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COMPARATIVE STUDY ON THE DRAINAGE REQUIREMENTS AND GROWTH PATTERN OF THREE NEOTROPICAL PIONEER SPECIES

L. Kammesheidt*

Institut für Waldbau, Abt. II: Waldbau der Tropen, Universität Göttingen, Büsgenweg 1, D-37077 Göttingen, Germany

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KAMMESHEIDT, L. 2000. Comparative study on the drainage requirements and growth pattern of three neotropical pioneer species. The spatial pattern, diameter distribution and height growth pattern of *Heliocarpus popayanensis*, *Ochroma lagopus* and *Cecropia peltata* were studied in logged stands of different ages along a drainage gradient in the Forest Reserve of Caparo, Venezuela. *Heliocarpus popayanensis* and *O. lagopus* were rare in the periodically flooded depressions but occurred commonly on well-drained levee sites. In contrast, *C. peltata* was equally abundant in both drainage types. *Heliocarpus popayanensis* and *O. lagopus* occurred only in large disturbed areas (> 300 m^2) and hence showed a clumped pattern, whereas *C. peltata* was found in a wide range of gap sizes, leading to a random distribution in both drainage types. Recruitment as well as height growth in *H. popayanensis* and *O. lagopus* ended earlier than in *C. peltata*. Overall, *C. peltata* showed a 'generalist' behaviour, while the other species were 'specialists' confined to a narrower ecological niche.

Key words: *Heliocarpus popayanensis* - *Ochroma lagopus* - *Cecropia peltata* - diameter distribution - drainage - height curves - logged stands - spatial pattern - Venezuela

KAMMESHEIDT, L. 2000. Kajian perbandingan terhadap keperluan saliran dan corak pertumbuhan tiga spesies perintis neotropika. Corak ruang, taburan garis pusat dan corak pertumbuhan ketinggian bagi *Heliocarpus popayanensis*, *Ochroma lagopus* dan *Cecropia peltata* dikaji di dirian yang dibalak yang berbeza umur di sepanjang cerun saliran di Hutan Simpan Caparo, Venezuela. *Heliocarpus popayanensis* dan *O. lagopus* jarang terdapat di tapak yang dibanjiri dari semasa ke semasa tetapi biasanya terdapat di tapak permatang yang disaliri dengan baik. Di sebaliknya, *C. peltata* terdapat sama banyak di kedua-dua jenis saliran. *Heliocarpus popayanensis* dan *O. lagopus* hanya terdapat di kawasan-kawasan rosak yang luas (>300 m^2) dan dengan ini menunjukkan corak berkelompok, manakala *C. peltata* didapati dalam saiz jurang yang luas, membawa kepada taburan secara rambang dalam kedua-dua jenis saliran. Penokokan dan pertumbuhan ketinggian *H. popayanensis* dan *O. lagopus* berakhir lebih cepat berbanding dengan *C. peltata*. Secara keseluruhannya, *C. peltata* menunjukkan tingkah laku 'umum' manakala spesies yang lain adalah 'pakar' yang terbatas kepada ruang ekologi yang lebih sempit.

**Present address: Institute for World Forestry, Federal Research Centre for Forestry and Forest Products, Leuschnerstrasse 91, D-21031 Hamburg, Germany.*

Introduction

Early successional stages in the neotropics are usually dominated by a few pioneer species, forming sometimes pure stands. Typical species at the first arboreal stage are *Heliocarpus* spp. and *Trema micrantha* which are eventually replaced by taller pioneers such as *Cecropia* spp. and *Ochroma lagopus* (Gomez-Pompa & Vázques-Yanes 1981). The role of neotropical pioneer species in succession was studied by focusing, for example, on the ecological life history (Silander 1979), growth and mortality pattern (Uhl & Jordan 1984), gap size requirement (Brokaw 1987), or the distribution in different zones of natural tree-fall gaps (Brandani *et al.* 1988). Presumably the most comprehensive study on the gap requirement, demography and allometry of a single pioneer species was done by Alvarez-Buylla and Martínez-Ramos (1992) on *Cecropia obtusifolia.* However, not much is known about the drainage requirement of pioneer species to date. As pioneer species are capable of ameliorating site condition for the establishment of late successional species (Silander & Lugo 1990), differences in their abundance pattern along a drainage gradient may result in different speeds of succession.

This study presents data on three pioneer species, i.e. *Heliocarpus popayanensis, Ochroma lagopus* and *Cecropia peltata,* common in early successional stages in logged forests on alluvial material. Specifically, I have asked the question: To what extent do these species differ in their recruitment, spatial distribution and height growth pattern along a drainage gradient in logged stands of different ages?

Material and methods

Study site

Research was conducted in logged stands in the Forest Reserve of Caparo (7° 30'N, 70° 45' W; *c.* 100 m above sea-level) which lies in the western plains of Venezuela about 40 km off the piedmont of the Andes. The climate is seasonal with the wettest period between May and August and a pronounced dry period from December to March. Mean annual rainfall is 1750 mm. The average annual temperature is 24.6 °C. Caparo forests are classified as 'moist semi-deciduous lowland forest' (Lamprecht 1989). Intensive sedimentation by river flooding has resulted in a fine-scaled microrelief of sandy levee sites (banco) and clay-rich depressions (bajio). The levee sites are well-drained throughout the year, while the depressions are flooded during the rainy season. The duration and depth of inundation depend on the soil texture, layering, relief, and ground water level. In the depressions, soils dry out during the dry season (Franco 1979). Therefore, water availability, rather than nutrient contents that are high in comparison with those of zonal neotropical forests (cf. Hase & Fölster 1982), may be the most important limiting factor at this site. Logging activities, which focused until the late 1980s mainly on four species, namely *Bombacopsis quinata, Swietenia macrophylla, Cedrela odorata* and *Cordia thaisiana* (all of these species are found both on well-drained and poorly-drained sites), removed on average 10 trees with a bole volume of 66.5 $m^3 ha^{-1}$ (Kammesheidt 1998).

Sampling and analysis

Two blocks of 100 ha each, logged-over 5 y (LG5) and 8 y (LG8) respectively prior to this study (done from November 1991 to January 1992), were selected. The actual logged area was delimited (LG5: 33 ha; LG8: 37 ha). In the delimited area, a grid of transect lines with equal distances between each other were established. Along these transect lines, 30 plots (400 m^2 each) in each of the logged stands were placed at systematic distances (30–60 m distance between neighbouring plots). In each plot, dbh (diameter at breast height = 1.3 m) and height (using a Suunto altimeter) of all trees ≥ 10 cm dbh were measured. Within the major sampling unit, saplings (130 cm tall, 10 cm dbh) were recorded in a 100 m^2 circle; seedlings (30–130 cm tall) were counted in eight 2 × 2 m quadrats (32 m^2). Dead standing stems > 1 cm dbh were recorded.

In each plot, a drilling was made for soil description. By determining the soil texture, soil colour, occurence of mottles and concretions, and horizons, the relative availability of water to plants and the degree of waterlogging could be derived (cf. Franco 1979). Based on these parameters, sites were classified according to Franco (1979) into levee sites (well-drained, not waterlogged) and depressions (poorly-drained, waterlogged for 3–6 months during the rainy season). In LG5 and LG8, 16 and 19 plots respectively were established on well-drained sites, and 14 and 11 plots respectively were located on poorly-drained sites. Overall, the slight dominance of well-drained sites reflects the proportion of drainage types within the high-forest area of Caparo (L. Vincent, pers. comm.).

The percentage of gap area (*sensu* Brokaw 1982: a gap is a 'hole' in the forest extending through all levels down to an average height of 2 m above ground) was determined from a scale map drawn in each plot. In addition, the distance between the nearest undisturbed forest and plot boundary was measured in the four main compass directions for plots established on skid trails and felling or landing areas. Due to the well-protected status of the study area managed by the Universidad de Los Andes in Mérida, any human disturbance ceased after logging. Based on this and the fact that neotropical pioneers establish themselves in general soon after gap creation (cf. Vázques-Yanes 1974, Holthuijzen & Boerboom 1982, Vázques-Yanes & Orozco-Segovia 1982), it can be assumed that the logged stands of different ages correspond to the age of the study species.

For *H. popayanensis* and *O. lagopus*, the best height curve fit was achieved with the Petterson equation (Kramer & Akça 1987):

$$ht = 1.3 + (dbh/(a + b \times dbh))^3 \qquad (1)$$

The Michailov equation (Prodan 1965) was used for *C. peltata:*

$$ht = 1.3 + a \times \exp(-b/dbh) \qquad (2)$$

The quantities *a* and *b* are both regression coefficients. As no sufficient data were available on poorly-drained sites for constructing a consistent height curve in *H. popayanensis* and *O. lagopus*, only curves for the well-drained site type are presented for both successional stages. Also, *H. popayanensis* was rare in LG5 and hence omitted for that stage.

The spatial pattern of species in the different site types was determined by the index of dispersion as the variance-to-mean ratio ($s^2/\bar{x}$) (Fowler *et al.* 1998).

Results

The left-skewed diameter distribution of *O. lagopus* in LG5 changed to a bell-shaped one in LG8, indicating that recruitment had ended (Figure 1). *Heliocarpus popayanensis* showed a similar diameter frequency distribution to *O. lagopus* in the older logged stand (Figure 2). Recruitment of *C. peltata*, by contrast, seemed to be going on even in the more advanced successional stage especially on the poorly-drained site type (Figure 3). This is due to the fact that *C. peltata* also successfully established itself in small gaps (150–300 m^2), while the other study species required large gaps (>300 m^2; L. Kammesheidt, unpubl. data). Gap area in the older logged stand ranged 10–60% ($\bar{x}$ = 22%, s.d. = 8.6, n =18) and 20–75% ($\bar{x}$ = 35%, s.d. = 17.5, n = 10) on well-drained and poorly-drained sites respectively, suggesting that further establishment of *C. peltata* is particularly likely on the latter site type. The mean diameter between drainage types was significantly different for *O. lagopus* in LG8 (t = 2.5, df = 105, $p < 0.01$), while in all other cases no significant differences were found ($p > 0.05$) (Table 1).

Table 1. Dbh (cm) and height (m) of three neotropical pioneer species on well-drained and poorly-drained sites at year 5 (LG5) and year 8 (LG8) in the Forest Reserve of Caparo, Venezuela. For the dbh all individuals > 1 cm dbh were considered, while the height represents only individuals ≥ 10 cm dbh.

	Well-drained			Poorly-drained		
	n	Range	$\bar{x} \pm$ sd	n	Range	$\bar{x} \pm$ sd
Dbh						
LG5						
Ochroma lagopus	23	4–28	16.5 ± 4.5	6	4–21	17.5 ± 1.8
Cecropia peltata	29	2–17	11.8 ± 2.3	31	3–15	10.6 ± 1.7
LG8						
Heliocarpus popayanensis	29	5–22	12.9 ± 3.3	16	8–21	13.2 ± 2.9
O. lagopus	89	9–31	17.3 ± 5.3	18	8–19	15.0 ± 2.6
C. peltata	67	4–33	13.2 ± 4.7	47	4–18	12.4 ± 2.5
Height						
LG8						
H. popayanensis	24	7–16	11.9 ± 2.4	14	11–15	12.3 ± 1.1
O. lagopus	79	11–20	16.2 ± 2.2	12	10–23	15.2 ± 4.2
C. peltata	36	9–24	13.8 ± 3.4	20	10–19	13.2 ± 2.1

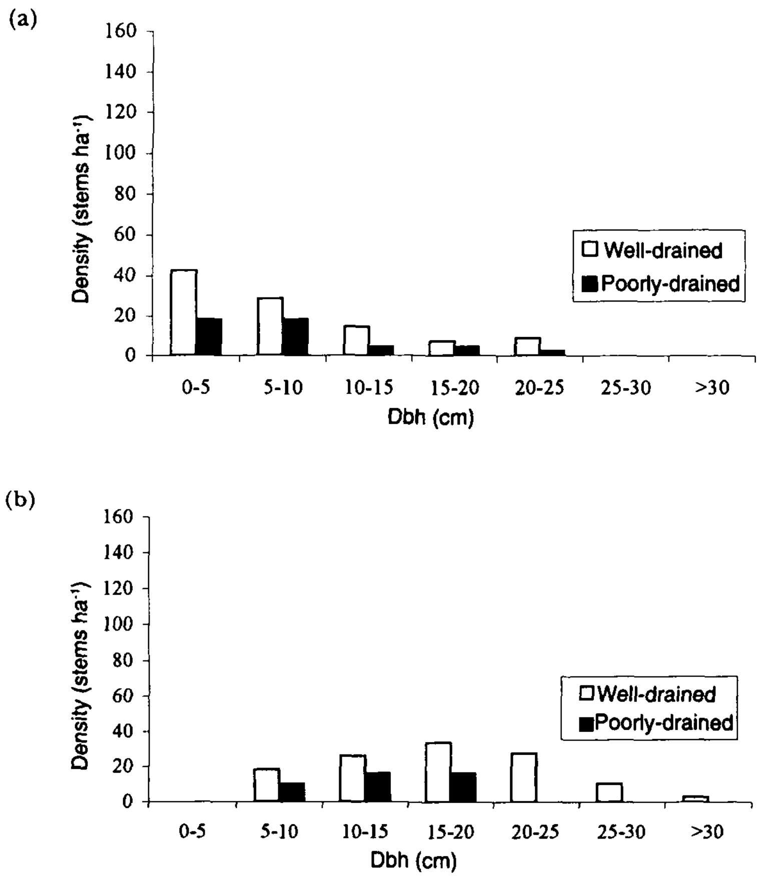

Figure 1. Diameter-class distribution of *Ochroma lagopus* on different drainage types in a (a) 5-y-old, and (b) 8-y-old logged-over stand respectively in the Forest Reserve of Caparo, Venezuela

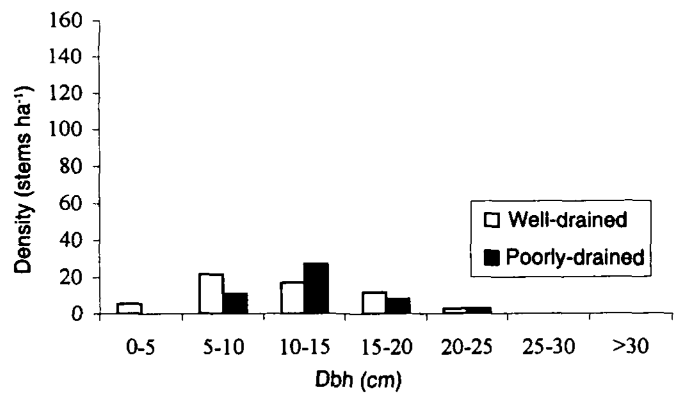

Figure 2. Diameter-class distribution of *Heliocarpus popayanensis* on different drainage types in a 8-y-old logged-over stand in the Forest Reserve of Caparo, Venezuela

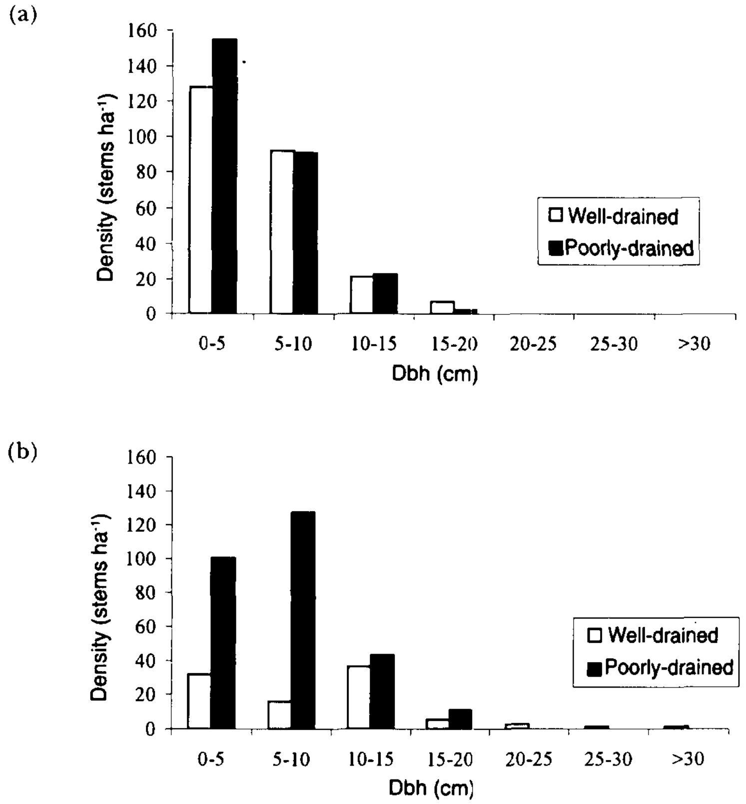

Figure 3. Diameter-class distribution of *Cecropia peltata* on different drainage types in a (a) 5-y-old, and (b) 8-y-old logged-over stand respectively in the Forest Reserve of Caparo, Venezuela

In both well-drained and poorly-drained sites, *O. lagopus* showed a clumped distribution, whereas *C. peltata* exhibited a slightly aggregated distribution pattern on well-drained sites and random distribution on poorly-drained sites (Table 2). *Heliocarpus popayanensis* was clumped on poorly-drained sites but showed a random pattern on well-drained sites. Theoretically, gaps in 12 plots on poorly-drained sites were found to be large enough (> 300 m^2) for establishment of *H. popayanensis* and *O. lagopus* but less than half were actually occupied. In contrast, on well-drained sites most of the plots with a gap size > 300 m^2 (in total 20) were occupied by *H. popayanensis* and *O. lagopus*. No significant difference of the stem density per plot between site types was found (Wilcoxon test; *H. popayanensis*: H = 1.37, p = 0.17; *O. lagopus*: H = 0.65, p = 0.52; *C. peltata*: H = 1.31, p = 0.19).

The height curve of *O. lagopus* at year 5 suggests that height growth culminated prior to this age (Figure 4). The population was split up into two cohorts that grew perhaps under optimal and suboptimal conditions. At year 8, height growth slowed down (Figure 5). The height curve of *H. popayanensis* in LG8 resembled the one of *O. lagopus* in LG5. However, *H. popayanensis* was clearly lower in stature than

O. lagopus. The height growth pattern of *C. peltata* was fairly distinct from the other study species, not least indicated by choosing a different equation to fit the curves. Height development of *C. peltata* in LG5 was slower than that of *O. lagopus*. In between the successional stages studied, however, the tallest individuals of *C. peltata* overtopped the latter species. The low r^2 in *H. popayanensis*, *O. lagopus* (LG8) and *C. peltata* (LG5) was not a failure of the curves to match the data but reflects the flat shape of the curves in conjunction with a similar standard deviation of residuals of the other stage. Established individuals showed hardly any difference in their height performance between drainage types in LG8 (Table 1).

Table 2. Sample size (n), maximum and mean stem number per plot (400 m^2), and the index of dispersion ($s^2/\bar{x}$) of three neotropical pioneer species ($\geq$ 10 cm dbh) on well-drained and poorly- drained sites in the Forest Reserve of Caparo, Venezuela; LG5 and LG8 combined

	Well-drained				Poorly-drained			
	n	max.	$\bar{x}$	$s^2/\bar{x}$[a]	n	max.	$\bar{x}$	$s^2/\bar{x}$[a]
Heliocarpus popayanensis	13	5	2.1	1.1	3	8	5.0	2.6
Ochroma lagopus	18	14	5.3	3.5	4	7	3.5	2.0
Cecropia peltata	25	9	2.1	1.7	14	6	2.5	1.0

[a]) > 1 indicates an aggregated pattern, 1 indicates a random distribution, and < 1 indicates a regular pattern.

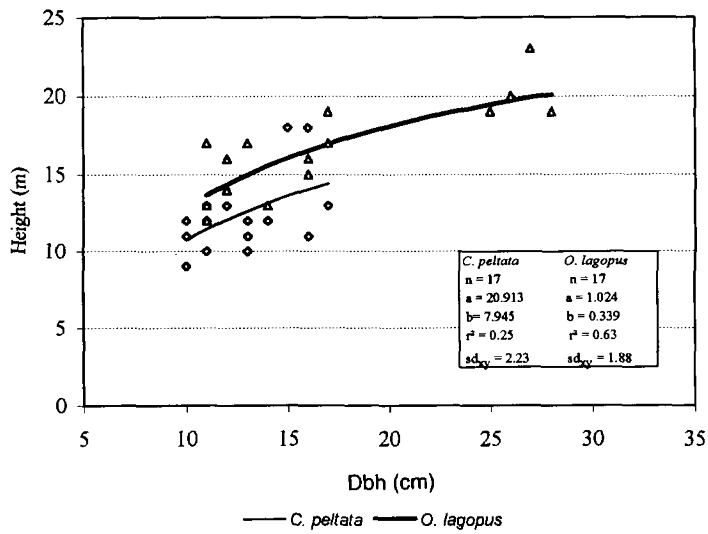

Figure 4. Height curves of *O. lagopus* and *C. peltata* in LG5 in the Forest Reserve of Caparo, Venezuela

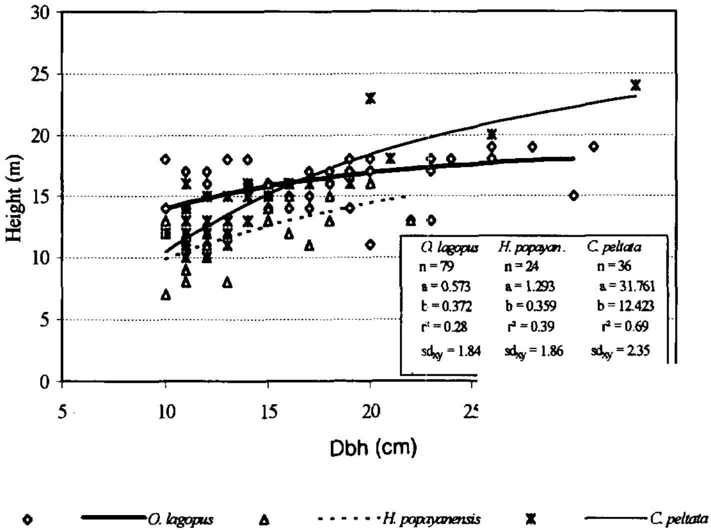

Figure 5. Height curves of *O. lagopus*, *H. popayanensis* and *C. peltata* in LG8 in the Forest Reserve of Caparo, Venezuela

Apart from the different height patterns (cf. Figures 4 and 5), the study species also have different life spans, indicated by the proportion of dead standing trees in LG8. Whereas in *H. popayanensis* 19 and 22% respectively were found to be dead standing stems on well-drained and poorly-drained sites, the corresponding figures in *O. lagopus* were 10 and 8% respectively, and in *C. peltata* 8 and 12% respectively.

Discussion

The study species represented a sequence of trees common in either the first (*H. popayanensis*) or second (*O. lagopus, C. peltata*) arboreal stage. The inferior stature of *H. popayanensis* has probably something to do with the timing of initial branching, phenology and photosynthetic rate. On average, *H. popayanensis* branched at lower levels than the other study species (L. Kammesheidt, unpubl. data). Mature individuals of *H. popayanensis* were leafless throughout the dry season, while *O. lagopus* and *C. peltata* developed new foliage continuously, irrespective of drainage conditions and season (pers. obs.). Continued and efficient development of new leaves is reported to be a major prerequisite for the rapid growth of pioneers (Coombe 1960, Coombe & Hadfield 1962). The photosynthetic rate of *O. lagopus* ranges 24–28 μmol m^{-2} s^{-1}, while *Heliocarpus appendiculatus* reaches only 8 μmol m^{-2} s^{-1} (Bazzaz 1991) and the photosynthetic rate of *C. peltata* is up to 16.4 μmol m^{-2} s^{-1} (Stephens & Waggoner 1970).

Cecropia peltata showed the widest ecological amplitude among the study species in terms of gap requirement. Also, *C. peltata* was equally abundant in both drainage types, while *H. popayanensis* and *O. lagopus* were rare in the periodically flooded depressions. Gräfe (1981) found similar differences in the abundance pattern of *C. peltata* and *O. lagopus* between drainage types in 1–19-y-old forest fallows in Caparo. It is not clear whether drainage plays a role in hampering the germination of *O. lagopus* and *H. popayanensis*. Perhaps these species germinate as well as *C. peltata* on poorly-drained sites but are less capable of surviving in the long run. Stilt roots, reported to be often covered with lenticells facilitating gas exchange with the atmosphere (Lüttge 1997), may be an adaptive tool for *C. peltata* to establish on sites with poor aeration. Silander and Lugo (1990) suggest that stilt roots in the superficially rooted *C. peltata* reduce the susceptibility to being uprooted. The other study species lack stilt roots. However, it is still questionable whether stilt roots are necessary for the plant to thrive in poorly-drained sites. Webb and Peralta (1998) report, for example, that *O. lagopus* was common in logged swamp forest in Costa Rica, while other pioneer species were found to be rare.

Maximum height is attained earlier in *O. lagopus* than in *C. peltata* (Figures 4 and 5). *Ochroma lagopus* formed the canopy of the study sites of Gräfe (1981) until year 9. As in this study, maximum height of *O. lagopus* is reached at about 20 cm dbh. Gräfe (1981) attributed the sharp decline of *O. lagopus* in more advanced successional stages to the intraspecific competition caused by the clumped distribution and early crown closure. In Gräfe's study, *C. peltata* overtopped the former species in older forest fallows. A similar trend can be observed from the height curves of these species in LG8. The dominance of *C. peltata* in older seral stages may be explained by the random distribution of individuals leading to less intraspecific competition, rather than to the slower growth and higher maximum height compared to *O. lagopus*.

This study showed that among pioneer species, there are both 'generalists' and 'specialists'. Periodic inundation is a limiting factor to some pioneer species. To what extent poor drainage influences forest recovery merits further investigations.

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