

## Capítulo 7

### Respuestas plásticas a la competencia en poblaciones de *Trema micrantha* [(L.) Blume, Ulmaceae] durante la sucesión temprana

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Velázquez, E., Gómez-Sal, A. *In preparation*. Plastic responses to competition in early successional populations of *Trema micrantha* [(L.) Blume, Ulmaceae]. *Journal of Integrative Plant Biology*.

#### Resumen

En este estudio se examinó el proceso de autoaclareo, así como el desarrollo de doseles estratificados y respuestas plásticas a la competencia a lo largo de dos años, en poblaciones de *Trema micrantha* [(L.) Blume, Ulmaceae] situadas en un deslizamiento de gran tamaño y con una gran heterogeneidad abiótica (Volcán Casita, Nicaragua). También se definieron las relaciones existentes entre el volumen y la densidad de los tallos, las estructuras de tamaño, y las relaciones alométricas entre la altura y el diámetro de los individuos existentes en las poblaciones presentes en las distintas zonas del deslizamiento. En las áreas más fértiles y geomorfológicamente estables, aunque la relación entre el volumen y la densidad de los tallos fue diferente a la de otras zonas del deslizamiento, esta no indicó la presencia de procesos de autoaclareo. Sí se observó el desarrollo de "jerarquías de tamaños" y se detectaron evidencias de competición asimétrica por la luz, así como de respuestas plásticas a la misma, en los individuos del sotobosque. En las áreas menos fértiles y estables, sin embargo, los individuos mostraron tallos más pequeños y tanto el volumen como la densidad de los mismos aumentaron simultáneamente respecto al tiempo. Los individuos de menor altura murieron debido a la dureza del ambiente físico y los de mayor altura crecieron lentamente, localizando la mayor parte de su producción fotosintética al crecimiento lateral más que al vertical. En el deslizamiento del Volcán Casita, los individuos de *T. micrantha* asignaron recursos al crecimiento y la supervivencia de forma diferente dependiendo de las características del área en la que estuvieran presentes. La posición en el deslizamiento también influyó la naturaleza de las interacciones entre los mismos.



---

## Plastic responses to competition in early successional populations of *Trema micrantha* [(L.) Blume, Ulmaceae].

Eduardo Velázquez\*<sup>1</sup>, Antonio Gómez-Sal\*

\*Departamento de Ecología, Facultad de Ciencias, Universidad de Alcalá, Autovía Madrid-Barcelona km. 33,600, s/n, 28871 Alcalá de Henares, Madrid, Spain. <sup>1</sup>E-mail: eduardo.velazquez@uah.es

### Abstract

This study examined the self-thinning processes, development of canopy-hierarchies, and plastic responses to competition over two years in populations of *Trema micrantha* [(L.) Blume, Ulmaceae] on a large, abiotically heterogeneous landslide (Casita Volcano, Nicaragua). The study also defined the relationships between stem volume and density, size-structures, and the allometric relationships between plant height and diameter within zones of the landslide. In the most fertile and stable areas of the landslide, although the stem volume/density relationship differed from that in other areas of the landslide, they did not point towards a self-thinning process. However, size-hierarchies and one-sided competition for light were apparent, and, among the stems of the understory, "plastic responses" were evident. In the less fertile and stable areas, however, stems were smaller, and both stem volume and density increased simultaneously over time. The shorter stems died because of the harshness of the environment, and the taller stems grew slowly, and allocated most of their photosynthetic production to lateral, rather than vertical, growth. In the landslide on the Casita Volcano, individuals of *T. micrantha* allocated resources to growth and survival differently depending on the area in which they were. Position on the landslide also influenced the nature of the interactions among them.

*Key words:* self-thinning, size-structure, allometric relationships.

### Introduction

Self-thinning or density-dependent mortality processes (Antonovics and Levin 1980) often occur in high-density populations as plants grow and their resource demands increase. As in other sessile organisms, the interactions between plants are essentially local (Harper 1977) and competitive stress is greatest between neighbours, whose growth rates decrease. Those effects can lead to a strong reduction in population growth rate such that subsequent increases in biomass will be subject to mortality of an equivalent amount of biomass coming from some individuals. The first formal analysis of that phenomenon was developed

for crowded, even-aged, monospecific crops using the "Self-thinning Rule" or "- 3/2 Power Law" (Yoda *et al.* 1963).

Initially, Self-thinning Rule Hypothesis received support but, more recently, has been criticized (Miyaniishi *et al.* 1979, Westoby 1984, Weller 1987, Zeide 1987). The hypothesis does not consider that size often varies among individuals within a population, even if they are the same age (Weiner and Thomas 1986). Indeed, the size of a plant relative to its neighbours can be more important than age in determining its fate (Westoby 1984). In populations in which size or canopy hierarchies develop, competition for light occurs often (Nagashima and

Terashima 1995) and usually is one-sided (Hara 1986) because light comes directionally from above such that tall plants can shade shorter plants, but ones not vice versa (Kikuzawa and Umeki 1996). Thus, taller individuals have an advantage over shorter individuals, which suppresses the growth of the latter (Cannell *et al.* 1984, Weiner 1990, Kikuzawa 1999). Canopy hierarchies and one-sided competition might be indicated if the frequency distribution of heights change from L-shaped (large positive values of skewness and kurtosis) to bimodal (large negative values of kurtosis) (Nagashima and Terashima 1995).

On the other hand, the early "geometrical" explanations of the Self-thinning Rule, which were based on the fact that a plant fills a volume and covers an area (Yoda *et al.* 1963, White and Harper 1970), were replaced by explanations based on allometric theory in which the availability of resources in the ecosystem and the rate of resource consumption by plants are the key factors (White 1981, Osawa and Allen 1993, Enquist *et al.* 1998). In recent interpretations, intraspecific competition in plant communities is determined by biomass optimization processes that operate at the level of the individual plant and follow a few allometric and biomechanical rules. Those rules dictate how metabolic production is partitioned among stems, leaves, and reproductive organs when space or other resources are limited (Enquist and Niklas 2001).

The implication is that, in some cases, density-dependent mortality or the suppression of shorter individuals by taller individuals through competition for light might be limited or not exist at all. The capacity of plants to manage competitive stress is higher than expected. Indeed, most plants have evolved sensory

mechanisms for detecting decreasing levels of available light (Smith 2000) and can allocate most of its photosynthetic gain into growing taller rather than into increasing diameter or forming new branches, leaves, or flowers (Ballaré 1999, Yang and Midmore 2005). Such changes in plant growth strategies or "plastic responses" to shade can retard the development of size hierarchies in the population and, thereby, impeding the suppression of shorter individuals by their taller neighbours (Schmitt and Wulff 1993, Gilbert *et al.* 2001, Stoll *et al.* 2002).

In this study, we examined the self-thinning processes and plastic responses to competition over two years in populations of *Trema micrantha* [(L.) Blume, Ulmaceae] on a large, abiotically heterogeneous landslide in Nicaragua that was surveyed in the first four years after disturbance. The genus *Trema* is widely distributed in the tropical areas of the world (Stevens *et al.* 2001) and is known for its shade-intolerant character, fast growth, and ability to colonize extremely hostile substrates (Swaine and Hall 1983, Dalling and Iremonger 1994, Li *et al.* 1999, Carrière *et al.* 2002). In the Neotropics, *T. micrantha* is very common in landslides (Garwood 1985, Guariguata 1990) and other disturbed areas (Vázquez-Yanes 1998, Vázquez-Yanes *et al.* 1999, de Souza and Batista 2004, Alvarez-Aquino *et al.* 2005). In our study area, *T. micrantha* was abundant in every year of the study, present in all of the zones of the landslide, and particularly dominant in the most fertile and geomorphologically stable areas. In these areas, *T. micrantha* had high stem densities but, throughout the 4-yr period, its biomass decreased, and mortality of some of the individuals occurred in the last two years of the study (2001-2002). In addition, adult individuals of this species were more

segregated than were dead standing individuals (personal observation).

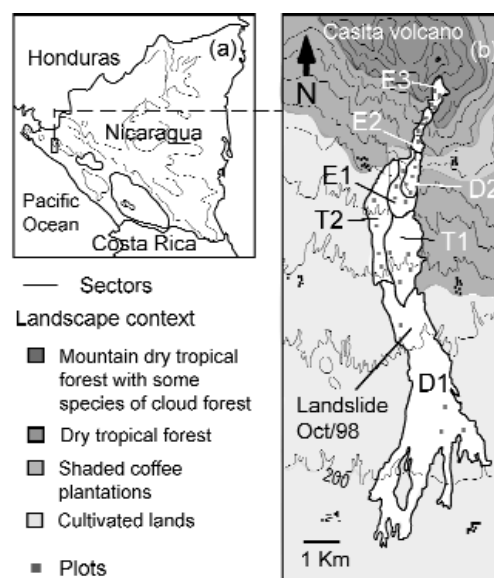
Collectively, the evidence suggested that intraspecific competition occurred in the *T. micrantha* populations that were in the most fertile and stable zones of the landslide, but not in other zones. The main objective of this study was to find evidence to support the last hypothesis. The specific questions addressed were: i) Did the death of some individuals lead to a simultaneous increase in biomass? If the answer was yes, was that increase rather important to consider a self-thinning process?, ii) Were the shortest individuals in the populations disproportionately affected by mortality? If the answer is yes, did it suggest the occurrence of one-sided, asymmetric competition for light?, and iii) Did the shortest individuals exhibit "plastic responses" to competition stress?

## Methods

### Study area

The study area was a landslide on the Casita Volcano (12,41 N; 85,57 W), which is part of the "Maribios" volcanic range in western Nicaragua (**Fig. 1a**). The landslide, which was triggered by an exceptional rainfall event (500 mm in 24 h) on 30 October 1998, during Hurricane Mitch (Sheridan 1998), formed an enormous lahar at mid-slope (Kerle 2002, Scott *et al.* 2005). With an altitude range of 150-1350 m a.s.l., and an area of 11.21 km<sup>2</sup>, the landslide on Casita Volcano is much larger than others studied in Central America and Caribbean region. In addition, the ecological and socioeconomic characteristics of the surrounding region are rather different (Velazquez and Gómez-Sal *in press*). Casita

Volcano is covered mostly by dry tropical forests that have been partially converted into "shaded" coffee plantations at mid-slope, and that, farther down, are interspersed with small-holding lands (Salas-Estrada 1999). At the base of the volcano, cultivated lands dominate the landscape. Local ecosystems have experienced substantial exploitation and reduction, and human disturbances, such as the clearcutting of forests and fire, are common in the area (Corrales-Rodríguez 1983).



**Figure 1.** Study area. a) Location in Nicaragua. b) Detailed map of the landslide indicating the different sectors based on abiotic heterogeneity (fertility and geomorphologic stability) and the landscape context; erosional (E1, E2, E3), transitional (T1 and T2), and depositional (D1 and D2). The locations of sampling plots are indicated.

In 1999, two criteria were used to define seven major sectors (D1, D2, T1, T2, E1, E2, and E3) in the landslide. (**Fig. 1b**). Based on their abiotic heterogeneity (fertility and geomorphological stability of substrates), the sectors were defined as i) stable depositional zones in which

formerly agricultural or forest soil remained after the landslide (D), ii) unstable erosional zones that had steep slopes in which soil was removed by the landslide (E), and iii) moderately stable "transitional" zones between the erosional and depositional zones, where the former soil remained in small patches, only (T). Within the context of landscape, we distinguished among sectors that i) had cultivated lands along the edges (D1), ii) were enclosed by mountain tropical dry forests that had some of the plant species that are typical of cloud forests (E3), iii) had tropical dry forests along their edges (T1 and E2), iv) had shaded coffee plantations along their eastern border (E1 and D2), or v) had cultivated lands that dominated beyond their western border (T2).

To document vegetation recovery in each sector of the landslide, we collected data in four consecutive years (1999, 2000, 2001, and 2002) following the disturbance. In a previous study, the sectors were characterized based on abiotic factors associated with the stability and fertility of substrates, and human disturbances, which occurred between 2001 and 2002 (Velazquez and Gómez-Sal *submitted*). Although all of the sectors were included in the study described here, the D2 sector was the primary focus. D2 was within the most fertile and geomorphologically stable area, and had the shallowest slope and highest nutrient content of all of the sectors in the Casita Volcano landslide (**Table 1**). In that sector, biomass accumulation decreased, mortality of some individuals occurred between 2001 and 2002, and adult *T. micrantha* were more segregated than were dead standing individuals, which suggests that intraspecific competition occurred in D2, but not in the other sectors (personal observation). Furthermore, that suggests the presence of a balance between negative

and positive (or neutral) interactions between individuals of *Trema*, which are influenced by the degree of physical stress in the substrates (Brooker and Callaghan 1998).

The presence and abundance of *T. micrantha*, and several characteristics of the structure of the communities of the landslide are summarized in **Table 2**. In D2, the *T. micrantha* populations were neither monospecific nor even-aged (an assumption required of the Self-thinning Rule, Yoda *et al.* 1963); rather, they exhibited features that rendered them prone to negative interactions. The D2 plots had a closed overstory canopy (mean total canopy cover > 50%) and, in the last two years of the study, *T. micrantha* was present in all of the plots, highly abundant, and contributed the most to the biomass of the sector (importance values > 50% in all years of study). Over the study, the number of standing and lying stems increased considerably, and stem density was high. Age differences were relatively small compared to the wide range of sizes among individuals (high standard deviations of mean stem height in 2001 and 2002).

#### **Fieldwork sampling**

In 2000, in each of the seven sectors, a long-term permanent 10\*10 m plot was established randomly and, in 2001, an additional three plots were added. Thus, in 2001 and 2002, the study included 28 plots. In each of three years (2000, 2001, and 2002), at the end of the rainy season (October to December), all of the *T. micrantha* stems in each plot were tagged. Stem diameter (to the nearest 0.05 cm) at 20 cm above ground (D) was measured using callipers. Stem height (HT) was measured using a clinometer (Mueller-Dombois and Elleberg 1974). During the study, human dis-

**Table 1.** Characterization of the different areas (sectors) in the landslide according to abiotic factors and presence of disturbances. Mean is at the top of the cells and Standard Deviation, in italics, is below. Asterisks show the statistical significance for each variable in the Kruskal-Wallis test.  $H > \chi^2$  with  $P < 0.001$  (\*\*) and  $P < 0.05$  (\*). Values within columns followed by the same superscript letters are not significantly different at  $P < 0.05$  in the Mann-Whitney U test.

Sector	Lc.	Stability variables				Productivity variables							Dist.
		Altitude** (m.a.s.l.)	Slope** (%)	Sc.** (%)	Mds.* (cm)	NO <sub>3</sub> ** (ppm)	K** (ppm)	P** (ppm)	Sand* (%)	Silt* (%)	Clay** (%)		
D1	CL	262.5 <sup>a</sup>	6 <sup>a</sup>	5 <sup>a</sup>	4.75 <sup>a</sup>	15.20 <sup>a</sup>	129.91 <sup>ab</sup>	55.9 <sup>a</sup>	72.34 <sup>a</sup>	9.35 <sup>a</sup>	20.52 <sup>a</sup>	Clear.	
		<i>43.37</i>	<i>2.16</i>	<i>2.04</i>	<i>3.57</i>	<i>1.86</i>	<i>13.98</i>	<i>5.09</i>	<i>1.76</i>	<i>1.09</i>	<i>2.80</i>		
D2	DTF,	649.5 <sup>b</sup>	5.75 <sup>a</sup>	38.50 <sup>b</sup>	11.18 <sup>ba</sup>	28.50 <sup>d</sup>	139.37 <sup>a</sup>	72.57 <sup>b</sup>	61.73 <sup>b</sup>	7.70 <sup>b</sup>	30.52 <sup>b</sup>	-	
		<i>43.43</i>	<i>1.07</i>	<i>15.80</i>	<i>4.24</i>	<i>8.93</i>	<i>13.32</i>	<i>6.21</i>	<i>5.32</i>	<i>2.7</i>	<i>3.78</i>		
T1	DTF	403.75 <sup>c</sup>	8.5 <sup>ba</sup>	33.75 <sup>b</sup>	10.23 <sup>a</sup>	10.12 <sup>ab</sup>	125.75 <sup>b</sup>	72.52 <sup>b</sup>	71.36 <sup>a</sup>	7.75 <sup>b</sup>	19.56 <sup>a</sup>	Clear. Burn.	
		<i>19.65</i>	<i>2.64</i>	<i>24.70</i>	<i>7.29</i>	<i>4.01</i>	<i>11.01</i>	<i>7.01</i>	<i>4.25</i>	<i>1.22</i>	<i>3.72</i>		
T2	CL	459.50 <sup>c</sup>	14.25 <sup>b</sup>	21.87 <sup>b</sup>	29.21 <sup>c</sup>	6.9 <sup>bc</sup>	93.52 <sup>bc</sup>	60.07 <sup>a</sup>	78.48 <sup>a</sup>	4.73 <sup>c</sup>	13.74 <sup>c</sup>	Burn.	
		<i>46.82</i>	<i>2.21</i>	<i>8.00</i>	<i>8.92</i>	<i>2.33</i>	<i>8.73</i>	<i>5.34</i>	<i>3.89</i>	<i>1.56</i>	<i>1.90</i>		
E1	DTF,	562.50 <sup>bc</sup>	26.50 <sup>c</sup>	88.75 <sup>c</sup>	27.33 <sup>c</sup>	4.7 <sup>c</sup>	66.37 <sup>d</sup>	5.15 <sup>c</sup>	64.60 <sup>b</sup>	9.53 <sup>a</sup>	26.68 <sup>b</sup>	-	
		<i>12.28</i>	<i>5.32</i>	<i>6.29</i>	<i>4.35</i>	<i>1.34</i>	<i>12.59</i>	<i>1.15</i>	<i>8.27</i>	<i>1.73</i>	<i>6.97</i>		
E2	DTF	849.5 <sup>d</sup>	59 <sup>d</sup>	91.87 <sup>c</sup>	17.14 <sup>b</sup>	5.42 <sup>c</sup>	87.40 <sup>c</sup>	37.42 <sup>c</sup>	76.57 <sup>a</sup>	7.06 <sup>b</sup>	15.62 <sup>c</sup>	-	
		<i>58.35</i>	<i>6.73</i>	<i>5.54</i>	<i>6.88</i>	<i>1.14</i>	<i>8.21</i>	<i>5.57</i>	<i>5.73</i>	<i>2.26</i>	<i>3.10</i>		
E3	DTF	1086.25 <sup>d</sup>	40.75 <sup>d</sup>	97.50 <sup>c</sup>	48.47 <sup>d</sup>	-	-	-	-	-	-	-	
		<i>- CF</i>	<i>59.15</i>	<i>17.07</i>	<i>2.04</i>	<i>25.10</i>							

Abbreviations; Lc. = Landscape context, Sc = Stone cover, Mds = Medium diameter of stones, Dist. = Presence of disturbances, Clear. = Clearcutting, Burn. = Burning, CL = Cultivated lands, DTF = Dry tropical forest, DTF - CF = Mountain dry tropical forest with some species of the cloud forest, SC = Shaded coffee plantations.

**Table 2.** Relevant structural characteristics of communities and *Trema micrantha* populations in the sectors of the landslide on Casita Volcano, Nicaragua, in 2001 and 2002. The third column refers to all of the plant species and all of the other columns refer to *Trema micrantha* populations.

Sector	Year	Mean Total canopy cover (%)	Np.	lv. <sup>1</sup>	Number of stems	Number of dead stems	Mean Stem density (n° / m <sup>2</sup> )	Mean Stem diameter (cm)	Mean Stem height (m) ± SDs <sup>2</sup>
D1	2001	70.32	3	34.74	27	-	0.77	10.66	7.41 ± 2.85
	2002	69.2	1	8.55	2	-	0.5	6.4	4.55 ± 0.77
D2	2000	68.7	1	72.91	45	-	0.9	2.82	1.38 ± 0.41
	2001	136.15	4	66.77	184	1	0.52	3.21	2.84 ± 1.22
T1	2002	108.72	4	55.52	171	13	1.89	3.39	3.36 ± 1.19
	2000	20	1	40.12	5	-	1.85	0.94	0.51 ± 0.38
T2	2001	63.47	4	37.95	29	-	0.33	4.39	3.36 ± 2.16
	2002	31.75	2	20.55	5	<sup>-3</sup>	0.25	1.71	1.25 ± 0.73
E1	2000	10.8	1	16.39	1	-	0.66	1.3	0.6 ± -
	2001	51.55	3	39.59	20	-	0.48	4.05	2.39 ± 1.58
E2	2002	37.1	3	13.75	8	<sup>-3</sup>	0.20	5.04	3.08 ± 1.86
	2000	10.1	1	82.91	25	-	12.5	0.99	0.54 ± 0.30
E3	2001	18.7	3	45.27	36	16	1.38	1.94	0.94 ± 0.41
	2002	41.27	4	31.66	29	7	0.58	2.54	1.34 ± 0.56
E3	2001	24.86	3	29.33	24	-	1.03	2.11	0.91 ± 0.36
	2002	43	3	24.43	20	3	0.69	2.8	1.07 ± 0.42
E3	2001	16.9	1	3.85	2	-	2.5	0.8	0.49 ± 0.05
	2002	40.9	1	1.66	1	1	1	1.1	0.86 ± -

Notes: <sup>1</sup> Importance value of *Trema micrantha* / Importance value of the other woody species. Importance value = relative density + relative cover / 2 (Kent and Cooker 1992). <sup>2</sup> Standard deviations. <sup>3</sup> There were no dead standing or lying stems in these sectors, but these sectors showed some burnt *Trema* individuals in 2002: 16 and 9 in the case of T1 and T2 respectively.

turbances occurred in the depositional and transitional sectors. In 2002, three plots were cleared. In addition, two other plots were cleared in both 2001 and 2002. In the dry season of 2002, peasants in the area lit fires that spread to the landslide and burned extensively seven of the plots in the transitional sectors.

### **Data Analysis**

In 2000, *T. micrantha* stems were absent from the majority of the plots; therefore, the analysis was based on the data from 2001 and 2002, only. It was impossible to use destructive methods for calculating biomass or weight of plants; therefore, rather than calculate relationships between biomass and density, we used total stem volume (sum of stem heights \* sum of stem diameters) and density in each plot of D2. For information on the suitability and usefulness of studying relationships using volume and density, see Lonsdale (1990), and Osawa and Allen (1993). A small number of plots could be included in the analysis; therefore, rather than fitting "thinning lines" using regression algorithms (Zeide 1987), self-thinning was identified using simultaneous decreases in density and increases in volume.

To determine whether mortality was more important to the shortest stems than to the others, and whether one-sided competition occurred, changes in the frequency distributions of height and diameter in D2 were compared to changes in the other sectors. Frequency histograms, skewness, and kurtosis of frequency distributions of height and diameter were analyzed in *T. micrantha* populations. To determine the equal-interval frequency histograms (Ford 1975) in all of the sectors, *Trema* stems were assigned to one of three groups based on height ("short",

"medium," and "tall" stems) and diameter ("thin", "medium thickness," and "thick" stems) using a K-means clustering method (Bishop 1995). That analysis was used to obtain three major-width intervals associated with each of the groups with the greatest possible distinction among them. Short and thin stems are important in assessing one-sided competition; therefore, several minor-width intervals were considered within them. To categorize frequency distributions, we used previously defined boundaries based on major- and minor-width intervals.

To detect plastic responses to competition for light, we examined the changes in allometric relationships between height and diameter of the short stems that appeared in 2001 and survived to 2002 (either as short or medium-height stems). Changes in the allometric relationships of medium-height stems that survived throughout the study period were also examined. To fit regression lines to the relationships between height and diameter, we used the RMA (Reduced Major Axis) algorithm (LaBarbera 1989) because its less sensitive to assumptions about the error structure of the data and it generates less biased estimates of the underlying functional relationships (Osawa and Allen 1993, Nikklas 1994).

When it was appropriate, variables were log-transformed to achieve normality and to eliminate the effects of differences in dimensions. All of the analyses were performed using STATISTICA software (Statsoft 2001).

### **Results**

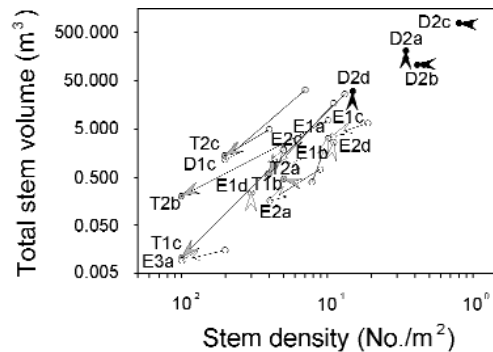
The stem density and total stem volume of *T. micrantha* populations were highest in the plots of the D2 sector (**Fig. 2**). In D2a and D2d,



density remained constant and total stem volume increased, whereas, in D2b, the opposite was true. In D2c, density decreased, but total stem volume increased slightly. In D1c, and in the most of the plots located in the transitional sectors and some of those that were in the erosional sectors, total stem volume and density decreased. In most of the plots located in the erosional sectors, density and total stem volume of *T. micrantha* increased slightly.

Within the *T. micrantha* individuals, K-means clustering that maximized the initial between-cluster distances generated three height-based groups: 0.0-2.56 m (short), 2.57-6.1 m (medium), and 6.3-14.0 m (tall stems), and three diameter-based groups: 0.0-3.2 cm (thin), 3.3-7.0 cm (medium diameter) and 7.6-15.7 cm (thick stems). Short- and thin-stemmed groups were particularly abundant. The boundaries for generating equal-interval frequency distributions were obtained using five minor-width intervals for the short stems (0.0-0.5 m, 0.5-1.0 m, 1.0-1.5 m, 1.5-2.0 m, 2.0-2.5 m), and one interval each for the medium height stems (2.5-6.1 m) and the tall stems (6.1-14 m). For stem diameter, four minor-width intervals were used for the thin stems (0.0-1.0 cm, 1.0-2.0 cm, 2.0-3.0 cm, 3.0-3.2 cm), and one each for the medium diameter (3.2-7.6 cm) and the thick stems (7.6-24.0 cm).

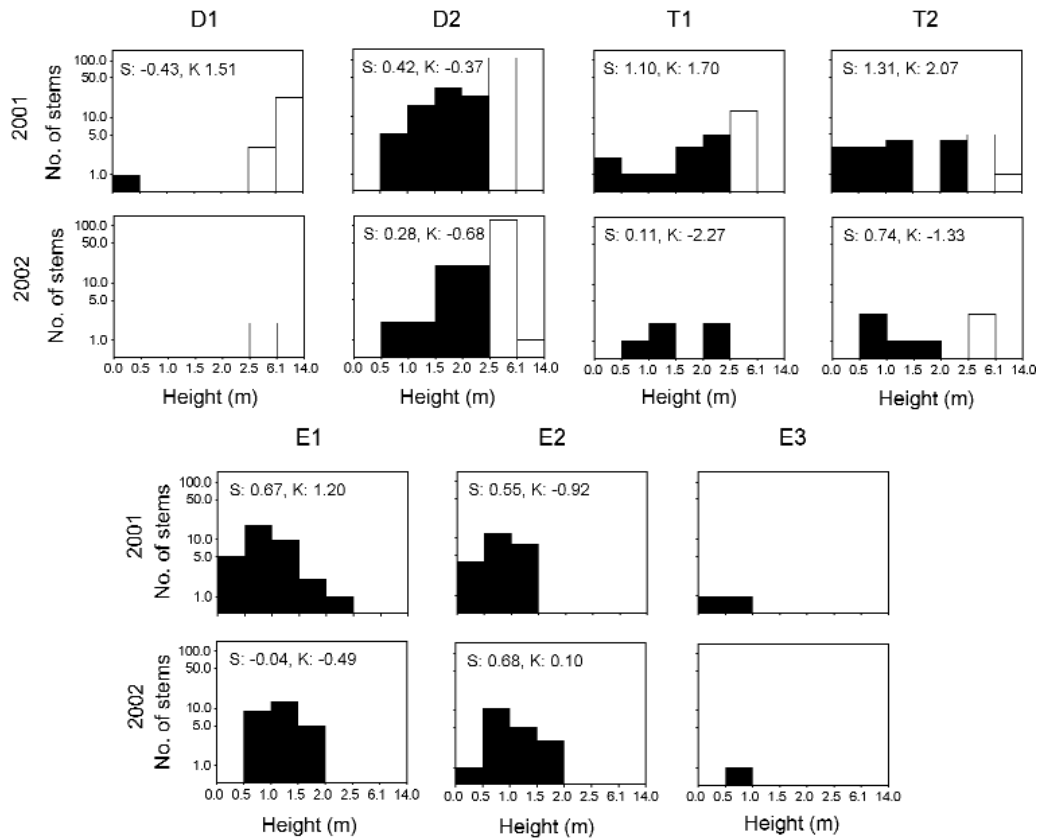
In D2, over the two years, the frequency of short stems decreased significantly, particularly within the four shortest intervals (0-0.5, 0.5-1, 1-1.5 and 1.5-2 m), the frequency of medium-height stems increased, and large stems appeared (Fig. 3). In the erosional sectors, only short-stemmed individuals of *Trema* were present. Within that group, the frequencies of the shortest intervals (0-0.5 and 0.5-1 m in E1, 0-0.5, 0.5-1 and 1-1.5 m in E2, and 0-



**Figure 2.** Log density and log total stem volume of *Trema micrantha* populations in the plots in which the species was present in 2001 and 2002 in the landslide on Casita Volcano, Nicaragua. Dots indicate values of density and stem volume in the plots, and arrows indicate the direction of changes in the 2-yr period. These arrows are labelled with the names of the sector and letters a, b, c, d). Black, grey, and white colours in dots and arrows indicate depositional, transitional, and erosional sectors, respectively.

0.5 m in E3) decreased, whereas those of the tallest-stemmed individuals (1-1.5, 1.5-2 m in E1, 1.5-2 m in E2, and 0.5-1m in E3) increased. In the transitional sectors and in D1, the frequencies of all of the groups decreased significantly, and tall-stemmed individuals were present no longer. The distributions were strongly positively skewed, although skewness decreased in most of the sectors and, in E1, became negatively skewed. In all of the sectors, with the exception of E2, the degree of kurtosis evolved toward strongly negative.

Temporal changes in the frequency distributions of stem diameter were similar among the different sectors of the landslide (Fig. 4). In D2, the frequency of thin-stemmed individuals decreased and that of medium-stemmed individuals increased between 2001 and 2002. In the erosional sectors, the frequencies of individuals in the lowest intervals in the thin group decreased and the frequencies in highest

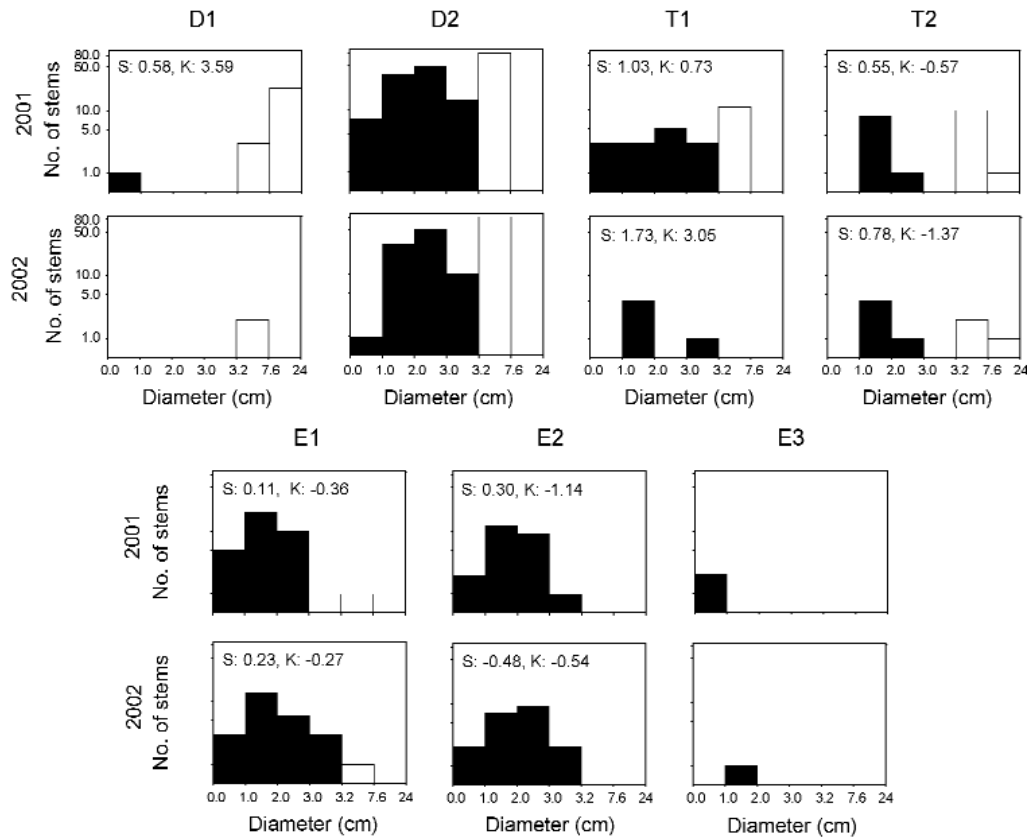


**Figure 3.** Changes in equal-interval frequency histograms, skewness, and kurtosis of the frequency distributions of height in the sectors of the landslide on Casita Volcano, Nicaragua. Black bars represent the five minor-width intervals defined for short stems (0-0.5 m, 0.5-1 m, 1-1.5 m, 1.5-2 m, 2-2.5 m) and white bars represent the intervals defined for the medium-height (2.5-6.1 m), and tall (6.1-14 m) stems. The values of Skewness (S) and Kurtosis (K) of the frequency distributions are indicated in the upper-left corner of each box.

intervals increased. The frequencies of medium-diameter stems remained unchanged. In the transitional sectors, the frequencies of all of the intervals decreased.

Regression lines of allometric relationships were not fitted to the data from the D1 and E3 sectors because of the small number of short-stemmed plants present in 2001 that survived to 2002. In D2, E1 and E2, the regression models indicated significant positive correlations between stem diameter and height in

2001 and 2002 (**Fig. 5**), however, diameter contributed much more to the variation in height in E1 and E2, than it did in D2 (**Table 3**). The slope of regression increased in D2 and decreased in E1 and E2 (**Table 3, Fig. 5**). In E1, E2 and particularly in D2, the number of short-stemmed plants decreased (**Table 3**). With regard to the medium-height stems, only the D2 sector contained enough stems to justify an analysis. In this sector, the slope of the regression line between height and diameter for the medium-height stems increased, but



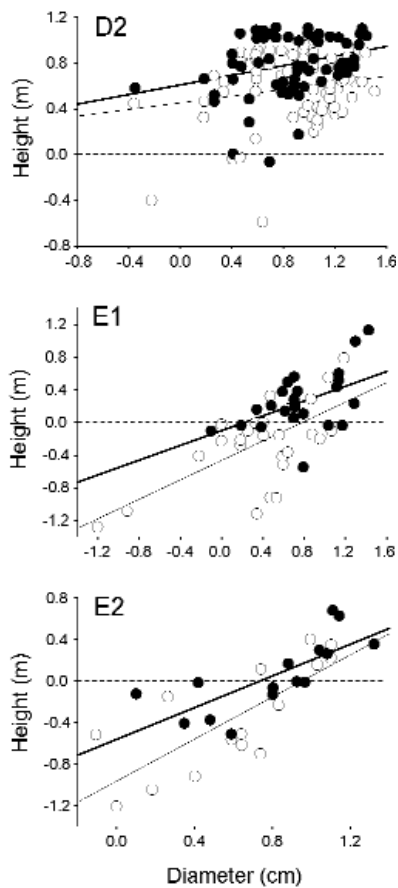
**Figure 4.** Equal-interval frequency histograms, skewness, and kurtosis of the frequency distributions of diameter in the sectors of the landslide on Casita Volcano, Nicaragua. Black bars represent the four minor-width intervals defined for thin stems (0-1 cm, 1-2 cm, 2-3 cm, 3-3.2 cm), and white bar represent the intervals defined for medium-diameter (3.2-7.6 cm) and thick stems (7.6-24 cm). The values of Skewness (S) and Kurtosis (K) of the frequency distributions are presented in the upper-left corner of each box.

less than it did in the short-stemmed group ( $\beta_1 = 0.4466$  in 2001 and  $\beta_1 = 0.4488$  in 2002). The number of medium-height stems increased from 104 in 2001 to 125 in 2002.

## Discussion

In the D2 plots of the landslide on Casita Volcano, Nicaragua, in which total stem volume and stem density of *T. micrantha* did not change in the same manner, populations of this species have become crowded. In D2c,

however, the decrease in density coincident with an increase in stem volume does not necessarily demonstrate self-thinning. According to Lonsdale (1990), to ensure that a population converges on the thinning line, density must decrease by more than a half an order of magnitude ( $\log [N_{\max} / N_{\min}] < 0.5$ ) and, in our study, density decreased less than an order of magnitude and stem volume increased slightly. Likewise, the slope of the line between the position of D2c in 2001 and in 2002 (Fig. 2) was much less steep than expected.



**Figure 5.** Allometric relationships between the height and diameter of *Trema micrantha* stems in the D2, E1 and E2 sectors in the landslide on Casita Volcano, Nicaragua, in 2001 and 2002. White and black dots indicate the height and diameter of stems in 2001 and 2002 respectively. Thin and thick lines denote the fitted regression lines for 2001 and 2002, respectively.

ted for the slope of the thinning line:  $-3/2$  (Yoda *et al.* 1963),  $-0.8 = -b = -0.3$  (White 1980), or  $-4/3$  (Enquist *et al.* 1998). Thus, in D2c, the short-stemmed individuals that perished between 2001 and 2002 probably died because of competition, but there was no strong evidence to confirm that self-thinning occurred.

In D2, the decrease in the frequencies of short-stemmed individuals and the increase in frequency of medium-height stems suggest one-sided competition for light. In D2 in 2001, *T. micrantha* populations exhibited an L-shaped distribution in which short-stemmed individuals were dominant over medium-height individuals, which created two distinct canopy- or size-hierarchies (understory and overstory). In addition, stem density was very high and, frequently, the crowns of medium-height stems overlapped. Consequently, the canopy was rather closed and prevented light from reaching the understory. In D2, between 2001 and 2002, short-stemmed *T. micrantha* experienced high mortality and in 2002, the frequency distributions of populations of this species were markedly bimodal. Collectively, those results imply the development of one-sided competition for light (Nagashima and Terashima 1995, Kikuzawa and Umeki 1996).

However, not all of the short-stemmed *T. micrantha* individuals in D2 died. The increase in the frequency of medium-height stems between 2001 and 2002 indicated that most short-stemmed individuals grew rapidly. Furthermore, the higher increase in height relative to diameter in short-stemmed individuals supports that interpretation, and suggests the existence of "plastic responses" to shade, as individuals modified their morphology to avoid being out-competed for light by their taller neighbours (Maliakal *et al.* 1999). In addition, individuals in the understory had fewer branches than did individuals in the overstory (personal observation), which suggests that, like other tropical light-demanding species (Popma and Bongers 1988), *T. micrantha* exhibits a complex growth response to low light levels, which allows it survive in the understory of forests .

**Table 3.** Allometric relationships between height and diameter (both log-transformed) of small stems of *Trema micrantha*, in the sectors of the landslide on Casita Volcano, Nicaragua. Regressions were not performed on the data from the D1 and E3 sectors because of the absence or scarcity of short stems.

Sector	Year	N <sup>1</sup>	Ns <sup>2</sup>	Statistic	P	r <sup>2</sup>	Slope
D2	2001	80	72	F <sub>1,70</sub> = 2.70	0.01	0.04	0.14
	2002	45		F <sub>1,70</sub> = 5.94	0.01	0.08	0.21
T1	2001	12	5	F <sub>1,3</sub> = 15.47	0.029	0.83	1.26
	2002	5		F <sub>1,3</sub> = 2.87	0.18	0.48	1.01
T2	2001	14	5	F <sub>1,3</sub> = 2.08	0.24	0.41	2.36
	2002	5		F <sub>1,3</sub> = 0.09	0.77	0.03	0.83
E1	2001	36	27	F <sub>1,25</sub> = 17.61	< 0.001	0.41	0.59
	2002	27		F <sub>1,25</sub> = 6.93	0.014	0.22	0.45
E2	2001	24	15	F <sub>1,13</sub> = 17.90	< 0.001	0.57	1.01
	2002	20		F <sub>1,13</sub> = 15.93	0.0015	0.55	0.76

Notes: <sup>1</sup> Number of short stems. <sup>2</sup> Number of short stems in 2001 that survive in 2002.

The decrease in the density of *T. micrantha* between 2001 and 2002 was less than the expected if self-thinning processes were operating, because, when shade increased in the understory, most of the seedlings and saplings allocated the most of their resources into increasing stem-length rather than into increasing diameter or forming new branches, leaves, or flowers. In short order, those short stems developed into medium-height stems (but, not necessarily into medium-diameter stems), which allowed them to better compete for light and increase their likelihood of survival.

In secondary succession in the tropics, some pioneer species produce longer stems when under the canopy of remnant trees (Guevara *et al.* 1992, Parrotta *et al.* 1997). The growth rate (> 10 m in four years) of *T. micrantha* in the landslide on Casita Volcano, Nicaragua, was very similar to the growth rate of this species (17 m in five years) observed in cleared forests in Ghana (Swaine and Hall 1983). Tall-stemmed *T. micrantha* were present in 2002, which indicates that the medium-height plants in 2001 continued to grow. The lower increase in the slope of the regression line of the medium-height individuals compared to that of the short-height individuals indicates that in the first case, the allocation of

resources into growth was less pronounced than in the second.

In the erosional sectors of the landslide, canopy hierarchies did not develop because, in most of the plots, stem densities and total cover were low, and only short-stemmed individuals were present. Thus, one-sided competition for light likely did not occur; rather, the decrease in the frequencies of shorter short-stemmed individuals and the increase in the frequencies of the taller short-stemmed individuals suggests mortality caused by two-sided competition for nutrients (Kikuzawa and Umeki 1996, Bergqvist 1999, Bravo *et al.* 2001) or strong environmental selection (Belyea and Lancaster 1999, del Moral and Jones 2002, del Moral and Lacher 2005, Houseman and Gross 2006).

Competition for nutrients occurs between individuals of similar size, and is considered as two-sided because affects primarily at the individuals that are close to established plants, where the availability of nutrients is relatively lower, and the effects of competition are greater. In the erosional sectors, however, dead individuals of *T. micrantha* were not more heavily concentrated near live stems (personal observation). This indicates that mortality of the shorter short-stem-

med plants that had recently germinated is not influenced by their location in the neighbourhood of established individuals, but by the site conditions (mainly slope, stoniness, and moisture) at small scale (presence of favourable micro-sites) (Titus and del Moral 1998, Jones and del Moral 2005).

*T. micrantha* is highly adapted for survival in hostile environments, but environmental selection might differ between the more and the least favourable micro-sites. Seedlings that arrived in the most favourable sites might germinate and would become established. In contrast, those that arrived in the least favourable sites might germinate, but they would not become established, which would lead to a decrease in the frequencies of the shorter short-stemmed individuals and a shift from L-shaped to bimodal frequency distributions. In addition, in the erosional sectors, the shortest of the short-stemmed plants grew slowly and the frequencies of the taller of the short-stemmed plants increased slightly between 2001 and 2002. In E1, medium-diameter stems, but not medium-height stems, were present and, in E1 and E3, stem diameter increased more than did stem height. This suggests that, unlike individuals in D2, *T. micrantha* individuals in the erosional sectors allocated resources mainly to survival and maintenance (radial extension) rather than to growth (elongation of stems). Greater investment in radial extension than in the elongation of stems occurs in several plant species when they grow in harsh substrates in temperate (Kaitaniemi and Ruohomaki 2003, Dehlin *et al.* 2004) and tropical (da Silva *et al.* 2002, Yan *et al.* 2006) zones.

In D1 and in the transitional sectors, the pronounced changes caused by human distur-

bances (fire and clercutting) in the relationships between total stem volume and density, the frequency distributions of size, and the allometric relationships between height and diameter, prevent a discussion about the development of size hierarchies or intraspecific interactions in *T. micrantha* populations in those zones.

### **Concluding remarks**

In the populations of *T. micrantha* located in the most fertile and stable zones of the landslide of Casita Volcano, Nicaragua, the decrease in density caused by the death of some individuals led to a simultaneous increase in biomass, but these changes were not pronounced enough to infer self-thinning. There was, however, evidence of one-sided competition for light and "plastic responses" by seedlings and saplings in the understory. Indeed, they grew much more in height than they did in diameter in an attempt to avoid being outcompeted by their neighbours.

However, in the less fertile and stable areas of the landslide, in general, stem volume increased and density decreased, and medium-height and tall-stemmed individuals were absent. In those areas, *T. micrantha* individuals died because of environmental selection, which primarily affected the shortest of the short-stemmed individuals. The other short-stemmed individuals allocated most of their resources to lateral, rather than vertical, growth. Our study suggests that *T. micrantha* individuals allocated resources to growth and survival, and developed different types of interactions among them depending on the abiotic characteristics of the area of the landslide in which occurred.

## Acknowledgements

This research was part of the collaborative program between the Universidad de Alcalá and the Universidad Nacional Autónoma de Nicaragua-León, and supported by a grant from the Third Scientific Research and Technological Innovation Program of the Regional Authority of Madrid. Pedrarias Dávila and Aníbal Rodríguez of the Universidad Nacional Autónoma de Nicaragua-León were extremely helpful with the fieldwork. Ricardo Rueda and Dania Paguaga helped us to identify plant species. We are very grateful to the Sevilla family in the community of Pikin Guerrero who provided accommodations and supported our fieldwork.

## Literature cited

- Alvarez-Aquino C., Williams-Linera G. and Newton A. 2005. Disturbance effects on the seed bank of Mexican cloud forest fragments. *Biotropica*. 37 (3): 337-42.
- Antonovics J. and Levin D.A. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*. 11: 411-52.
- Ballaré C.L. 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. *Trends in Plant Sciences*. 4: 97-102.
- Belyea L.R. and Lancaster J. 1999. Assembly rules within a contingent ecology. *Oikos*. (86): 402-16.
- Bergqvist G. 1999. Wood volume yield and stand structure in Norway spruce understorey depending on birch shelterwood density. *Forest Ecology and Management*. 122 (3): 221-29.
- Bishop C.M. 1995. Neural networks for pattern recognition. Clarendon Press, London.
- Bravo F., Hann D.W. and Maguire D.A. 2001. Impact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir trees in southwestern Oregon. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*. 31 (12): 2237-47.
- Brooker R.W. and Callaghan T.V. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos*. 81 (1): 196-207.
- Cannell M.G.R., Rothery P. and Ford E.D. (1984): Competition within stands of *Picea sitchensis* and *Pinus contorta*. *Annals of Botany*. 53: 349-62.
- Carrière S.M., Letourmy P. and McKey D.B. 2002. Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology*. 18: 375-96.
- Corrales-Rodríguez D. 1983. Impacto ecológico sobre los recursos naturales renovables de Centroamérica. Instituto Nicaragüense de los Recursos Naturales y del Ambiente (IRENA), Managua.
- da Silva R.P., dos Santos J., Tribuzy E.S. *et al.* 2002. Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *Forest Ecology and Management*. 166 (1-3): 295-301.
- Dalling J.W. and Iremonger S. 1994. Preliminary estimate of landslide disturbance in the Blue Mountains, Jamaica. *Caribbean Journal of Science*. 30: 290-92.
- de Souza F.M. and Batista J.L.F. 2004. Restoration of seasonal semideciduous forests in Brazil: influence of age and restoration design on forest structure. *Forest Ecology and Management*. 191 (1-3): 185-200.
- Dehlin H., Nilsson M.C., Wardle D.A. *et al.* 2004. Effects of shading and humus fertility on growth, competition, and ectomycorrhizal colonization of boreal forest tree seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*. 34 (12): 2573-86.
- del Moral R. and Jones C. 2002. Vegetation development on pumice at Mount St. Helens, USA. *Plant Ecology*. 162 (1): 9-22.
- and Lacher I.L. 2005. Vegetation patterns 25 years after the eruption of Mount St. Helens Washington, USA. *American Journal of Botany*. 92 (12): 1948-56.
- Enquist B.J., Brown J.H. and West G.B. 1998. Allometric scaling of plant energetics and population density. *Nature*. 395: 163-5.
- and Niklas K.J. 2001. Invariant scaling relations across tree-dominated communities. *Nature*. 410 (6829): 655-60.
- Ford E.D. 1975. Competition and stand structure in some even-aged plant monocultures. *Journal of Ecology*. 63: 311-333.

- Garwood N.C. (1985): Earthquake-caused landslides in Panama: recovery of the vegetation. National Geographic Society Research Reports 21. National Geographic Society, Washington DC.
- Gilbert I.R., Jarvis P.G. and Smith H. 2001. Proximity signal and shade avoidance differences between early and late successional trees. *Nature*. 411: 792-5.
- Guariguata M.R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *Journal of Ecology*. 78: 814-32.
- Guevara S., Meave J., Moreno-Casasola P. *et al.* 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *Journal of Vegetation Science*. 3: 655-64.
- Hara T. 1986. Effects of density and extinction coefficient on size variability in plant populations. *Annals of Botany*. 57: 885-92.
- Harper J.L. 1977. *The population biology of plants*. Academic press, London.
- Houseman G.R. and Gross K.L. 2006. Does ecological filtering across a productivity gradient explain variation in species pool-richness relationships? *Oikos*. 115 (1): 148-54.
- Jones C. and del Moral R. 2005. Effects of microsite conditions on seedling establishment on the foreland of Coleman Glacier, Washington. *Journal of Vegetation Science*. 16 (3): 292-300.
- Kaitaniemi P. and Ruohomaki K. 2003. Factors controlling resource allocation in mountain birch. *Perspectives in Plant Ecology Evolution and Systematics*. 5 (4): 231-49.
- Kent, M. and Cooker, P. 1992. *Vegetation description and analysis: a practical approach*. Belhaven, London.
- Kerle N. 2002. Volume estimation of the 1998 flank collapse at Casita volcano, Nicaragua: A comparison of photogrammetric and conventional techniques. *Earth Surface Processes and Landforms*. 27 (7): 759-72.
- Kikuzawa K. 1999. Theoretical relationships between mean plant size, size distribution and self-thinning under one-sided competition. *Annals of Botany*. 83: 11-8.
- and Umeki K. 1996. Effect of canopy structure on degree of asymmetry of competition in two forest stands in northern Japan. *Annals of Botany*. 77: 565-71.
- LaBarbera M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics*. 20: 97-117.
- Li X., Wilson S.D. and Song Y. 1999. Secondary succession in two subtropical forests. *Plant Ecology*. 143: 13-21.
- Lonsdale W.M. 1990. The Self-Thinning Rule - Dead or Alive. *Ecology*. 71 (4): 1373-88.
- Maliakal S.K., McDonnell K., Dudley S.A. *et al.* 1999. Effects of red to far-red ratio and plant density on biomass allocation and gas exchange in *Impatiens capensis*. *International Journal of Plant Science*. 160: 723-33.
- Miyaniishi K., Hoy A.R. and Cavers P.B. 1979. A generalized law of self-thinning in plant populations. *Journal of Theoretical Biology*. 78: 439-42.
- Mueller-Dombois D. and ElleMBERG H. 1974. *Aims and methods of vegetation ecology*. Wiley Publishers, New York.
- Nagashima H. and Terashima I. 1995. Relationships between height, diameter and weight distributions of *Chenopodium album* plants in stands: effects of dimension and allometry. *Annals of Botany*. 75: 181-88.
- Nikklas K.J. 1994. *Plant Allometry*. University of Chicago Press, Chicago.
- Osawa A. and Allen R.B. 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. *Ecology*. 74 (4): 1020-32.
- Parrotta J.A., Turnbull J.W. and Jones N. 1997. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management*. 99: 1-7.
- Popma J. and Bongers F. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia*. (75): 625-32.
- Salas-Estrada J.B. 1999. Biodiversidad en Nicaragua, un estudio de país. Ministerio de los Recursos Naturales y del Ambiente (MARENA)-Ministerio Agropecuario y Forestal (MAGFOR). Managua.
- Schmitt J. and Wulff R.D. 1993. Light spectral quality, phytochrome and plant competition. *Trends in Ecology and Evolution*. 8: 47-51.
- Scott K.M., Vallance J.W., Kerle N. *et al.* 2005. Catastrophic precipitation-triggered lahar at Casita volcano, Nicaragua: occurrence, bulking and transformation. *Earth Surface Processes and Landforms*. 30 (1): 59-79.



- Sheridan M.F. 1998. Report on the October 30, 1998 avalanche and breakout flow of Casita Volcano, Nicaragua, triggered by hurricane Mitch. United States Geological Service (USGS), Washington DC.
- Smith H. 2000. Phytochromes and light signal perception by plants-an emerging synthesis. *Nature*. 407: 585-91.
- Statsoft 2001. STATISTICA. Data analysis software system. 6. Tulsa.
- Stevens W.D., Ulloa-Ulloa C., Pool A. *et al.* 2001. Flora de Nicaragua. Missouri Botanical Garden Press, St. Louis.
- Stoll P., Weiner J., Muller-Landau H. *et al.* 2002. Size symmetry of competition alters biomass-density relationships. *Proceedings of the Royal Society of London, Series B*. 269: 2191-95.
- Swaine M.D. and Hall J.B. 1983. Early succession on cleared forest land in Ghana. *Journal of Ecology*. 71: 601-27.
- Titus J.H. and del Moral R. 1998. Seedling establishment in different microsites on Mount St. Helens, Washington, USA. *Plant Ecology*. 134: 13-26.
- Vazquez-Yanes C. (1998): *Trema micrantha* (L.) Blume (Ulmaceae): A promising neotropical tree for site amelioration of deforested land. *Agroforestry Systems*. 40 (1): 97-104.
- , Batis-Muñoz A.I., Alcocer-Silva M.I. *et al.* 1999. Árboles y arbustos potencialmente valiosos para la restauración ecológica y la reforestación. CONABIO-Instituto de Ecología (UNAM), México DF.
- Weiner J. 1990. Assymmetric competition in plant populations. *Trends in Ecology and Evolution*. 5: 360-64.
- and Thomas S.C. 1986. Size variability and competition in plant monocultures. *Oikos*. 47: 211-22.
- Weller D.E. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. *Ecological Monographs*. 57: 23-43.
- Westoby M. 1984. The self-thinning rule. Academic Press, London.
- White J. 1980. Demographic factors in populations of plants. In: Solbrig O.T. (ed), *Demography and evolution in plant populations*. Blackwell Publishing, Oxford.
- 1981. The allometric interpretation of the self-thinning rule. *Journal of Theoretical Biology*. 89: 475-500.
- and Harper J.L. 1970. Correlated changes in plant size and number in plant populations. *Journal of Ecology*. 58: 467-85.
- Yan J.H., Zhou G.Y., Zhang D.Q. *et al.* 2006. Different patterns of changes in the dry season diameter at breast height of dominant and evergreen tree species in a mature subtropical forest in South China. *Journal of Integrative Plant Biology*. 48 (8): 906-13.
- Yang Z.J. and Midmore D.J. 2005. Modelling plant resource allocation and growth partitioning in response to environmental heterogeneity. *Ecological Modelling*. 181 (1): 59-77.
- Yoda K., Kira T., Ogawa H. *et al.* 1963. Self-thinning in overcrowded pure stands under cultivated natural conditions. *Journal of the Institute of Polytechnics. Osaka City University Series D*, 14: 107-29.
- Zeide B. 1987. Analysis of the 3/2 power law of self-thinning. *Forest Science*. 33: 517-37.

