Ann. Sci. For. 55 (1998) 727–742

Original article

Physical damage on tropical tree saplings: quantification and consequences for competition through height growth in a neotropical rain forest of French Guiana

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(Received 29 July 1996; revised 2 April 1997; accepted 25 May 1998)

Abstract – This paper deals with the quantification and the effects of physical damage on tree regeneration dynamics in the tropical rain forest. We define physical damage as breakage resulting in a greater than 20 % reduction in stem diameter and its associated effects. A study of physical damage at the community level was made in March 1994 in primary forest and forest disturbed by silvicultural treatments at the Paracou research site in French Guiana. The frequency of damage varies with diameter class and the degree of forest disturbance due to the silvicultural treatments, ranging from 14.9 % for saplings greater than 6 cm DBH in undisturbed forest to over 50 % for smaller saplings in disturbed forest. Study at the specific level was made at the same site on saplings of three tree species with contrasting ecological temperaments, *Bocoa prouacensis, Pradosia cochlearia* and *Goupia glabra,* from March 1994 to March 1996. Damage frequencies varied from 34 % for saplings of the pioneer species *Goupia glabra* to 64 and 60 %, respectively, for the more shade tolerant species *Bocoa prouacensis* and *Pradosia cochlearia.* Physical damage does not directly influence height or diameter growth rates nor mortality within a species except for *Pradosia cochlearia.* However, diameter growth rates irrespective of damage are significantly different between species. Under certain circumstances, stem breakage may be an influential factor affecting the long term survival of pioneer species saplings because it modifies their social status. (© Inra/Elsevier, Paris.)

growth / saplings / competition / mortality / stem breakage / tropical rain forest

Résumé – Casse mécanique sur des jeunes arbres tropicaux : quantification et conséquences sur la compétition par la croissance en hauteur dans une forêt néotropicale humide de Guyane française. Ce travail portant sur la quantification et les effets de la casse mécanique sur la dynamique de la régénération des arbres en forêt dense humide tropicale, a été envisagé à

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deux niveaux de perception sur le dispositif de recherche de Paracou, en Guyane française. Une étude au niveau peuplement sans prise en compte des espèces a été réalisée en mars 1994 en forêt primaire et en forêt perturbée par des traitements sylvicoles. Le pourcentage de casse varie selon les classes de diamètre et l'importance de la perturbation due aux traitements, depuis 14,9 % pour les jeunes arbres de DBH supérieur à 6 cm en forêt naturelle, à plus de 50 % pour ceux de petits diamètres dans des sites perturbées. L'étude au niveau spécifique a été réalisée sur trois espèces aux tempéraments écologiques contrastés, *Bocoa prouacensis, Pradosia cochlearia* et *Goupia glabra,* entre mars 1994 et mars 1996.
Les jeunes arbres de l'espèce pionnière *Goupia glabra* sont moins fréquemment endommagées (34 %) que celles des espèces plus tolérantes d'ombre, *Bocoa prouacensis* (64 %) et *Pradosia cochlearia* (60 %). La casse mécanique n'influence pas directement les taux de croissance des tiges en hauteur ou en diamètre pour une espèce, sauf pour *Pradosia cochlearia.* Cependant, la croissance en diamètre, sans prendre en compte des dégâts mécaniques, est significativement différentes entre espèces. La casse mécanique, dans certaines circonstances, peut avoir une influence importante sur la survie à long terme des jeunes arbres d'espèces pionnières, car elle modifie leur statut social. (© Inra/Elsevier, Paris.)

croissance / jeune arbre / compétition / mortalité / casse mécanique / forêt tropicale humide /

1. INTRODUCTION

Studies on population dynamics and tree regeneration in tropical rain forests have shown the importance of physical damage on seedling and sapling mortality [1, 7–9, 14, 29, 30]. Physical damage is the mechanical breakage of a stem by an animal (due to tramping, scraping, pushing, biting or boring for example) or by material falling from a higher stratum of the vegetation. Whereas seedlings are more likely to be completely crushed, saplings most frequently suffer from breakage or stem deformations resulting in significant modification of future growth. This damage may either lead to increased mortality or, in the case of survival, to changes in growth trajectories. We can surmise that individuals reaching the young tree stage and emerging from the understory may already have a long and eventful past history.

If we take into account the notion of species in the study of physical damage on saplings, we can evaluate how it influences mortality, growth and competition dynamics. This approach is interesting in light of the nuances revealed by some studies contrasting the differences between pioneer species and shade tolerant ones [1, 9]. We ask the following questions.

1) In what way does the ecological temperment of a species influence the frequency of damage to saplings?

2) For a given individual of a given species, is physical damage automatically detrimental in comparison to another individual of the same species with no breakage, especially under conditions of active competition?

3) In which terms does physical damage affect sapling growth, in height or diameter, and in what proportion? Is there a direct or indirect consequence of stem breakage on these parameters?

We undertook a study of the effects of damage by breakage on the growth and survival of saplings of three tropical rain forest tree species in native and silviculturally treated forest in order to answer these questions.

2. MATERIALS AND METHODS

2.1. Study site

This study was carried out at the Paracou Tropical Forest Research Site of Silvolab, a co-ordination unit set up by French research institutes (current members are CIRAD-Forêt, Inra, ENGREF, ORSTOM, ONF and MNHN) for forest ecosystem studies in French Guiana. Located in the dense upland rain forest of north-eastern South America (2–6° N, 51°30'53°30W) (*figure 1*), the climate is considered as equatorial, characterised by perennial high (80–90 %) humidity, low temperature variation centred around 26 °C and a rarity of violent winds [15]. Mean annual rain fall for the last 10 years is 4 976 +/– SD 243 mm (CIRAD-Forêt à Kourou, unpublished data). Rainfall distribution is unequal over the year (*figure 2*). The main dry season occurs between August and November, with another short dry season during March or April. Average annual temperature is 26 °C.

The forest structure and composition are generally similar to other upland rain forest sites in South America, all the while possessing a Guianian character by virtue of a small number of relatively abundant tree species in a nonetheless species-rich forest. The three most representative families of trees attaining at least 10 cm in diameter at breast height (DBH) in the Paracou forest are the Lecythidaceae (18 % of the individuals), the Caesalpinaceae (13 %) and the Chrysobalanaceae (12 %) [11]. The principal tree species are the *Eschweilera* spp. (Lecythidaceae), the *Licania* spp. (Chrysobalanaceae), *Eperua falcata*, mouamba, *Bocoa prouacensis* (this study), bouchi mango, *Iryanthera* spp., bakouman, *Eperua grandiflora, Symphonia globulifera*, moni, *Vouacapoua americana, Pradosia cochlearia* (this study), *Qualea rosea Carapa procera,* patawa, and *Dicorynia guianensis* [24]. From a structural point of view there are on the average 618 stems/ha, with a mean basal area of 31 m^2/ha [10]. Approximately 60 % of the stems are 20 cm in DBH or less [24]. While emergents may reach 45 m in height, the general level of the canopy is around 40 m (B. Ferry, pers. com.).

The experimental site is composed of 12 plots of 9 ha (each surrounded by a 25 m wide buffer zone) distributed over three replicated blocks consisting of four silvicultural treatments, including a control [27]. The treatments, applied once in October 1986 to May 1987 for logging and December 1987 to January 1988 for poison girdling, are:

– treatment 0: control (mean basal area (ba) = 32 m^2/ha);

– treatment 1: selective logging above 50 cm DBH (mean remaining ba after logging = 24 m^2/ha;

– treatment 2: selective logging plus thinning by poison girdling (ba after logging = 19 m^2/ha);

– treatment 3: selective logging plus thinning by poison girdling and fuel wood extraction (ba after logging = 16 m^2/ha).

2.2. Methods

Frequency of breakage, survival, height and diameter growth rates for damaged and undamaged stems were analysed at both the community level and the specific level.

At the community level, the frequency of breakage on saplings regardless of species was estimated on randomly oriented transects 20 m long and 2 m wide, with origins located every 40 m on a square grid. A total of 96 transects were censused on three parcels (control, first level and second level treatments; with 32 transects per parcel). Measurements were made on individuals of more than 1.5 m in height and less than 10 cm DBH. Diameter was measured by classes of 1 cm intervals with a notched gauge (*figure 3*). Frequencies of damage were assessed using Clark and Clarks method based on comparison of main stem diameters above and below breakage points as indicated by major discontinuity or scarring [9]. From this a discontinuity ratio can be established as:

discontinuity ratio = 100 * (diameter above scar/diameter below scar).

Clark and Clark [9] fixed the lower limit of discontinuity at 25 %. This means that a stem with a discontinuity less than 25 % was considered as undamaged. But, as they recognise themselves, this criterion is quite conservative, leading to under-estimates. After a preliminary investigation of different critical levels for breakage acceptance (10, 15, 20 and 25 %), we decided to lower the level of acceptance to 20 %. However, results at the community level were not different for the two limits. Measures above and below the scar were made with a caliper every time discontinuity was doubtful. It is difficult to distinguish vertebrate damage from limbfall or treefall effects and we assume that the greatest contributions to any observed species differences depends on the species themselves and not the cause of the damage.

The species level effects of damage were studied for three tree species of contrasting ecological temperaments. The individuals studied were tagged saplings located on circular plots (radius 3.72 m) located throughout the 12 plots of 9 ha mentioned above, and forming part of the Inra (Institut national de la recherche agronomique) natural tree regeneration study (see [27] for the site description and

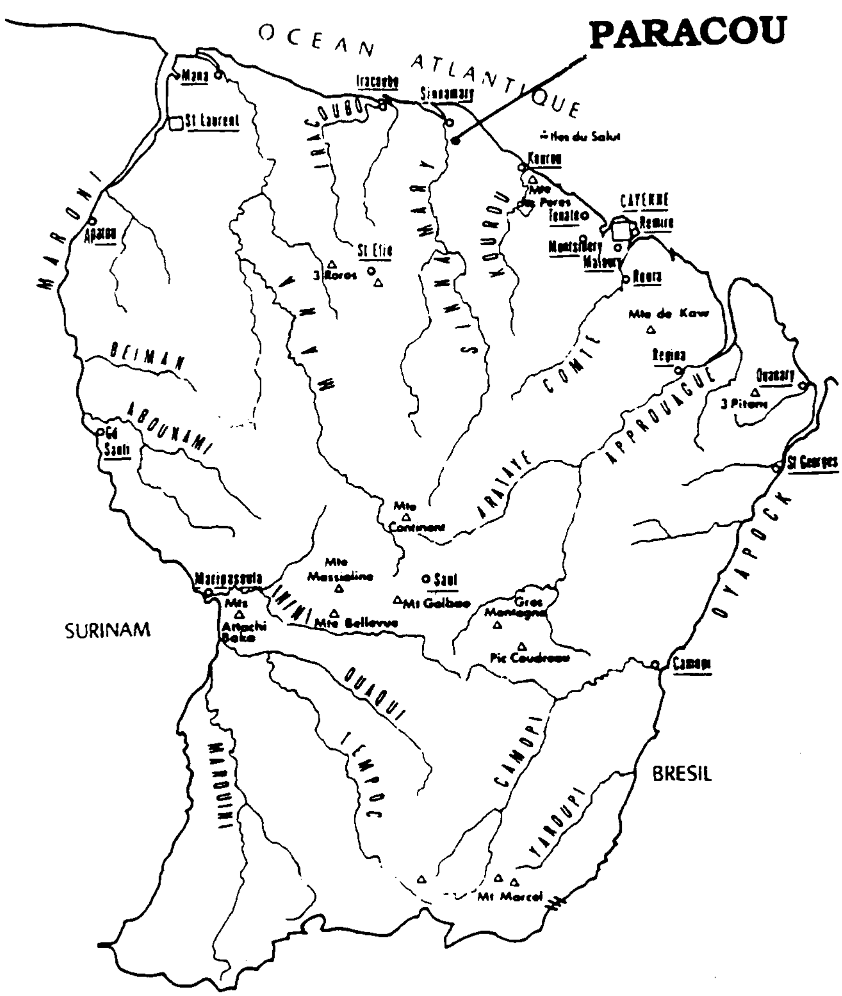


Figure 1. Localisation of the Paracou research site in the coastal tropical rainforest zone, French Guiana.

[26] for details of the inventory protocol and data base). The positions of the plots correspond to the origins of the community level transects on the 40 by 40 m square grid, thus the observations at these two levels were conducted in the same zones. All the saplings (n = 80 for each species) were more than 1.5 m in height and less than 5 cm DBH, the upper limit being determined by the difficulties in accurately measuring heights of more than 7 m, the maximum length of our calibrated telescopic pole. Height measurements were thus made to the centimetre for heights up to 7 m. Measurements of DBH for all the saplings and the diameter above and below scar for damaged saplings considered as damaged were made twice with a millimetric caliper, each diameter being the mean of two perpendicular diameters. All measurements were made once in March 1994 and were repeated in March 1966 in order to evaluate the diameter and height growth.

2.3. Species studied

Bocoa prouacensis Aubl. (Caesalpiniaceae) is a relatively common mid-canopy tree species which attains 30 m in height and is shade tolerant as an adult [4, 11]. Seed dispersal is endozoochorous (spider monkeys) and synzoochorous (bats, such as Artiibeus) [31].

Pradosia cochlearia (Lecomte) Pennington (Sapotaceae) is an emergent tree with an adult height of about 40–45 m. Its large typically sapotaceous berries are dispersed by monkeys [31]. Like Boco, the saplings of Kimboto are relatively shade tolerant [19] yet growth can be stimulated by increased light following forest canopy opening [25].

Goupia glabra Aubl. (Celastraceae) is a long-lived pioneer tree species [6] with very small fruits of about 1 cm and few seeds [2, 3, 13] present throughout the rain forest soil seed bank [21]. It is a light-demanding species

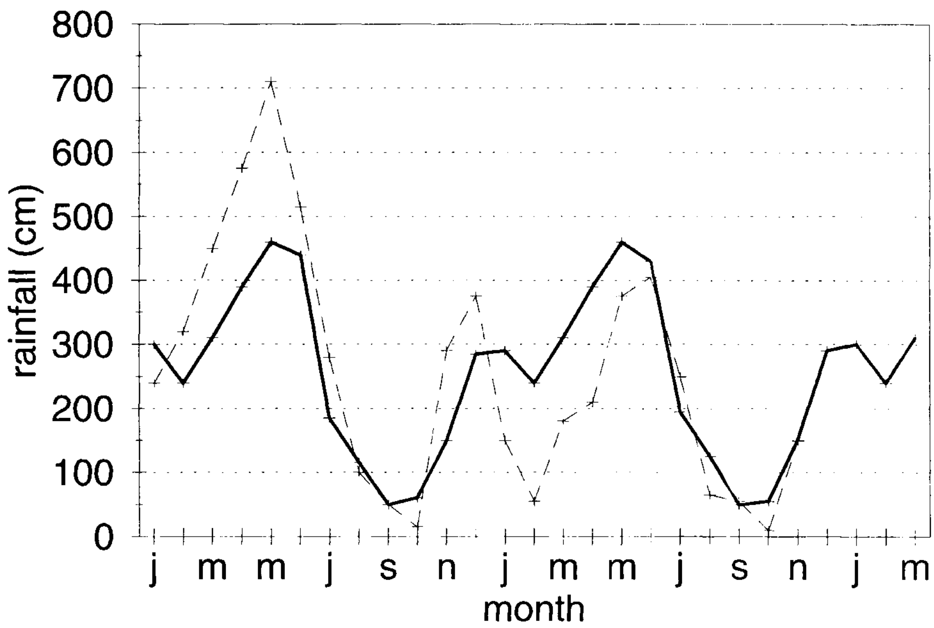


Figure 2. Monthly rainfall at the Paracou research site, French Guiana. The dashed line shows the rainfall observed during the period of the present study. The solid line represents the mean monthly rainfall for the last 10 years (CIRAD-Forêt à Kourou, unpublished data.)

from germination until death and grows rapidly [18]. It quickly colonises gaps and open sites [6], especially on disturbed soils [28] such as logging trails. For these reasons, *Goupia glabra* usually appears on favourable sites in dense groups of relatively numerous individuals among other pioneer species [17]. Mature trees are emergent, with a maximum height surpassing 40 m [12, 20] and a lifespan of more than 100 years.

Bocoa prouacensis, Pradosia cochlearia and *Goupia glabra* are among the 14 more common species (for all diameter classes) at Paracou in the control parcels [3, 10]. The number of *Goupia glabra* saplings increased steadily on treated parcels after logging and silvicultural interventions [3, 19] while *Bocoa prouacensis* remained unchanged or decreased [19, 25].

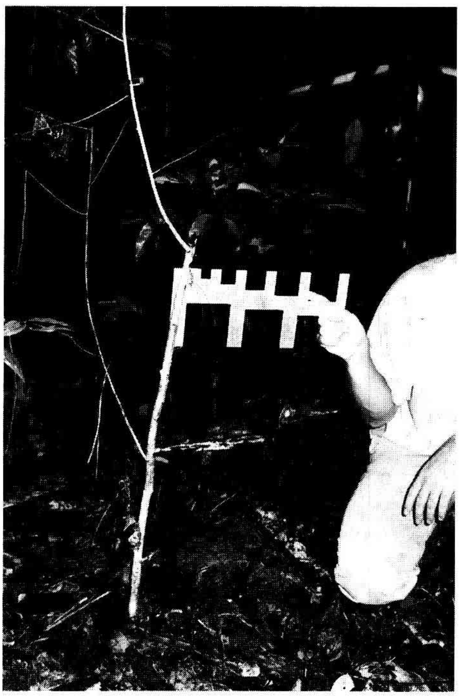


Figure 3. Measurements of diameter class on transects were made with a notched gauge, seen here pointing out a discontinuity on a broken and healed stem of *Goupia glabra*.

3. RESULTS

3.1. Frequency of damage in 1994

The overall frequency of damage observed on the transects, all species considered, is 40.6 % (n = 3 681). Damage frequency is essentially equal for the control and treatment level 1 (41.9 and 41.5 % for n = 968 and 1 421, respectively) and only slightly less for treatment level 2 (38.5 %, n = 1 292).

For saplings ≤ 4 cm DBH, damage frequency is 43.9 % (n = 852) on control plots in our study (*table I*) as compared to 19.5 % (n = 794) in Clark and Clark's study [9] limited to nine canopy tree species at the La Selva Biological Station, Costa Rica. The difference for saplings > 4–10 cm DBH on control plots is somewhat less, with a damage rate of 27.6 % (n = 116) in our study compared to 22.8 % (n = 281) in Clark and Clark's study [9]. These figures remain virtually identical whether using our 20 % discontinuity threshold or theirs at 25 %.

As already mentioned by these authors, frequency of damage and diameter class are not independent. At Paracou, we find that the ratio of broken to intact stems varies by more than chance among the four diameter classes under all conditions (*table I*: for df = 3, in the control, chi-square = 16.5, $P < 0.001$; in level 1, chi-square = 14.7, $P = 0.01$; in level 2, chi-square = 24.7, $P = 0.001$). In the control plots there is a greater occurrence of damage in the two lower size classes while damage is greatest for the intermediate sizes in the treatment plots (*table I*). For saplings < 2 cm DBH, the frequency of damage is significantly higher in the control over the treated plots (df = 2, chi-square = 12.3, $P < 0.001$). The least damage (14.9 %) is encountered for the largest saplings > 6–10 cm DBH in undisturbed forest. However, no significant differences exist between this and the frequencies observed in the first and second treatment levels for this size class (df = 2; chi-square = 5.8; $P > 0.05$), nor for any of the other size classes.

We also examined the initial overall frequency of stem damage for the three species chosen for the growth and survivorship studies. Differences in frequency of damage among species are highly significant (df = 2, chi-square = 17.3; $P < 0.001$) because frequency of damage is very high for *Bocoa prouacensis* (64 %; $n = 72$) and *Pradosia cochlearia* (59.5 %; $n = 78$) and nearly double that observed for *Goupia glabra* (34 %; $n = 85$).

3.2. Two year mortality rates

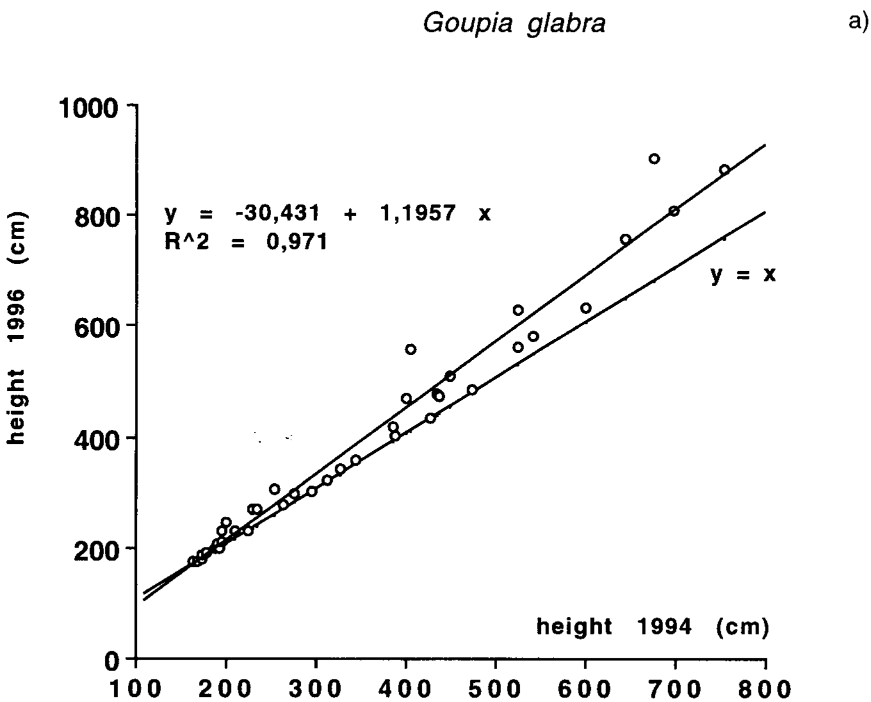
Mortality between 1994 and 1996 due to physical damage varied widely between the three species studied. Mortality was high for *Goupia glabra* (21 of 85 individuals) but less than half of this is apparently due to physical damage: nine saplings broken among the 21 which died over the period. Six of the seven *Pradosia cochlearia* that died (of 78 initially) had their stems broken. Only one *Bocoa prouacensis* of 72 tagged stems died and that individual had its stem broken in 1994, and thus does not figure in the following analysis.

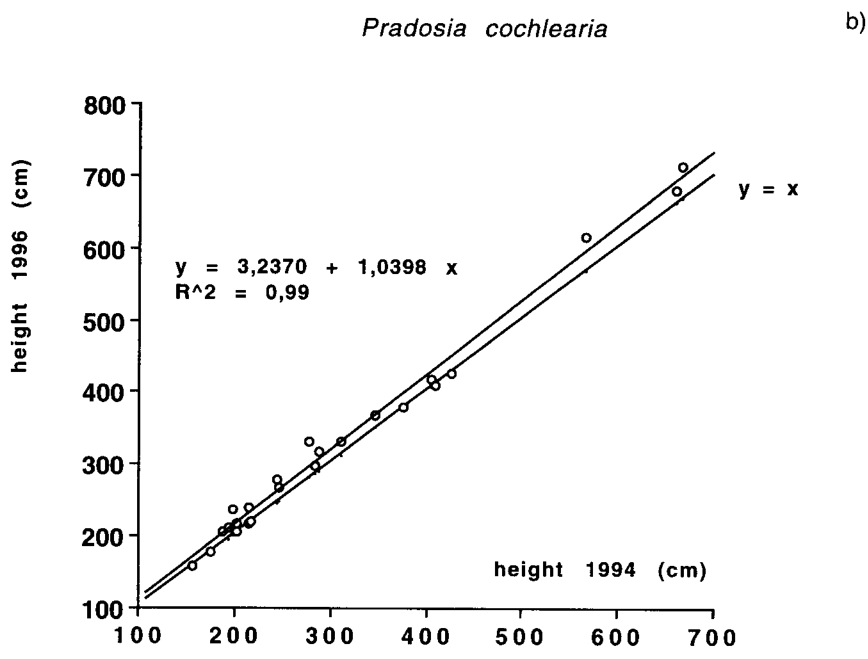
The comparison of heights and diameters in 1994 between stems dying during the subsequent 2 year period and those surviving (*table II*) shows certain significant differences by species, with those dying have smaller initial heights and diameters (for initial diameters: median 1-way analysis chi-square = 7.228; df = 1; $P < 0.01$ for *Goupia glabra*; analysis chi-square = 5.745; df = 1; $P < 0.05$ for *Pradosia cochlearia;* for initial height: median 1-way analysis chi-square = 4.789; df = 1; $P < 0.05$ for *Goupia glabra*; analysis chi-square = 3.873; df = 1; $P < 0.05$ for *Pradosia cochlearia*). The median value was used in this comparison, being more representative of location due to distribution skewness.

3.3. Rates of growth in height and diameter

Growth rate between March of 1994 and March 1996 were measured for the saplings that did not die, suffer disease and/or physical damage during the period, as far as we were able to discern. For this reason, the sample size for this part of the study was reduced as compared to the initial sample of tagged seedlings. True values of mean diameter growth are difficult to establish due to difficulty in accurately repeating measurements on an irregular stem where the site of measurement can not be permanently marked without risk of damage to the plant, and due to the great difference in overall diameter and actual diameter growth over the observation period (*table III*). Moreover, regarding stem shrinkage [16], for a short observation period such as 2 years, true gains may be masked if the second measure is made when the stem is significantly less hydrated or under greater hydric stress than at the first measure. In this study, this problem was minimised by taking the measurements during the same seasonal period.

Nevertheless, we can observe highly significant differences among species (*table III*) in diameter growth rates (Kruskall-Wallis test; df = 2; chi-square = 10.5; $P < 0.01$) and height growth rates (Kruskall-Wallis test; df = 2; chi-square = 11.9; $P < 0.01$) with *Goupia glabra* greatly outpacing *Pradosia cochlearia* for both parameters and *Pradosia cochlearia* outpacing *Bocoa prouacensis*.


Goupia glabra
a)
y = -30,431 + 1,1957 x
R^2 = 0,971
y = x
height 1996 (cm)
height 1994 (cm)
0
200
400
600
800
1000
100
200
300
400
500
600
700
800


Pradosia cochlearia
b)
y = 3,2370 + 1,0398 x
R^2 = 0,99
y = x
height 1996 (cm)
height 1994 (cm)
100
200
300
400
500
600
700
800
100
200
300
400
500
600
700

There is no significant difference between damaged and undamaged stems of the same species (*table IV*) in diameter growth (median 1-way analysis chi-square = 0.072; df = 1; P = 0.79 for *Goupia glabra;* chi-square = 0.282; df = 1; P = 0.59 for *Pradosia cochlearia*, chi-square = 1.38; df = 1; P = 0.24 for *Bocoa prouacensis*).

Spearmans correlation between height growth rate over 2 years and the initial 1994 DBH is high and significant for the undamaged *Goupia glabra* (*table V*). The same kind of correlation is observed between height growth rate and initial height (*table VI*). No correlation is observed between the variables mentioned above for *Bocoa prouacensis* (damaged or undamaged), the damaged *Goupia glabra* and the undamaged *Pradosia cochlearia*. There is a significant but not strong correlation between these variables for damaged *Pradosia cochlearia*.

Sapling height in 1994 can be partitioned into the following components:

height (1996) = height (1994) + height growth (1994–1996)

The comparison of a linear regression model between stem height in 1994 and

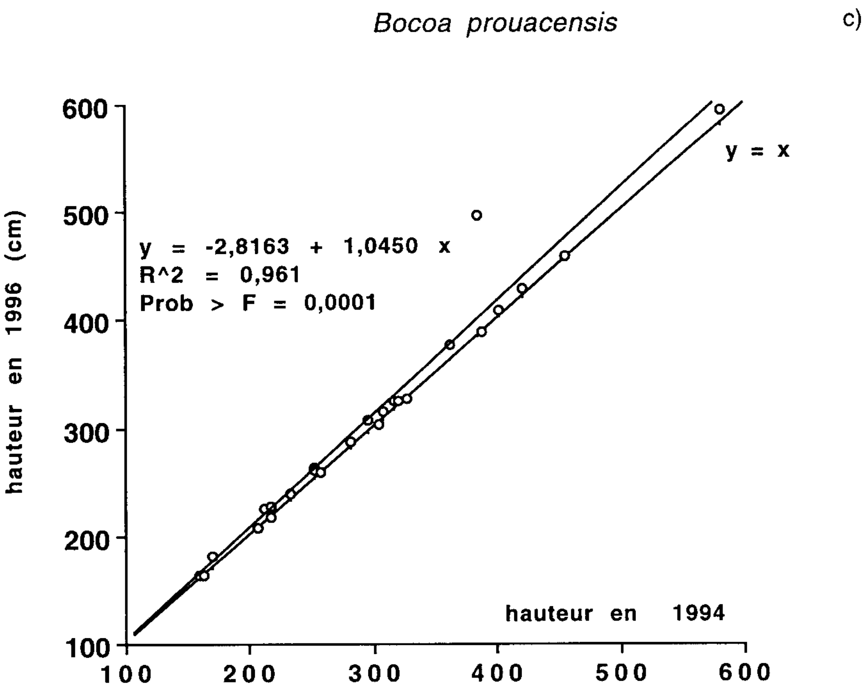


Figure 4. a) Comparison of the linear regression model height (1996) = a + b * height (1994) with the line y = x for undamaged *Goupia glabra* (n = 39) at the Paracou research site, French Guiana. b) Comparison of the linear regression model height (1996) = a + b * height (1994) with the line y = x for undamaged *Pradosia cochlearia* (n = 30) at the Paracou research site, French Guiana. c) Comparison of the linear regression model height (1996) = a + b * height (1994) with the line y = x for undamaged *Bocoa prouacensis* (n = 25) at the Paracou research site, French Guiana.

Table I. Frequency of damage for all saplings less than or equal to 10 cm DBH on transects as a function of diameter (cm) and treatment level at the Paracou research site, French Guiana.

	Diameter class (cm)								
	≤ 2		> 2–4		> 4–6		> 6–10		
Treatment level	% stems damaged	*N stems examined*	% stems damaged	*N stems examined*	% stems damaged	*N stems examined*	% stems damaged	*N stems examined*	*N total row*
Control	43.4	*650*	45.1	*202*	36.2	*69*	14.9	*47*	*968*
First level	38.7	*945*	49.8	*311*	46.8	*94*	33.8	*71*	*1 421*
Second level	34.7	*857*	50.5	*309*	37.2	*78*	33.3	*48*	*1 292*
Mean damaged, *N* total examined	38.5	*2 452*	48.9	*822*	40.6	*241*	28.3	*166*	

Table II. Comparison of the 1994 median height and diameter values for the stems that died between 1994 and 1996 with the 1994 median height and diameter of the viable stems.

	Median			
	Dead stems		Viable stems	
	DBH (cm)	Height (cm)	DBH (cm)	Height (cm)
Goupia glabra	0.65	219	1.00	290
	$n = 21$		$n = 64$	
Pradosia cochlearia	0.45	170	1.25	252
	$n = 7$		$n = 71$	

stem height in 1996 for undamaged stems with the line y = x is one way to evaluate the relationship between initial height and subsequent height growth (*figure 4a–b–c*). For *Goupia glabra*, the regression coefficient is significantly > 1 (comparison of the regression coefficient value to 1; one-tailed test: n = 39; df = 37; a = 0.025; t = 5.793; P < 0.001). Difference is not significant for the *Bocoa prouacensis* (n = 25; df = 23; t = 1.027) nor for *Pradosia cochlearia* (n = 30; df = 28; t = 1.892). Thus for a species such as *Goupia glabra,* stem breakage acts to reduce subsequent growth as well as current height, among other effects. This alters the saplings immediate and future social status in the stand and its ability to compete.

4. DISCUSSION

The frequencies of damage observed are relatively high, due in part to the decision criterion we used. Our method considers as damaged stems that have been broken a long time ago. Such stem traumas have partially healed with time and may not be taken into account with a more conservative criterion [9]. This way of tackling physical damage leads us to consider this phenomena not just simply as frequency at a given time, but also as a function of time spent in the understory. It reveals both the importance and the effect of physical damage in the history of a young tree.

The low rate of damage in the higher diameter classes is consistent with the greater mechanical resistance of larger stems and the fact that they occupy progressively higher levels within the forest and are thus subject to less material falling from overhead.

The importance of canopy overhead concurs with the results from the transects: saplings < 2 cm DBH are more damaged on the control parcel because this kind of stem is very fragile and exposed to falling debris. Furthermore, on treated parcels, the increase in light reaching the soil leads to a very important recruitment of pioneer species. Such stems grew fast in open sites with concomitantly fewer limbfalls. Both characteristics are presented by Clark and Clark [9] and Aide [1] as the best way for avoiding physical damage by limbfalls. Thus the competitive sorting processes potentially at work on saplings (damage, disease, competition for light and nutrients) intervene in a different sequence and certainly with different degrees of influence in native versus disturbed tropical rain forest.

The higher mortality of the smaller stems may lead us to underestimate the importance of physical damage in primary forest for the first diameter class. This would explain why the second DBH class presents higher frequencies of damage in each treatment. The other explanation for the higher frequencies in this diameter class is the fact that these saplings are older. If we consider physical damage as a function of time spent in the understory [1], they must be more broken than the younger ones.

Frequency of damage of the 6–10 cm DBH class is less in the control. This can probably be explained by the greater resistance of these individuals in the control parcels as compared to the treated parcels in the early years after logging, where slower growth rates characteristic of a lower light environment favour the formation of denser woody structures and thus greater resistance to breakage.

Table III. Mean values of growth rate in diameter (mm) and height (cm) between March 1994 and March 1996, for intact saplings of three tree species in tropical rain forest at the Paracou research site, French Guiana.

		Mean ± standard deviation	
	n	Diameter growth (mm)	Height growth (cm)
Goupia glabra	60	0.12 ± 0.21	39.0 ± 50.70
Pradosia cochlearia	56	0.07 ± 0.16	21.6 ± 30.16
Bocoa prouacensis	63	0.03 ± 0.08	13.5 ± 18.43

Table IV. Median growth rates for diameter (mm) and height (cm) of three tree species as a function of physical damage occurrence on stems in 1994, in a tropical rain forest at the Paracou research site, French Guiana.

	Median			
	Undamaged stems		Damaged stems	
	Diameter (mm) growth	Height (cm) growth	Diameter (mm) growth	Height (cm) growth
Goupia glabra	0.08	19	0.1	25
	n = 39		*n* = 21	
Pradosia cochlearia	0.04	13.5	0.05	9
	n = 26		*n* = 30	
Bocoa prouacensis	0	7	0.1	9
	n = 25		*n* = 38	

The differences in damage frequency between pioneer species, such as *Goupia glabra*, and shade tolerant ones can thus also be due to differences in the micro-habitat and height growth rate [1]. Frequency of damage is less for pioneer species such as *Cecropia* spp. or *Simaropuba amara* Aubl. [9]. Overall, *Goupia glabra* was found here to grow much faster than *Pradosia cochlearia* and *Bocoa prouacensis*. Moreover, it is well known that this species reiterates easily after physical trauma [20]. Thus we can assert that a *Bocoa prouacensis* and a *Goupia glabra* with the same height do not share the same age nor the same history.

Our results on stem breakage as a factor contributing to mortality of saplings are not unanimous regarding species. *Bocoa prouacensis* has the highest rate of breakage among the three species studied here but only one individual died between 1994 and 1996, showing that this species has an important capacity to survive after breakage. Frequency of damage for *Pradosia cochlearia* is nearly the same as for *Bocoa prouacensis* but its influence on mortality seems to be important regarding the percentage of broken

Table V. Spearman's correlation between DBH growth rate (1994–1996) and initial sapling DBH (1994) in a tropical rain forest at the Paracou research site, French Guiana. *P* values refer to the significance of the correlation ($\alpha = 0.05$).

	Undamaged	Damaged
Goupia glabra	0.855 *P = 0.0001*	0.318 *P = 0.1602*
Pradosia cochlearia	0.109 *P = 0.595*	0.489 *P = 0.0071*
Bocoa prouacensis	0.144 *P = 0.2460*	0.0724 *P = 0.6657*

Table VI. Spearman's correlation between height growth rate (1994–1996) and initial sapling height (1994) in a tropical rain forest at the Paracou research site, French Guiana. *P* values refer to the significance of the correlation ($\alpha = 0.05$).

	Undamaged		Damaged	
Goupia glabra	0.842	*P = 0.0001*	0.288	*P = 0. 2051*
Pradosia cochlearia	0.205	*P = 0.3152*	0.472	*P = 0.0097*
Bocoa prouacensis	0.209	*P = 0.3149*	–0.022	*P = 8938*

stems (86 %) among the dead ones. In the case of *Goupia glabra*, while fewer stems were broken and a greater percentage died over the 2 year observation period, overall mortality from all causes was also high, giving the impression of a less resistant and less vigorous species.

The differences in ecological temperament described in the methods can be illustrated in the specific case of stem breakage. *Goupia glabra* is a pioneer species whose waiting stage is the seed, while *Bocoa prouacensis* and *Pradosia cochlearia* are primary forest species and their waiting stage is the seedling or young plant. *Goupia glabra* and *Bocoa prouacensis* are not affected by physical damage in their mortality and growth while *Pradosia cochlearia* seems to be affected directly in its survival but not in its growth. Except for the *Pradosia cochlearia*, these results do not imply a direct effect of physical damage on competition between individuals of the same or different species. Of course, the breaking of a stem is effectively a height reduction and implies more time before the individual will reach the canopy stratum, especially for a slow-growing species, but in what way does it affect competition and its outcome?

Observations on *Goupia glabra* showed the importance of initial height for mortality and growth rate in our sample. This is due to this species' heliophile temperament: its main stem grows very fast because, in a competitive environment, vertical growth is the only way to satisfy its needs in light energy. For this reason, competition within and between it and other species is very important [2, 22]. Lacoste [17] showed that selective logging in favour of *Goupia glabra* seedlings and saplings significantly lowers mortality and stimulates growth. He underlines the importance of initial social status, determined by its height, of individuals for this species. Physical damage acts by modifying this social status of the individual. When a stem is damaged, the reduction in height entails a change in microhabitat: the undamaged stems dominate the broken one which receives less light and so grows less rapidly. This domination increases with time and the damaged stem declines and ultimately dies. This scenario is valid only in the case of growth under direct competition in groups on a small area. We observed damaged *Goupia glabra* which had a high growth rate due to the open unencumbered nature of the site. According to Brokaw [5], on the basis of numerous experimental studies " (...) canopy opening occasions accelerate seedling and sapling growth in perhaps all middle- and upper-story tree species". *Bocoa prouacensis*, because it is adapted to shade conditions, is able to persist in low light environments and still react to the arrival of better light conditions as shown by its low mortality rates. For this species, competition for height growth is not vital during the sapling stage and physical damage, even if it implies more time species in the understory, has no effect on sapling survival. *Pradosia cochlearia* is an opportunist like *Bocoa prouacensis* and a sapling exposed to good light conditions will surely grow better than another in shade conditions, even if it has been broken before; however *Pradosia* seems to be sensitive to the trauma caused by physical damage.

5. CONCLUSION

This study shows in what way physical damage can interfere at the specific level, in regeneration and plant competition dynamics. It reveals how ecological temperaments will determine a reaction, significant or not, in the face of this phenomenon. It also reveals growth mechanisms that permit the characterisation of behaviours in a stage of tropical tree species dynamics that has rarely been studied in situ and using a demographic protocol with tagged individuals, by establishing the relationship between height or diameter growth rate and the social status of a sapling as expressed by its initial height. This should help us in the definition of functional groups [11] for juvenile stages of tree growth.

ACKNOWLEDGEMENTS

We would like to thank P.-M. Forget and M.-F. Prevost plus the anonymous reviewers for their helpful comments and criticisms concerning this manuscript. We would also like to thank P. Imbert, D. Duchant and A. Patient of the Inra Station de recherches forestières in French Guiana for their help with the data collection in the field.

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