

## Regeneration patterns of *Cedrela lilloi* (Meliaceae) in northwestern Argentina subtropical montane forests

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**ABSTRACT.** All individuals of *Cedrela lilloi* (a valuable timber species of Meliaceae) > 4 cm DBH were sampled in three rectangular plots (c. 15 000 m<sup>2</sup> each) in northwestern Argentina subtropical montane forests between 850 and 1350 m. Regeneration dynamics of *C. lilloi* was characterized by testing two hypotheses: (i) *C. lilloi* has a gap-phase regeneration mode, which implies a negative exponential size/age distribution at forest stand scale, growth releases due to canopy openings, and juvenile trees clumped at spatial scales of treefall gaps. (ii) There is a negative spatial association between adults and juveniles of *C. lilloi* which could be caused by density dependent mortality. Despite differences in age structure, diameter distribution approximated a negative exponential curve at all sites. Radial growth, measured as tree-ring widths, averaged between 2 and 4 mm y<sup>-1</sup> which is comparable to fast growing tropical species in mature forests. Aggregation of juveniles peaked at radial distances of 8 to 15 m. Size structure, growth and spatial patterns of juveniles support the first hypothesis. In support of the second hypothesis, juveniles showed a negative spatial association with conspecific mature trees at spatial scales of less than 20 m. The Janzen–Connell model of density-dependence is one potential explanation for this pattern. Although regeneration and growth patterns of *C. lilloi* suggest a potential for sustainable management based on small-scale gaps, spatial dynamics at stand-scale need to be considered to ensure the regeneration of mature trees.

**KEY WORDS:** Argentina, *Cedrela lilloi*, dendroecology, Janzen–Connell model, neotropical montane forests, regeneration dynamics, Ripley's *K*-function, tropical forest management, *Yungas*

### INTRODUCTION

Regeneration dynamics of tree species can be characterized by the scale of disturbances and environmental heterogeneity to which the species responds,

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and by the spatial relationship between adults and juveniles. In the absence of large-scale catastrophic disturbances, regeneration dynamics is strongly influenced by endogenous factors (vegetation structure and species interactions), which operate at scales of thousands of square metres or smaller. Factors controlling regeneration dynamics at these scales include treefall gaps, density-dependent mortality of seeds and juveniles due to pathogens, herbivores, and seed predators; short distance dispersal, allelopathy, and local heterogeneity in the physical environment (Augspurger 1984, Forget 1994, Grubb 1986, Veblen 1992, Willson 1993). Species differ in their response to canopy gaps and susceptibility to pathogens, herbivores and predators. These variations in species performance reduce competitive exclusion at a community scale and they have been hypothesized as factors contributing to the maintenance of biodiversity in species-rich forests (Connell 1971, 1978; Denslow 1987, Huston 1994, Janzen 1970).

Treefall gaps, seed dispersal and density-dependent mortality generate spatial patterns at scales that depend on the height and canopy projected area of the adult trees. Treefall gaps are canopy openings produced by the death of one or a few canopy trees. In most neotropical forests, treefall gaps range between 100 and 400 m<sup>2</sup> (Denslow 1987). The main ecological effect of treefall gaps is the increase in resources availability (light and soil nutrients), which promotes seed germination and growth release of suppressed juveniles (Brokaw 1985, Denslow 1987, Veblen 1992). Consequently, juveniles of species that recruit in canopy gaps tend to be spatially aggregated at the scale of a few hundred m<sup>2</sup> (Armesto *et al.* 1986, Itoh *et al.* 1997, Read & Hill 1988, Stewart 1986, Veblen *et al.* 1981). A gap-phase regeneration mode (Veblen 1992) is characterized by recruitment mostly in treefall gaps. Since treefall gaps are disturbances typical of mature forests, species having a gap-phase regeneration mode should have a size distribution reflecting continuous regeneration (i.e. negative exponential) at spatial scales that include several treefalls.

Seed dispersal distance from the source tree (particularly in wind-dispersed species) typically decreases following a negative exponential curve. This implies that seed rain is strongly aggregated within a few metres around mature trees (Willson 1993). Consequently, density-dependent mortality due to pathogens, herbivores and predators is expected to be much higher in the proximity of mature trees (Connell 1971, Janzen 1970). One expected outcome of the increased mortality in adult proximity is a spatial pattern characterized by the lack of juvenile individuals in the vicinity of adults (Clark & Clark 1984, Condit *et al.* 1992, Itoh *et al.* 1997, Okuda *et al.* 1997, Sterner *et al.* 1986).

*Cedrela lilloi* C. DC. (Meliaceae) is a common species in subtropical montane forests of NW Argentina and it is the most valuable timber species in the region (Brown & Grau 1993). Preliminary studies and field observations suggest that, although small seedlings can be found in the understorey of a closed canopy, recruitment of saplings and juveniles depends on disturbances (Grau &

Brown 1998, Grau *et al.* 1997). In a 20-m  $\times$  100-m plot, we observed that seedling density of *C. lilloi* was much lower in the proximity of adults of the same species than under the canopy of other species, suggesting a negative spatial association between adults and juveniles (Grau & Pacheco 1996).

In this study, I describe the population structure, growth, and spatial patterns of *C. lilloi* at spatial scales of more than 1 ha in three sampling plots in the subtropical montane forests of NW Argentina. The objectives of this study were to test the following hypotheses: (i) *Cedrela lilloi* has a gap-phase regeneration mode (*sensu* Veblen 1992), which implies that the population can be in equilibrium at stand scale, as long as gap events within the stand are sufficiently frequent. (ii) Juveniles and mature trees have a negative spatial association at small spatial scales.

#### STUDY SITE AND SPECIES

This study was conducted in the subtropical montane forests of El Rey National Park, Salta Argentina, located at 24°50'S and 64°50'W. The vegetation of the area corresponds to the 'Yungas' biogeographic province, which is the southernmost extension of the tropical Andean montane forests (Cabrera & Willink 1980). Average annual rainfall for the study area is between 1200 and 1500 mm, and mean annual temperature is between 15 and 17 °C. Rainfall is distributed in a monsoonal seasonal regime, with 80% of the precipitation occurring in the late winter, summer and early autumn months (December to April; Brown 1995).

Vegetation of the area is a semi-evergreen forest dominated by Lauraceae, Myrtaceae, Fabaceae, Juglandaceae and Nyctaginaceae. There are between 30 and 40 species of trees > 10 cm DBH per hectare. The canopy is relatively heterogeneous and it is not easy to discriminate canopy openings from closed canopy situations. However, fall of dominant trees clearly increase light availability at understorey and ground levels. In terms of general structural descriptors such as height of canopy trees (30–40 m), density of stems larger than 10 cm of diameter (300–400 ind. ha<sup>-1</sup>) and basal area (30 m<sup>2</sup> ha<sup>-1</sup>), forest structure is very similar to lower latitude neotropical forests (Brown *et al.* 1985). Given these similarities in vegetation structure, size of treefall gaps is expected to be also similar to other tropical forests, although there are no quantitative descriptions of disturbance regime in this study area.

*Cedrela lilloi* C. DC. is a common canopy (30–40 m) tree species of the Argentinean Yungas. It occurs along an elevational range between 400 and 2000 m, and between 18 °S in southern Bolivia and 28 °S in the southern end of Argentine Yungas (Killeen *et al.* 1993, Morales *et al.* 1995, Smith 1960). *Cedrela lilloi* is a deciduous species which drops leaves between June and August (dry winter). The fruit is a dehiscent capsule that reaches maturity at the end of the autumn. Winged seeds disperse during the winter (Brown 1995) and seed

germination occurs during the late spring and early summer (Brown & Grau 1993). *Cedrela* species (tropical cedars) are among the most valuable timber species in the neotropics (Smith 1960) and *Cedrela lilloi* is the most important timber species of NW Argentina humid forests (Brown & Grau 1993).

Little is known about the regeneration dynamics of this species. Although seedlings can be found frequently in the understory, their growth is very slow under closed canopy (5–10 mm  $y^{-1}$  in height). However, seedlings and saplings grow between 30 and 60 cm  $y^{-1}$  in height under conditions of higher solar radiation (Grau & Pacheco 1996). Field observations and secondary succession chronosequences suggest that this species is dependent on canopy disturbances for reaching maturity (Brown & Grau 1993, Grau & Brown 1998, Grau *et al.* 1997).

As with all the species of the genus, larvae of *Hypsipyla grandella* Zeller ('shoot borer', Lepidoptera) frequently attack terminal buds (Brown & Grau 1993). Infestation is more intense under conditions of high density of young individuals. Although the attack of *H. grandella* usually does not cause immediate mortality, it is likely to weaken young individuals and to limit recruitment of saplings and juveniles. Observations on *Cedrela odorata*, a closely related species, suggest that *H. grandella* attacks may increase mortality of seedlings (Griypma & Gara 1970).

*Cedrela lilloi* produces reliable annual tree rings, making it a useful species for dendrochronological and dendroecological studies (Villalba *et al.* 1985). Whereas climate has an important effect on *C. lilloi* radial growth at relatively high elevation (above 1600 m), in the lower montane forests (where this study was conducted) dendrochronological reconstructions show that the relationships between growth and climate are weak, and growth is probably more controlled by local factors such as competition with other trees (Villalba *et al.* 1987).

## METHODS

### *Sampling*

Between March and June 1997, I sampled all trees > 4 cm of diameter at breast height (DBH) in three rectangular plots in El Rey National Park. Site 1 (120-m  $\times$  140-m) was located in the 'Aguas Negras' trail, between 850–900 m of elevation in a forest dominated by *Ocotea puberula* (L.C. Rich) Nees, (Lauraceae), *Tipuana tipu* (Benht) O. Kuntze (Fabaceae) and *Parapiptadenia excelsa* (Griseb.) Burkhart (Fabaceae). Site 2 (120-m  $\times$  120-m) was located in the 'Poza Verde' trail between 1000 and 1050 m elevation in a forest dominated by *Cinnamomum porphyria* (Griseb.) Kosterm (Lauraceae), *Pisonia ambigua* Heimerl (Nyctaginaceae) and *Juglans australis* Griseb. (Juglandaceae). Site 3 (140-m  $\times$  150-m) was located in the 'Poza Verde' trail, between 1300 and 1350 m in a forest dominated by *J. australis*, *Blepharocalyx salicifolius* (H.B.K.) Berg. (Myrtaceae), and *Myrcianthes pungens* (Berg.) Legrand (Myrtaceae). El Rey National Park was created in 1948. Therefore, the forests studied had no

anthropogenic disturbances for at least 50 y and no evidence of logging activities was found in the study sites. Sites were selected to have relatively high densities of *C. lilloi* and relatively low slope inclination ( $< 20\%$ ), in order to facilitate the spatial mapping. Trees were mapped based on measurements of coordinates within 20-m  $\times$  20-m quadrats. The DBH of each tree was measured, and each tree was cored with an increment borer at the base, aiming to encounter the pith below 10 cm of height from the ground. *Cedrela lilloi* seedlings usually reach between 10 and 20 cm of height during the first growing season (Grau & Pacheco 1996). Therefore, samples taken at 10 cm were not corrected for time to reach sampling height. Individual trees were mapped in an (x, y) coordinate system to the closest m. In addition to all *C. lilloi* trees, I also mapped all large trees ( $> 50$  cm DBH) of other species.

Increment-borer cores were processed according to standard dendrochronological procedures (Stokes & Smiley 1968). Ring visibility was enhanced by treating the samples with phloroglucinol. This procedure consists of soaking the samples in a 1% solution of phloroglucinol in 95% ethyl alcohol for 1 min, then placing the samples for 1 min in 50% hydrochloric acid, and finally washing the samples with water. The combination of phloroglucinol and hydrochloric acid stains the lignin red and increases visibility of annual rings, particularly in the softer wood of young trees.

Establishment dates were assigned to the calendar year in which the growing season begins (i.e. establishment dates assigned to year x include both individuals which germinated during spring of year x and during summer of year x+1). Pith was encountered in 57% of the samples. When pith was not encountered (28% of cases), establishment dates were determined following geometrical procedures based on the curvature and width of the innermost rings (Duncan 1989). Trees with rotten cores (15% of the cases) were not used for the analysis of age. Ring widths were measured using a computer-compatible tree-ring measuring system (Velmex Inc. Bloomfield N.Y. USA), with a precision of 0.01 mm.

#### *Data analysis*

To describe the population structure and the potential for reaching future canopy abundance, age and DBH frequency distributions are presented as histograms of 5-y and 5-cm classes respectively. Whereas age structure better reflects the history of recruitment, size structure may be a better predictor of the future composition of the forest (Enright 1982, Veblen 1992). A negative exponential decline in number of individuals with increasing size (or age) can be interpreted as evidence of a pattern of continuous recruitment and probable persistence of the species population (Rollet 1979, Veblen 1992).

To describe growth patterns and growth variability, I present the frequency distributions of average individual tree radial growth, and mean and standard errors of individual growth for each site. Most assessments of radial growth of neotropical trees use simulated curves based on permanent-plot measurements

of trees of different diameters larger than 10 cm (Lieberman *et al.* 1985). When data on smaller individuals are available, it is possible to describe growth trajectories than can be expressed as time to reach a determined diameter (Condit *et al.* 1993). For comparative purposes, average rates of tree growth from the year they become > 10 cm in diameter (according to measures of tree rings), and average time to reach both 10 and 30 cm of diameter in individuals larger than these sizes are presented. Growth releases can be interpreted as evidence of response to canopy disturbances (Lorimer 1985). To explore the response of *C. lilloi* to canopy openings, the average number of growth releases per tree and the percentage of trees showing releases at each plot are presented. Growth releases were arbitrarily defined as a sustained threefold increase in radial growth for at least 5 y when compared to the previous 5 y.

Spatial distribution patterns were analysed by means of the Ripley's  $K$ -functions (Diggle 1983, Haase 1995, Ripley 1976). The  $K(t)$  function describes the spatial patterns of one category of points (clumped, random, or regular), whereas the  $K_{(12)}$  function describes the spatial relationship between two categories of points (co-occurrence, random or repulsion). The high and low confidence intervals at a 0.05 probability level were determined by running 19 Monte Carlo randomizations of  $K$ -functions (Besag & Diggle 1977) computed at 1-m intervals for 't' distances from 1 to 60 m (half the length of the shortest side of the smallest plots). All the analyses were performed using the toroidal edge correction (Haase 1995) in the program SPATIAL (Duncan 1990, 1991). For better visualization, results are presented as the linearized  $L$ -functions (Diggle 1983, Haase 1995).

To describe spatial patterns of juveniles, the  $K(t)$  function of *C. lilloi* individuals between 4 and 12.5 cm of DBH (juveniles) was analysed. This size range included more than 50% of the sampled individuals in all plots. Gaps produced by the fall of large canopy trees have areas of 200 to 400 m<sup>2</sup> (Brokaw 1985, Denslow 1987), which (assuming a circular shape) corresponds to diameters between 8 and 25 m. If spatial pattern of juveniles is controlled by treefall gaps, aggregation should occur at the corresponding radial distances 't' < 12 m. Spatial patterns of juveniles, age and size structure, and growth patterns together were used to determine whether *C. lilloi* is a species with a gap-phase regeneration mode (hypothesis 1).

To assess hypothesis 2 of negative spatial association (repulsion) between mature trees and juveniles of *C. lilloi*, I used the  $K_{(12)}$  function of juveniles and large trees (> 50 cm DBH). This size was chosen to represent the minimum size of mature canopy trees which are large enough to produce substantial treefall-originated canopy openings. Negative spatial association can be expected also due to intraspecific competition. For example if juveniles are light-demanding, they may be less abundant near large trees independently of species, and a negative association between mature trees and juveniles of *C.*

*lilloi* would be a spurious correlation instead of indication of species-specific pattern. However, if the negative association is due to a species-specific factor, advanced regeneration of *C. lilloi* should not be negatively associated with canopy trees of other species. The spatial relationship of juveniles of *C. lilloi* and mature trees of other species was used as a control to test whether the repulsion of juveniles and mature trees was species-specific. I computed the  $K_{(12)}$  function between *C. lilloi* juveniles and other-species trees > 50 cm DBH.

## RESULTS

### *Age and size structure*

A total of 89, 106 and 64 individuals of *C. lilloi* were sampled at sites 1, 2 and 3 respectively, ranging from 4 to 139 cm of DBH and from 6 to 143 y of estimated age. The three sites showed different age structure patterns (Figure 1). Sites 1 and 3 had peaks between 20 and 30 y of age, corresponding to establishment peaks in the 1960s and 1970s. Site 1 also had a high number of trees > 55 y of age. Site 2 had a distribution with regularly decreasing number of individuals, in which 70% of the individuals were < 20-y-old. Despite the differences in age structure, size structure showed similar patterns in the three sites: individuals decrease as DBH class increases. At site 2, 84% of the individuals were < 12.5 cm DBH. In sites 1 and 3, 51–56% of the individuals were < 12.5 cm DBH.

### *Growth*

Individual radial tree growth averaged between 2.1 and 3.8 mm  $y^{-1}$  at the different sites, with individuals averaging > 5 mm  $y^{-1}$  at all sites (Table 1). Average individual radial tree growth ranged from less than 0.5 mm  $y^{-1}$  to more than 7 mm  $y^{-1}$ . Growth was consistently lower at site 3 than at the other two sites (Figure 2, Table 1). Radial growth in trees > 10 cm of diameter was faster than the average growth considering all sizes. Average time to reach 10 and 30 cm of diameter was 21 and 68 y respectively, which corresponds to average annual radial increments of 2.4 and 2.2 mm  $y^{-1}$  respectively. At sites 1 and 3, more than half of the trees showed growth releases, whereas at site 2, only 36% did. Average number of releases per tree was more than 0.5 at all sites (Table 1).

### *Spatial patterns*

At the three sites, juveniles were clumped at almost all analysed scales. The only exception was site 2, which showed no significant aggregation at more than 50 m of  $t$  (radius). In the three sites, the  $K(t)$  function showed a first peak of aggregation at the scale of tree-fall gaps (< 15 m). Sites 1 and 2 showed a first peak of aggregation *c.* 10 m and a second one at *c.* 40 and 30 m respectively. At site 3 there was only one peak of aggregation between 12 and 17 m (Figure 3).

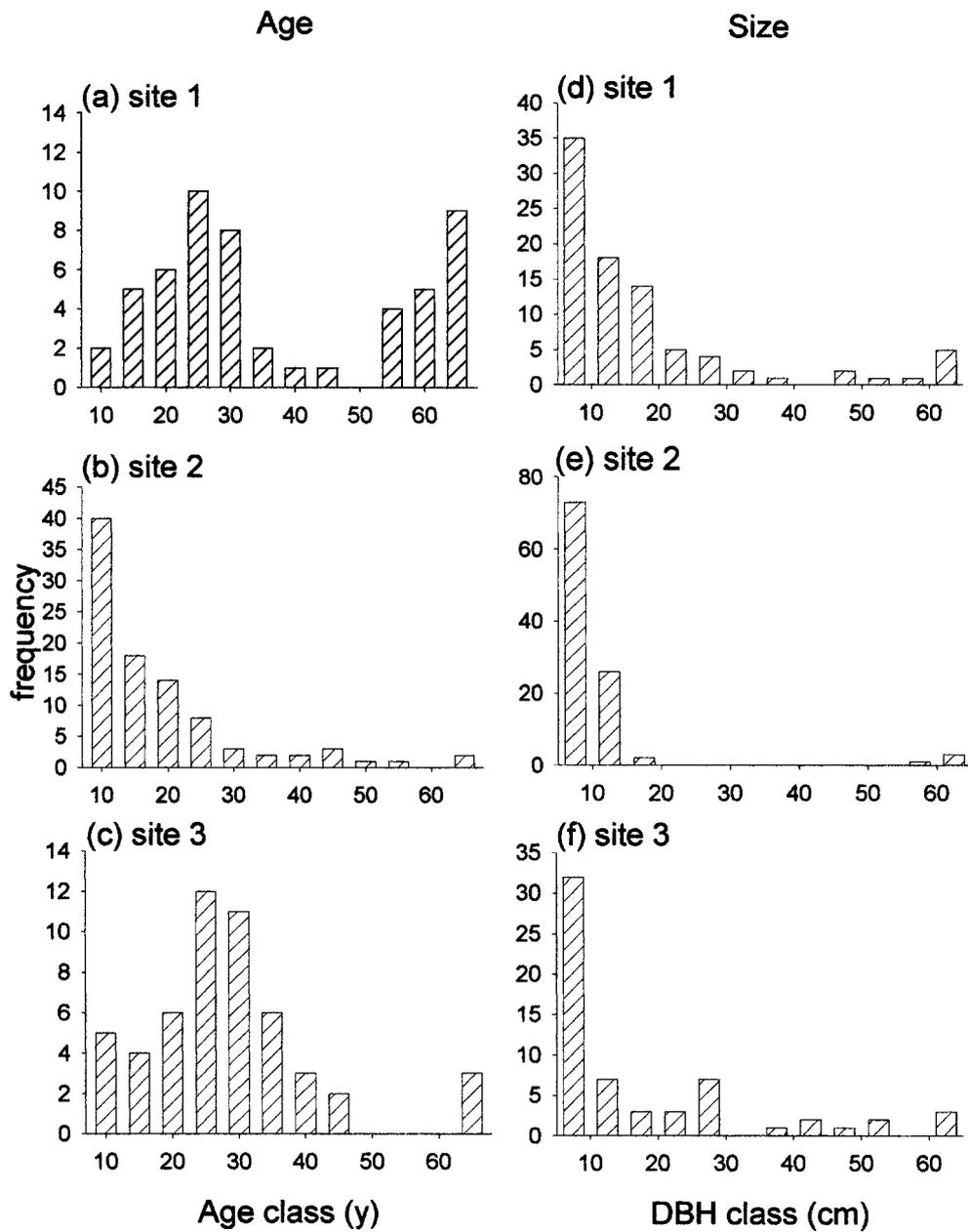


Figure 1. Age (left) and DBH (right) frequency distributions of *Cedrela lilloi* in the three study sites in NW Argentina. The oldest/largest classes of both age and diameter includes all individuals equal to or larger than this class.

Table 1. Mean ( $\pm$  SE) of parameters of radial growth of *Cedrela lilloi* in the three study sites in NW Argentina.

	Site			Average of the three sites
	1	2	3	
Radial growth (mm $y^{-1}$ )				
All trees (> 4 cm DBH)	3.8 $\pm$ 0.20	3.6 $\pm$ 0.17	2.1 $\pm$ 0.17	3.2
Trees > 10 cm DBH	4.3 $\pm$ 0.36	4.9 $\pm$ 0.34	2.7 $\pm$ 0.36	4.0
Age to reach 10 cm (y)	18 $\pm$ 1.0	17 $\pm$ 2.1	28 $\pm$ 3.0	21
Age to reach 30 cm (y)	73	46	84	68
Mean number of releases per tree	0.71	0.54	0.89	0.71
% of trees showing releases	52	36	56	48

The  $K_{(12)}$  function between juveniles and large trees of *C. lilloi* showed a consistent pattern at the three sites (Figure 4). In all cases there was a negative association (repulsion) at small spatial scales and positive association (aggregation) at larger spatial scales. At site 1, the negative departure of the  $K_{(12)}$  was significant between 0 and 31 m with a peak at 9 m. After 40 m, the derived spatial function became positive. At site 2, a non-significant negative departure peaked at 7 and 12 m, and the positive spatial association reached statistical significance at 53 m. At site 3, a significant negative association peaked at 11 m, and a positive association peaked at 52 m. In all three cases, the peaks in negative association between large trees and juveniles roughly coincided in scale with the peaks in aggregation of the juveniles (Figures 3, 4). All three sites showed spatial independence (no significant association) of juveniles of *C. lilloi* and large trees of other species.

#### DISCUSSION

##### *Size, age and growth*

Size and age distributions showed different patterns (Figure 1). Two of the three sites showed peaks of recruitment in the age classes between 20 and 35 y. Peaks in establishment may be attributed to climatic conditions controlling seed or seedling ecophysiology, fluctuations in seed production, seed predation, herbivory, or increased canopy disturbances during this period. Differences in establishment dates, however, did not produce large differences in size structure and, consequently, in the probable future composition of the forest (Enright 1982, Veblen 1992). In the three cases the size distribution, characterized by a regularly decreasing number of individuals that approximate a negative exponential decline at increasing DBH classes, implies a continuous pattern of future recruitment. There is a large number of small trees that can potentially replace mature trees, and maintain *C. lilloi* as a relatively abundant canopy species. Since these plots were not randomly selected, this size distribution should not be necessarily interpreted as representative of *C. lilloi* stands. However, these results support previous observations that *C. lilloi* is able to regenerate in mature forest stands without large scale disturbances (Grau & Brown 1998, Grau & Pacheco 1996).

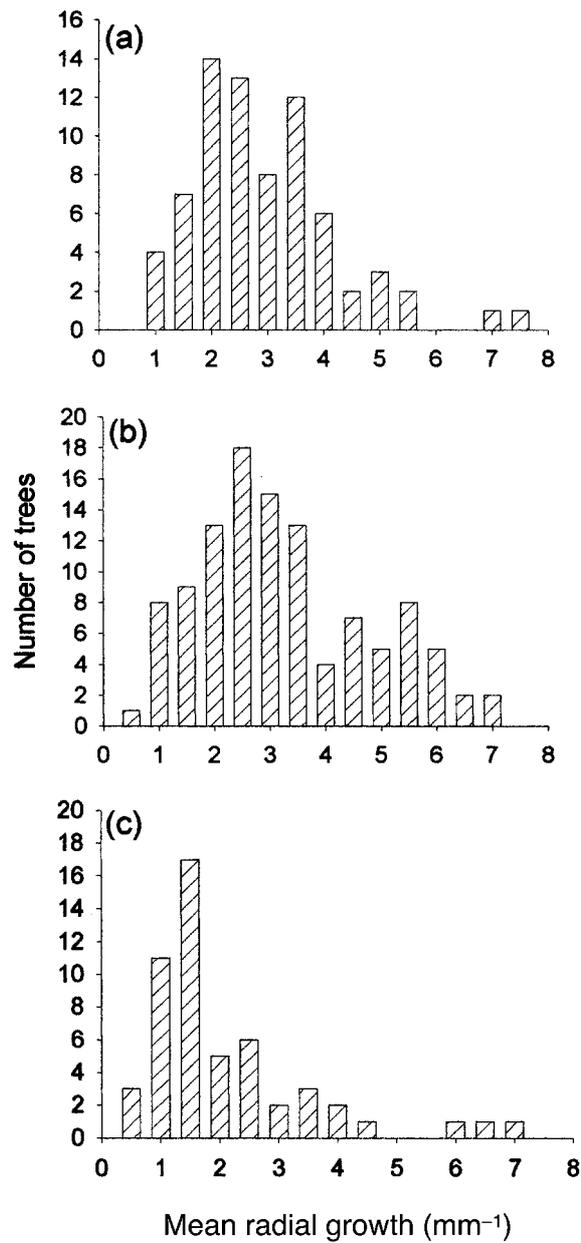


Figure 2. Frequency distributions of mean individual radial growth rates of *Cedrela lilloi* at (a) site 1, (b) site 2 and (c) site 3 in NW Argentina.

According to the observed radial growth patterns (Table 1, Figure 2) *C. lilloi* can be characterized as a fast growing species. Comparison of growth rates with those observed in other studies is limited by differences in methods and sample characteristics (e.g. differences in age/size structure can influence the estimates of growth). However, even the conservative estimates in this study

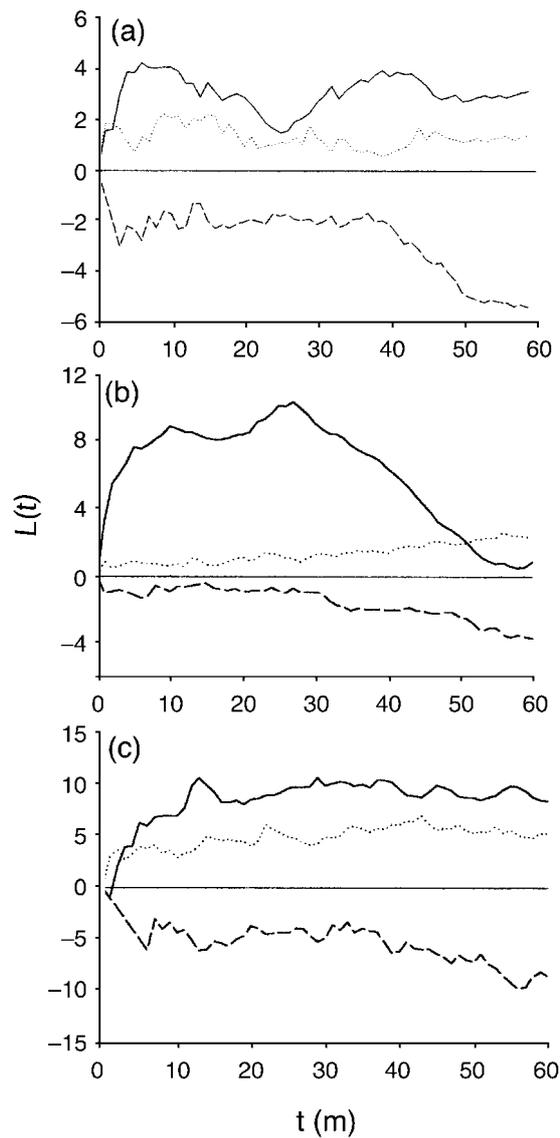


Figure 3. Sample statistic  $L(t)$  for *Cedrela lilloi* juveniles (solid line) at (a) site 1, (b) site 2 and (c) site 3 in NW Argentina. Dotted and dashed lines are positive and negative limits to the 95% confidence intervals for spatial randomness.

show high values of *C. lilloi* growth when compared to growth rates of other neotropical tree species. For example, the average time for *C. lilloi* to reach 10 and 30 cm of diameter was less than the threshold used to define the top 15% fastest growing trees and shrubs among 160 species in Panama (Condit *et al.* 1993). Average and median growth rates of individuals of *C. lilloi* greater than 10 cm of diameter at site 3 (which showed the lowest growth rates, Figure 2, Table 1) are greater than threshold values that define the top 10–25% fastest

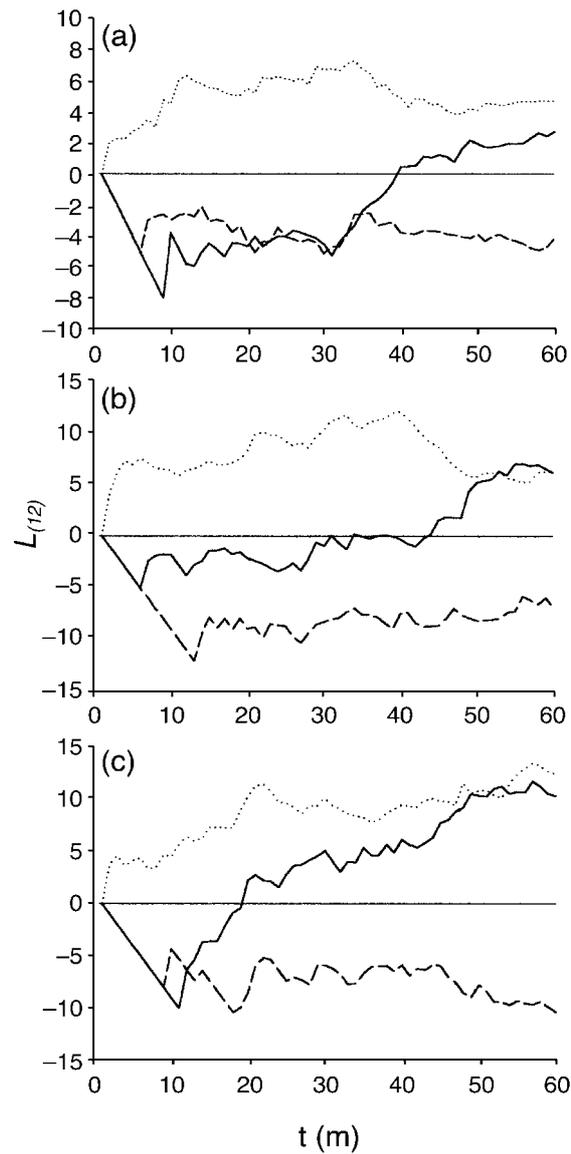


Figure 4. Sample statistic  $L_{(12)}$  for *Cedrela lilloi* juveniles and large trees (solid line) at (a) site 1, (b) site 2 and (c) site 3 in NW Argentina. Dotted and dashed lines are positive and negative limits to the 95% confidence intervals for spatial randomness.

growing canopy trees in three compared studies (Felfili 1995, Korning & Balslev 1994, Lieberman *et al.* 1985). In the mentioned studies, many of the species that show growth rates greater than *C. lilloi* are typical pioneer genera with reduced timber value and reduced regeneration in the absence of large-scale disturbances (e.g. *Ochroma*, *Cecropia*, *Jacaranda*, *Trema*, *Solanum*; Whitmore 1990).

At sites 1 and 3, more than half of the trees showed growth releases, suggesting that canopy openings are important controls of growth of *C. lilloi* (Table 1). Consistently, growth rates of trees > 10 cm of diameter were higher than average, which can be attributed to smaller proportion of suppressed individuals as trees become larger. The percentage of individuals with growth releases was lower at site 2, characterized by a larger number of trees in the young/small classes (Figure 1). It is possible that many of the individuals in site 2 were not old enough to have experienced changes in canopy cover.

#### *Spatial patterns*

Juveniles were significantly clumped at different spatial scales (Figure 3). Peaks of clumping at less than 15 m of radial distance  $t$ , suggest that spatial distribution of juveniles is influenced by treefall gaps, as has been observed in other studies of gap-phase regeneration-mode species (Armesto *et al.* 1986, Itoh *et al.* 1997, Read & Hill 1988, Stewart 1986, Veblen *et al.* 1981). Together with the data on growth and population structure, spatial patterns of juveniles support hypothesis 1 that *C. lilloi* can be considered a species with a gap-phase regeneration mode.

The  $K_{(12)}$  function between mature and juveniles of *C. lilloi* showed a consistent pattern in the three sites (Figure 4). There was a positive association at spatial scales > 50 m and a negative association at scales < 15 m of radius. In each case these associations were statistically significant at two of the three sites. The positive association at large spatial scales may be associated with both dispersal distances and microenvironmental preferences (soil, topography) of the species (e.g. Forget 1994, Hubbell & Foster 1990, Itoh *et al.* 1997, Okuda *et al.* 1997, Sterner *et al.* 1986).

The lack of spatial relationship between juveniles of *C. lilloi* and mature trees of other species suggests that the negative spatial association between juveniles and mature *C. lilloi* trees is not a consequence of canopy cover, but of some species-specific factor. One potential explanation for this pattern is density-dependent mortality due to herbivores, pathogens and seed predators (Clark & Clark 1984, Condit *et al.* 1992, Connell 1971, Janzen 1970). *Cedrela* seedlings are severely attacked by larvae of *Hypsipyla grandella* in conditions of high density (Brown & Grau 1993, Griypma & Gara 1970). Although the attack of *H. grandella* generally does not kill the individuals in the short term, it may produce weakening, favour mortality, and decrease recruitment in larger size classes. Seeds of *C. lilloi* are also commonly attacked by larvae and adults of Coleoptera species. These factors, as well as other potential causes of negative spatial associations (e.g. pathogens, allelopathic compounds), require further study.

#### *Conclusions*

Size structure suggests that *C. lilloi* regenerates in the absence of large-scale disturbances. Growth patterns suggest that this species can be characterized

as fast growing in comparison to other neotropical tree species. Both recruitment into large size classes and fast growth seem to be dependent on fine-scale canopy openings, and therefore, the species can be characterized as having a gap-phase regeneration mode (*sensu* Veblen 1992). Results suggest that *C. lilloi* has the potential to overcome two major limitations for sustainable management of tropical tree species: lack of regeneration and reduced growth rates (Hartshorn 1995, Whitmore 1990). Gap-based approaches (Attiwill 1994, Coates & Burton 1997, Hartshorn 1995) provide a conceptual basis for sustainable management of this species.

Advanced regeneration of *C. lilloi* tends to have a negative spatial association with mature trees of the same species, giving support to the Janzen–Connell model (Connell 1971, Janzen 1970) of small-scale spatial patterns. This pattern implies that selective logging of mature *C. lilloi* trees is likely to produce canopy openings that will not improve growth of *C. lilloi* juveniles because of their low density in these locations. Consequently, sustainable management of this species needs to consider the mechanisms causing the negative spatial association between mature and juvenile individuals. This study suggests that treefall gaps and density-dependent mortality may generate spatial patterns at similar spatial scales (Augsburger 1984, Veblen 1992). Consequently, the interactions between these two factors need to be better understood in order to explain and to manage tree regeneration and diversity.

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#### LITERATURE CITED

- ARMESTO, J. J., MITCHELL, J. D. & VILLAGRAN, C. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18:1–11.
- ATTIWILL, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management* 63:247–300.
- AUGSPURGER, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps and pathogens. *Ecology* 65:1705–1712.

- BESAG, J. & DIGGLE, P. 1977. Simple Monte Carlo tests for spatial patterns. *Applied Statistics* 26:327–333.
- BROKAW, N. L. V. 1985. Treefalls, regrowth, and community structure in tropical forests. Pp. 53–69 in Pickett, S. T. A. & White, P. S. (eds). *The ecology of natural disturbances and patch dynamics*. Academic Press, Orlando, Florida.
- BROWN, A. D. 1995. Fenología y caída de hojarasca en las selvas montañas del Parque Nacional El Rey, Argentina. Pp. 93–102 in Brown, A. D. & Grau, H. R. (eds). *Investigación, conservación y desarrollo en selvas subtropicales de montaña*. Universidad Nacional de Tucumán, Tucumán, Argentina.
- BROWN, A. D., CHALUKIAN, S. E. & MALMIERCA, L. 1985. Estudio florístico-estructural de la selva semidecídica del Noroeste Argentino. I. Composición florística, densidad y diversidad. *Darwiniana* 26:27–41.
- BROWN, A. D. & GRAU, H. R. 1993. *La naturaleza y el hombre en las selvas de montaña*. Colección Nuestros Ecosistemas, Proyecto de Desarrollo Forestal en Comunidades Campesinas. Salta, Argentina. 121 pp.
- CABRERA, A. L. & WILLINK, A. 1980. *Biogeografía de América latina*. Organization of American States. Washington DC. 132 pp.
- CLARK, D. A. & CLARK, D. B. 1984. Spacing dynamics of a tropical rainforest tree: evaluation of the Janzen–Connell model. *American Naturalist* 124:769–788.
- COATES, K. D. & BURTON, P. J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management* 99:337–334.
- CONDIT, R., HUBBELL, S. & FOSTER, R. B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a Neotropical forest. *American Naturalist* 140:261–286.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1993. Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecology and Management* 62:123–143.
- CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and rainforest trees. Pp. 298–312 in den Boer, J. (ed.). *Dynamics of populations*. Center of Agriculture Publishing and Documentation, Wageningen, The Netherlands.
- CONNELL, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310.
- DENSLOW, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431–451.
- DIGGLE, P. J. 1983. *Statistical analysis of spatial point patterns*. Academic Press, London.
- DUNCAN, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrydium dacrydioides*). *New Zealand Natural Sciences* 16:31–37.
- DUNCAN, R. P. 1990. SPATIAL analysis program. Department of Plant Science, Lincoln University, New Zealand.
- DUNCAN, R. P. 1991. Competition and coexistence of species in a mixed podocarp stand. *Journal of Ecology* 79:1073–1084.
- ENRIGHT, N. J. 1982. Recognition of successional pathways in forest communities using size-class ordination. *Vegetatio* 48:133–140.
- FELFILI, J. M. 1995. Growth, recruitment and mortality in the Gama gallery forest in central Brazil over a six-year period (1985–1991). *Journal of Tropical Ecology* 11:67–83.
- FORGET, P. M. 1994. Recruitment pattern of *Vouacapoua americana* (Caesalpinaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26:408–419.
- GRAU, H. R., ARTURI, M. F., BROWN, A. D. & ACENOLAZA, P. G. 1997. Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests. *Forest Ecology and Management* 95:161–171.
- GRAU, H. R. & BROWN, A. D. 1998. Structure, composition, and inferred dynamics of a subtropical montane forest of northwestern Argentina. Pp. 715–726 in Dallmeier, F. & Camiskey, J. (eds). *Forest biodiversity in North, Central and South America, and the Caribbean. Research and monitoring*. Parthenon Publishers and UNESCO, Chichester, UK.
- GRAU, H. R. & PACHECO, S. E. 1996. Demografía y crecimiento de renovales de *Cedrela lilloi* durante dos años en un bosque subtropical de montaña de Tucumán, Argentina. *Iyryareta* 7:11–15.
- GRIYMA, P. & GARA, R. 1970. Studies in the shoot borer *Hypsipyla grandella* Zeller. 1. Host selection and behavior. *Turrialba* 20:233–240.
- GRUBB, P. J. 1986. Problems posed by sparse and patchily distributed species in species rich plant communities. Pp. 207–225 in Diamond, J. & Case, T. J. (eds). *Community ecology*. Harper & Row, New York, USA.
- HAASE, P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods for edge correction. *Journal of Vegetation Science* 6:757–582.
- HARTSHORN, G. S. 1995. Ecological basis for sustainable development in tropical forests. *Annual Review of Ecology and Systematics* 26:155–175.
- HUBBELL, S. P. & FOSTER, R. B. 1990. Structure, dynamics and equilibrium status of old-growth forest on Barro Colorado Island. Pp. 522–541 in Gentry, A. (ed.). *Four neotropical rainforests*. Yale University Press, New Haven, CT, USA.

- HUSTON, M. 1994. *Biological diversity. The coexistence of species in changing landscapes*. Cambridge University Press, Cambridge, UK. 430 pp.
- ITOH, A., YAMAKURA, T., OGINO, K., LEE, H. S. & ASHTON, P. S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest of Sarawak, Malaysia. *Plant Ecology* 132:121–136.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–527.
- KILLEN, T., GARCIA, E. & BECK, S. G. (eds) 1993. *Guía de árboles de Bolivia*. Herbario Nacional de Bolivia and Missouri Botanical Garden, St Louis, MO, USA. 958 pp.
- KORNING, J. & BALSLEV, H. 1994. Growth rates and mortality patterns of tropical lowland tree species and the relation to forest structure in Amazonian Ecuador. *Journal of Tropical Ecology* 10:151–166.
- LIEBERMAN, D., LIEBERMAN, M., HARTSHORN, G. & PERALTA, R. 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology* 1:97–109.
- LORIMER, C. G. 1985. Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* 15:200–213.
- MORALES, J. M., SIROMBRA, M. & BROWN, A. D. 1995. Riqueza de árboles en las Yungas Argentinas. Pp. 163–174 in Brown, A. D. & Grau, H. R. (eds). *Investigación, conservación y desarrollo en selvas subtropicales de montaña*. Universidad Nacional de Tucumán, Tucumán, Argentina.
- OKUDA, T., KACHI, N., YAP, S. K. & MANOKARAN, N. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rainforest—implications for regeneration and maintenance of species diversity. *Plant Ecology* 131:155–171.
- READ, J. & HILL, R. S. 1988. The dynamics of some rainforest associations in Tasmania. *Journal of Ecology* 76:558–584.
- RIPLEY, B. D. 1976. The second order analysis of stationary point processes. *Journal of Applied Probability* 13:255–266.
- ROLLET, B. 1979. Application des diverses methodes d'analyse de donnees a des inventaires forestieres detaillés leves en foret tropicale. *Oecologia Plantarum* 14:319–344.
- SMITH, C. E. 1960. A revision of *Cedrela* (Meliaceae). *Fieldiana* 29:295–341.
- STERNER, R. W., RIBIC, C. A. & SCHATZ, G. E. 1986. Testing for life-history historical changes in spatial patterns of four tropical tree species. *Journal of Ecology* 74:621–633.
- STEWART, G. 1986. Population dynamics of a montane conifer forest, western Cascada range. *Ecology* 67:534–544.
- STOKES, M. A. & SMILEY, T. L. 1968. *An introduction to tree ring dating*. University of Chicago Press, Chicago.
- VEBLEN, T. T. 1992. Regeneration dynamics. Pp. 152–187 in Glenn-Lewin, D. C., Peet, R. K. & Veblen, T. T. (eds). *Plant succession: theory and prediction*. Chapman & Hall, London.
- VEBLEN, T. T., DONOSO, A. C., SCHLEGEL, F. M. & ESCOBAR, R. B. 1981. Forest dynamics in south-central Chile. *Journal of Biogeography* 8:211–247.
- VILLALBA, R., BONINSEGNA, J. A. & HOLMES, R. L. 1985. *Cedrela angustifolia* and *Juglans australis*: two new tropical species useful for dendrochronology. *Tree-Ring Bulletin* 45:25–35.
- VILLALBA, R., BONINSEGNA, J. A. & RIPALTA, A. 1987. Climate, site conditions and tree growth in subtropical north-western Argentina. *Canadian Journal of Forest Research* 17:1527–1544.
- WHITMORE, T. C. 1990. *An introduction to tropical rain forest*. Clarendon Press, Oxford.
- WILLSON, M. F. 1993. Dispersal mode, seed shadows and colonization patterns. *Vegetatio* 107/108:261–280.