1) suggest that the formation of large gaps is an unfrequent event in this forest-type. Therefore, the compositional equilibrium (predicted from seedlings and juvenile trees) can be explained by the small-sized gaps, created by the disturbance regime of the area. The

establishment of light-demanding pioneers (*Drymis winteri, Embothrium coccineum, Nothofagus dombeyi* and *Raphithamnus spinosus*; Tabla 1) is limited in the mid-elevation forests, but the establishment, growth and reproduction of shade-tolerant tree species (*Laureliopsis philippiana, Amomyrtus luma, Mirceugenia planipes* and *Myrceugenia ovata*) is favorable (Table 2 and 3). How then could shade-intolerant trees still persist in this forest? These species may be the remnant colonizers of medium to large gaps which are formed at a very low frequency. As prevailing conditions are unfavourable for subsequent germination and establishment of offsprings, we predict that, all things equal, these species will disappear from the forest after the death of adults, by senescence. *Myrceugenia ovata*, the third most important component of the forest, deserves special attention (Table 1). We did not find any gaps formed by gap-makers of this species. This scarcity suggests a high resistence of adults to windthrow or uprooting (Armesto & Fuentes 1988), or the death of trees without fall to the floor, which make gaps very rare or inexistent in the forest. Nevertheless, the regeneration of this species is assured in the forest as seedlings and juveniles are abundant in other gaps (Table 2 and 3).

Natural communities have often been assumed to be in a non-equilibrium condition (Pickett 1980, Sousa 1984), because the occurrence of disturbances alter resources and species composition (Pickett & White 1985). In temperate forests, the compositional equilibrium is posible if large gaps are infrequent, and the time elapsed between one large gap and the next one is larger than the life span of the longest-living shade-tolerant tree. Other studies made in similar forests, and using similar protocols, have arrived at similar conclusions (Barden 1981, Barden 1989, White et al. 1985). More studies are needed in order to determine the extent to which conditions for a compositional equilibrium in temperate forests occur in nature.

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