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Stand dynamics and basal area change in a tropical dry forest reserve in Nicaragua

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Abstract

Stand dynamics and basal area change were determined in deciduous and gallery forest types at the Chacocente Wildlife Reserve, Nicaragua. All stems ≥10 cm dbh in 4 ha were tagged and identified by species and measured in 1993 and 2000. In year 2000 totally 519 stems ha^{-1} with a basal area of 15.62 m^2 ha^{-1} were recorded in the deciduous forest type and corresponding figures were 308 stems ha^{-1} and 23.13 m^2 ha^{-1} for the gallery forest type. Comparison of stem diameter and basal area distribution during this study period revealed no changes. Both forests types had a reversed J-shape diameter distribution dominated (>80%) by small stems (<30 cm dbh). In the deciduous forest small stems contributed to more than half of the basal area, whereas in the gallery forest large stems (>70 cm dbh) contributed to almost half the basal area. Based on a logarithmic model the mortality and recruitment rates were calculated at 4.5 and 2.5% $year^{-1}$, respectively, in the deciduous forest type and 4.2 and 4.0% in the gallery forest type. The decrease in stand density in the deciduous forest type was significant whereas it was not the case for the gallery forest type. There was also a significant decrease in basal area of 1.2% $year^{-1}$ in the deciduous forest and no change in the gallery forest. The recorded median diameter (dbh) increment was 0.14 cm $year^{-1}$ with a range of 1.21 cm $year^{-1}$ in the deciduous forest type and corresponding figures for the gallery forest were 0.24 cm $year^{-1}$ and 0.71 cm $year^{-1}$. Three of the five most common species in the deciduous forest, *Lonchocarpus minimiflorus*, *Gyrocarpus americanus* and *Stemmadenia ovovata* had mortality rates above 9%. Although *L. minimiflorus* and *S. ovovata* had recruitment rates above average the net balance was negative. Among the five most common species only *Tabebuia ochracea* a timber species had an annual recruitment higher than its mortality rate. Non-timber species as a group had the largest calculated negative balance between mortality and recruitment as well as between loss and gain of basal area indicating a possible anthropogenic influence. In the gallery forest *Capparis pachaca* was the only species, out of the most common, with a positive annual balance. In both forest types there was a higher than average calculated recruitment and basal area growth for species with no local use.

Keywords: Chacocente Wildlife Reserve; Dry deciduous forest; Gallery forest; Mortality; Recruitment; Gain; Loss; Ingrowth; Diameter increment

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1. Introduction

Central America has approximately 3.4 million ha of tropical dry forest (Sabogal, 1992) mainly along the Pacific coast and it has been reduced to less than 0.1% of its original extent and it is considered the most endangered ecosystems in the tropics (Janzen, 1988; Gillespie, 1999). The main reason for this deforestation is the conversion of forests to agricultural land. Degradation in existing unprotected forest is caused by accidental and intentional fires, wood collection, grazing by livestock and selective logging of valuables species (Gerhardt and Hytteborn, 1992; Murphy and Lugo, 1995).

Out of the 0.1 million ha of dry forest in Nicaragua about 60% was declared conservation area (Alves-Milho, 1996) and the remaining dry forest was managed for production of timber and woodfuel. Given the high population density of more than 100 inhabitants km^{-2} in the Pacific Region the demand for woodfuel from the dry forest is high (Roldan, 2001). Historically Nicaraguan dry forests have provided timber like *Swietenia humilis*, *Cederia odorata*, *Bombacopsis quinatum*, *Dalbergia retusa* and *Guaiacum sanctum* for the domestic market and for export (Sabogal, 1992). The selective logging was made without consideration of the species-specific regeneration requirements and the long-term consequences on the species composition. At present there is a limited experience in sustainable dry forest management, which has mainly been carried out in development projects in the 1990s (Anon., 2002). Management plans in these areas were based on a polycyclic silvicultural system in which each logging operation was limited to certain species or species groups (Lamprecht, 1990; Alves-Milho, 1996).

In general, information about the dry forest dynamics and growth of economically valuable species, or the entire tree population, was lacking or inferred from a single survey based on size-class description of the population structure. Studies on changes of stocking, basal area distribution and growth over a longer time period is necessary to provide the manager with knowledge about the magnitude of change in population size, i.e., in mortality and recruitment rates, growth and yield (Díaz et al., 2000).

To develop sound management systems for harvesting and/or conservation of forest resources, it is fundamental to understand the dynamics of the forest (Sokpon and Biaou, 2002; Obiri et al., 2002). As the forest ecosystem is not stable in time in terms of size and structure, long-term observations are one of the best ways to provide new insights (Takahashi et al., 2003). The measurement of recruitment, mortality and growth rates provides useful information to analyze factors affecting population dynamics. Studies on population dynamics and growth have been carried out in permanent sample plots of different size according to type of forest (Manokaran and Kochummen, 1987; Finegan and Camacho, 1999; Gray, 2003).

Research on tropical dry forest has been performed in Mexico and Costa Rica providing information on species ecology of the same tree species that grow in the Nicaraguan dry forest (Rico-Gray et al., 1988; Janzen, 1988; Gerhardt, 1996; Mizrahi-Perkulis et al., 1997). However, there are only few studies available on the country's dry forest resources and little information on species ecology, biology, silviculture and utilization. A few floristic surveys have been carried out, mainly for conservation purposes (Sabogal and Valerio, 1995; Gillespie et al., 2000).

The objective of this study was to assess the forest dynamics and growth parameters in the Chacocente Wildlife Reserve. These parameters were analyzed per deciduous and gallery forest types, at species level as well as for aggregation of species into use groups. Changes in use groups were considered as a proxy for the anthropogenic influence.

2. Methods

2.1. Study area

This study was carried out in the Chacocente Wildlife Reserve (11°36N–11°30N and 86°08′–86°15W) located on the Pacific Coast, in the department of Carazo. In the period 1981 to 2001, the annual precipitation and temperature was 1431 ± 369 mm and 26.6 ± 0.34 °C, respectively. The dry period spans over 5 months, from December to April, and the altitude varies from sea level to ca. 300 m.a.s.l. (Sabogal, 1992). The total area of the wildlife reserve was ca. 4650 ha of which two-third were dry deciduous forests types and one-tenth was gallery forest type. The remaining area was scrubs, pasture and agriculture land (Anon., 2002). According to Sabogal (1992), the Chacocente Wildlife Reserve constituted one of the backbones of the dry forest along the Central American Pacific coast.

Soils in the deciduous dry forest type were classified as Vertic and Ferric Luvisol (FAO-system) (Sabogal and Valerio, 1998). One of the two plots was located on a slightly ondulating terrain with deep soil whereas the other plot was located on a hilly terrain with shallow soil. Based on at least one stem with a diameter $\geq$10 cm dbh (diameter breast height) the number of trees were 432 and 534 ha^{-1} and the basal areas were 15.4 and 21.5 m^2 ha^{-1} in 1993 at two 1 ha plots. Tree crown heights varied between 5 and 20 m and the most common species were *Gyrocarpus americanus*, *Tabebuia ochraceae* ssp. *neochrysantha* and *Lysiloma* sp. (Sabogal, 1992).

The gallery forest type is located along semi-permanent watercourses and is distinguished from the deciduous forest by a species composition dominated by evergreen or semi-deciduous trees, whereas the deciduous forest type is dominated by totally deciduous species (Tercero and Urrutia, 1994). Soils were classified as Eutric fluvisol (FAO) and at two 1 ha plots there were 328 trees ha^{-1} with a basal area of 27 m^2 ha^{-1} with crown heights varying between 5 and 30 m in an inventory made 1993 (Sabogal and Valerio, 1998). The most abundant species were *Trichilia martiana* (13%), *Thounidium decandrum* (11%) and *Capparis pachaca* (9%).

2.2. Data collection

In 1993 girths of all trees with a least one stem $\geq$10 cm dbh were measured, identified by species and tagged on four permanent sample plots (PSP), two in the dry deciduous forest and two in the gallery forest. Each plot was one ha in size and subdivided in 25 squares of 20 m $\times$ 20 m. Girths were measured with a tape and the point of measurement was marked on each tree with paint, as was the code identifying each individual. In year 2000, the girth of all tagged stems were re-measured and all newly recruited stems $\geq$10 cm dbh were measured and identified by species. A detailed description of data collection can be found in Sabogal and Valerio (1995, 1998).

2.3. Data analysis

Stand structure in terms of number of trees per hectare (N ha^{-1}) and basal area (m^2 ha^{-1}) and their distribution in 10-cm diameter classes were presented for year 1993 and 2000 for the deciduous forest and the gallery forest. Average annual changes in the 7-year time period were estimated by demographic parameters, i.e., mortality and recruitment and the growth parameters, loss in basal area, ingrowth and gain in basal area. The annual rates of mortality (m), recruitment (r), loss (l), gain (g) and ingrowth (i) were estimated using a logarithmic model (Lieberman and Lieberman, 1987; Sheil et al., 1995; Hoshino et al., 2002) as follows:

$$m = \frac{\ln N_{93} - \ln N_s}{T}$$

$$r = \frac{\ln N_{00} - \ln N_s}{T}$$

where N_{93} is the number of live stems in 1993, N_s the number the live stems in 2000 (N_{93}: number of dead stems), $N_{00} = N_s$ + number of recruited stems and T the time interval.

$$l = \frac{\ln \mathrm{BA}_{93} - \ln \mathrm{BA}_{s93}}{T}$$

$$g = \frac{\ln \mathrm{BA}_{00} - \ln \mathrm{BA}_{s93}}{T}$$

$$i = \frac{\ln \mathrm{Ba}_{s00} - \ln \mathrm{BA}_{s93}}{T}$$

where BA_{93} is the basal area of live stems in 1993, BA_{s93} the basal area in 1993 of live stems in 2000, BA_{s00} the basal area in 2000 of live stems in 2000 and $\mathrm{BA}_{00} = \mathrm{BA}_{s00}$ + BA of recruitment stems in 2000. The diameter annual increment (dai) was estimated from the following equations (Valerio, 1997):

$$\mathrm{dai} = \frac{\mathrm{dbh}_{00} - \mathrm{dbh}_{93}}{T}$$

where dbh_{93} is the diameter at breast height in year 1993 and dbh_{00} is the diameter at breast height of the same tree in year 2000. When the annual diameter increment data show asymmetrical distribution, it is recommended to use the median to estimate the annual increment of the period (Lieberman and Lieberman, 1987; Silva et al., 1995; Finegan and Camacho, 1999 and Venegas and Camacho, 2001).

Medians were calculated for species with at least 27 observations. In the calculations of diameter increments extreme outliers defined by deviating >50 mm above or below the mean (dbh_{93}, dbh_{00}) were deleted. A comparison of stem density and basal area during the study period for each of the two forest types was made with a Student's *t*-test using 25 subplots of 400 m^2 (20 m × 20 m) per 1 ha plot, in total fifty 400 m^2 per forest type. All species were classified into four groups according to their main use given by the settlers around the forest (Morales and Rueda, 1989; Sabogal, 1992; Carrillo, 1993) as,

(1) TW (timber): species used mainly for rural construction, furniture and sawn wood;
(2) FW (firewood): species used mainly for firewood;
(3) NT (non timber forest products): species used mainly for other uses different from timber and firewood (medicine, tannin);
(4) UN (use not known locally): species not used by the local population. For the most common species the stocking (stems ha^{-1}) and basal area ($m^2\ ha^{-1}$) were computed for 1993 and 2000 for the deciduous and the gallery forest.

3. Results

3.1. Dry deciduous forest

3.1.1. Dynamics

3.1.1.1. Stand dynamics and diameter distribution. In total 899 stems were recorded in year 2000 at 2 ha, which was 13% less than in 1993 and this corresponds to an annual loss of 11.5 trees per hectare. The decrease in stand density was significant ($t = 4.75$, d.f. = 49, $p = 0.00$). The negative balance was due to 282 dead or missing stems and 144 newly recruited stems corresponding to a mortality and recruitment rate of 4.5 and 2.5% $year^{-1}$, respectively, yielding a net annual decrease of 2%. Both in year 1993 and 2000, the diameter distribution showed a reversed-J shape curve and 88% of the stems had less than 30 cm dbh (Fig. 1). There was a transition of stems between the 10-cm diameter classes. On average one-tenth of the stems shifted but no large (≥50 cm) stems were involved. No clear pattern could be found in mortality linked to diameter classes and the variation was large among the four largest classes (Fig. 2; Table 1).

3.1.1.2. Dynamics of the most common species and use groups. Three of the five most common species *Lonchocarpus minimiflorus*, *G. americanus* and *Stemmadenia ovovata* had mortality rates above 9% $year^{-1}$, i.e. more than twice the overall average (Table 2). Two of these species, *L. minimiflorus* and *S. ovovata,* also had high recruitment rates, 5.4 and 7.2% $year^{-1}$, respectively, equivalent to ca. twice and three-fold all species included. Among the five most common species only *T. ochracea* had an annual recruitment higher than its mortality rate (Table 2). Among the four use groups the NT had the highest mortality rate with 7.2% $year^{-1}$ and a low recruitment rate of 2.3% $year^{-1}$ resulting in the largest decrease in stocking with 4.9% $year^{-1}$ (Table 3). Recruitment rates for species belonging to the FW and the UN use groups were higher than average by about 50% (3.7% $year^{-1}$) and more than twice (5.4% $year^{-1}$), respectively (Table 3). The UN group had the largest increase in stem density among the four use groups with 2.1 (5.4–3.3)% $year^{-1}$.

Table 1
Changes in basal area

Forest type	Basal area					
	$m^2\ ha^{-1}$			% $year^{-1}$		
	Loss mortality	Gain		Loss mortality	Gain	
		Recruitment	Growth		Recruitment	Growth
Deciduous	4.32	0.80	2.15	4.2	0.8	2.2
Gallery	3.97	0.98	3.45	2.7	0.6	2.4

Changes in basal area ($m^2\ ha^{-1}$ and % $year^{-1}$) from 1993 to 2000 of stems ≥10 cm dbh a dry forest reserve in Nicaragua.

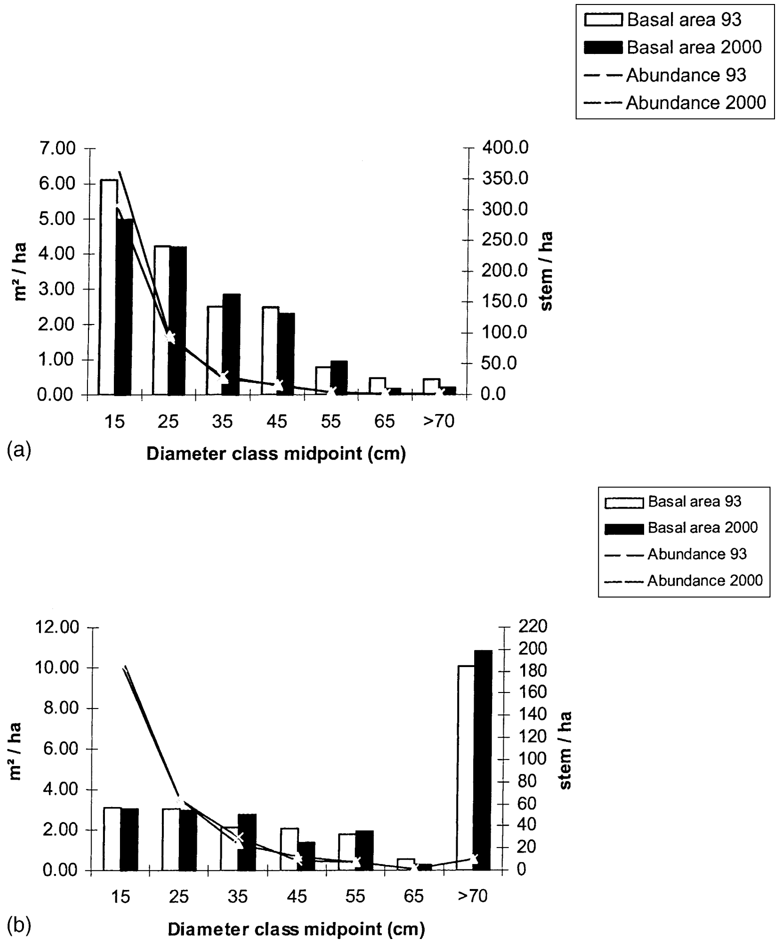

Fig. 1. Diameter distribution and basal area per diameter classes (10 cm) 1993 and 2000 of stems ≥10 cm dbh in a dry forest reserve in Nicaragua, (a) deciduous forest (b) gallery forest.

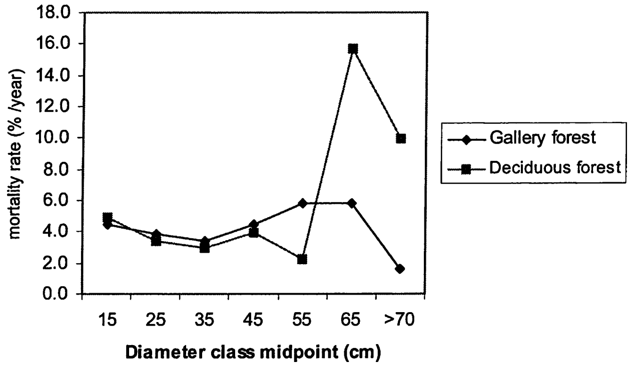

Fig. 2. Annual mortality (% year^{-1}) from 1993 to 2000 of stems ≥10 cm dbh per diameter class (10 cm) in a deciduous and gallery forest in a dry forest reserve in Nicaragua.

Table 2
Annual mortality and recruitment

Forest type and species	Use Group	Mortality (% $year^{-1}$)	Recruitment (% $year^{-1}$)
Deciduous			
Caesalpina exostema	TW	6.0	2.4
Gyroscarpus americanus	NT	9.3	1.7
Lonchocarpus minimiflorus	TW	9.9	5.4
Stemmadenia ovovata	NT	9.5	7.2
Tabebuia ochracea	TW	1.9	2.9
Gallery			
Capparis pachaca	UN	2.1	8.1
Guarea glabra	TW	2.3	1.6
Stemmadenia ovovata	NT	4.4	3.8
Thichilia hirta	UN	3.7	3.2
Thounidium decandrum	FW	4.8	4.4

Annual mortality (%) and recruitment (%) from 1993 to 2000 of stems≥10 cm dbh for the five most common tree species per deciduous and gallery forest in a dry forest reserve in Nicaragua.

3.1.2. Growth

3.1.2.1. Basal area growth and distribution. In year 2000 a basal area of 15.62 m^2 ha^{-1} was recorded which was 1.38 m^2 ha^{-1} less than in 1993 (Appendix A). The change in basal area was significant ($t = 2.34$, d.f. = 49, $p = 0.023$). The loss of 4.32 m^2 ha^{-1} due to mortality was larger than the gain of 0.80 m^2 ha^{-1} due to recruitment of new stems and the gain of 2.15 m^2 ha^{-1} due to growth of stems present since 1993 (Table 1). On a percentage basis the balance between the loss of 4.2% $year^{-1}$ and the gain of 3.0% $year^{-1}$ was a decrease with 1.2% $year^{-1}$.

Distribution of basal area in 10 cm-diameter classes had a similar structure on both occasions (Fig. 1). The two smallest size classes (midpoint 15 and 25) contributed to more than half, whereas the largest size classes (>50 cm) contained less than one-tenth of the total basal area.

3.1.2.2. Basal area growth per use group. The largest loss of basal area was found in the NT use group with 6.4% $year^{-1}$ and smallest in the FW use group with 2.6% $year^{-1}$ (Table 3). These percentages were ca. 50% above and below, respectively the overall average. The FW and UN use groups had the highest basal area gain 5.3 and 4.8% $year^{-1}$, respectively, both due to high growth of the live stems, 3.1 and 2.2% $year^{-1}$ and high rates of recruited stems 2.2 and 2.6% $year^{-1}$, respectively. FW had the largest increase in basal area with 2.7% $year^{-1}$ whereas the NT had the largest decreased by 3.8% $year^{-1}$.

3.1.2.3. Median diameter increment. The Kolmoroz–Smirmov test showed that the annual stem diameter increment did not have a normal distribution ($Z = 1.857$, $N = 361$, $p = 0.02$) and therefore the median was applied which was calculated at 0.14 cm $year^{-1}$ with a range of 1.21 cm $year^{-1}$. The largest increment (0.21 cm $year^{-1}$) was in the diameter class 20–29 and the smallest increments (0.06 and 0.07 cm $year^{-1}$) were found in the two largest diameter classes (30–39 and 40–49) (Table 4).

Among the seven most abundant species *Caesalpinia exostema* and *G. americanus* had the highest

Table 3
Stand dynamics and basal area increment

Forest type	Dynamics (1% stems $year^{-1}$)			Basal area (% of m^2 $year^{-1}$)		
	Use group	Mortality	Recruitment	Loss Mortality	Gain	
					Recruitment	Growth
Deciduous	TW	3.8	2.2	3.3	0.6	2.3
	FW	3.4	3.7	2.6	2.2	3.1
	NT	7.2	2.3	6.4	0.6	2.0
	UN	3.3	5.4	4.7	2.6	2.2
Gallery	TW	3.0	2.3	2.1	0.2	2.2
	FW	4.9	4.0	5.3	1.5	3.2
	NT	7.4	6.2	5.5	1.9	3.6
	UN	3.2	6.1	3.5	1.9	3.1

Stand dynamics (% stems $year^{-1}$) and basal area increment (% of m^2 $year^{-1}$) from 1993 to 2000 of stems ≥10 cm dbh in a dry forest reserve in Nicaragua per forest type and use groups TW (timber), FW (firewood), NT (non-timber forest products), UN (use not known locally).

Table 4
Median annual diameter increment for deciduous and gallery forest

Diameter class	Deciduous		Gallery	
	Median (cm $year^{-1}$)	Range (cm $year^{-1}$)	Median (cm $year^{-1}$)	Range (cm $year^{-1}$)
10–19	0.13	1.21	0.23	0.76
20–29	0.21	0.94	0.23	1.17
30–39	0.06	0.89	0.29	0.71
40–49	0.07	0.64	0.31	0.59

Median annual diameter increment from 1993 to 2000 of stems ≥10 cm dbh per diameter class (10 cm) for deciduous and gallery forest in a dry forest reserve in Nicaragua.

median increments (0.26 and 0.24 cm $year^{-1}$) with about twice the average all species included and *T. ochraceae* and *L. minimiflorus* had the lowest (0.04 and 0.04 cm $year^{-1}$) (Table 5). Among the four use groups, FW and NT had the largest annual increments with 0.20 and 0.17 cm $year^{-1}$, respectively (Table 6).

3.2. Gallery forest

3.2.1. Dynamics

3.2.1.1. Stand dynamics and diameter distribution. In total 616 stems were recorded in year 2000 at 2 ha which was 1% less than in 1993 (Appendix B). The change in stand density was not significant ($t = 0.290$,

Table 5
Median annual diameter increment for the most common species per forest type

Forest type and species	Use group	Diameter class (cm)					
		10–19	20–29	30–39	40–49	50–59	Total
Deciduous							
Achatocarpus nigricans	TW	0.07	0.07	–	–	–	0.07
		(37)	(11)				(48)
Caesalpinia exostema	TW	0.29	0.21	–	–	–	0.26
		(32)	(16)				(48)
Gyrocarpus americanus	NT	0.30	0.30	0.01	–0.09	–	0.24
		(33)	(20)	(8)	(3)		(64)
Lonchocarpus minimiflorus	TW	0.04	0.03	–	–	–	0.04
		(53)	(1)				(54)
Myrospermun frutescens	TW	0.13	0.23	0.10	–	–	0.14
		(35)	(11)	(1)			(47)
Tabebuia ochraceae	TW	0.06	0.03	0.00	–0.01	–	0.04
		(50)	(10)	(4)	(1)		(65)
Stemmadenis ovovata	NT	0.13	0.01	–	–	–	0.13
		(42)	(5)				(47)
Gallery							
Capparis pachaca	UN	0.29	0.24	–	–	–	0.28
		(44)	(2)				(46)
Guarea glabra	TW	0.26	0.21	0.36	–	–	0.24
		(18)	(8)	(1)			(27)
Stemmadenia ovovata	NT	0.15	0.29	–	–	–	0.16
		(30)	(1)				(31)
Thounidium decandrum	FW	0.40	0.15	0.26	0.23	–	0.27
		(25)	(8)	(3)	(1)		(37)
Trichilia hirta	UN	0.19	0.16	0.02	0.47	0.29	0.16
		(20)	(10)	(2)	(1)	(1)	(34)

Median annual diameter increment (cm $year^{-1}$) from 1993 to 2000 per diameter class (10 cm) for the most common species per forest type in a dry forest reserve in Nicaragua. Figures in brackets are the number of increments used in the calculation. Blank entries: no data.

Table 6
Median and range of annual diameter increment

Use group	Forest type			
	Deciduous		Gallery	
	Median (cm $year^{-1}$)	Range (cm $year^{-1}$)	Median (cm $year^{-1}$)	Range (cm $year^{-1}$)
TW	0.13	0.71	0.24	0.79
FW	0.20	0.66	0.21	0.79
NT	0.17	0.71	0.21	0.61
UN	0.13	0.70	0.29	1.14

Median and range of annual diameter increment (cm $year^{-1}$) from 1993 to 2000 of stems $\geq$10 cm dbh per four use groups in a dry forest reserve in Nicaragua.

d.f. = 49, $p = 0.773$). There were 158 dead or missing stems and 144 new stems were recruited corresponding to a mortality of 4.2% $year^{-1}$ and a recruitment of 4.0% $year^{-1}$. The diameter distribution remained the same in year 2000 as in 1993 with a reversed-J shape curve and ca. 80% of the stems had less than 30 cm dbh (Fig. 1). There was a difference in annual mortality among diameter classes with the highest and lowest mortality among the three largest diameter classes (Fig. 2). On average 29% of the stems in a diameter class passed to another class during the study period.

3.2.1.2. Dynamics of the most common species and use groups. Two of the five most common species *Guarea glabra* and *C. pachaca* had mortality rates (2.3 and 2.1% $year^{-1}$, respectively) about half the overall mortality of 4.2% $year^{-1}$ all species included (Table 2). In addition to low mortality *C. pachaca* had a high annual recruitment rate with 8.1% $year^{-1}$ which was twice the overall (4.0% $year^{-1}$) and it was the only species among the most common with a positive annual balance. *G. glabra* had the lowest recruitment rate with 1.6% $year^{-1}$, which was less than half of the overall average.

Among the four use groups only the UN had a recruitment rate (6.1% $year^{-1}$) higher than its mortality rate (3.2% $year^{-1}$) resulting in a positive balance of 2.9% $year^{-1}$ (Table 3). The NT use group had mortality and recruitment rates above and the TW use group below overall average.

3.2.2. Growth

3.2.2.1. Basal area growth and distribution. In year 2000 a basal area of 23.13 $m^2\,ha^{-1}$ was recorded which was 0.46 $m^2\,ha^{-1}$ more than in year 1993 (Appendix B). The calculated change in basal area was not significant ($t = 0.518$, d.f. = 49, $p = 0.607$). The loss of 3.97 $m^2\,ha^{-1}$ due to mortality was less than the gain of 0.98 $m^2\,ha^{-1}$ due to recruitment of new stems and the gain of 3.45 $m^2\,ha^{-1}$ due to stems present since 1993 (Table 1). On a percentage basis the balance between the loss of 2.7% and the gain of 3.0 (0.6 ± 2.4)% was an increase by 0.3% (Table 1). Almost half of the basal area was found in the largest diameter classes (>70 cm dbh) and the basal area distribution remained the same during the study period.

3.2.2.2. Basal area growth per use group. The UN use group had a positive basal area balance (1.5% $year^{-1}$) five times above overall average which and the largest increase among all use groups (Table 3). Largest decrease in basal area (0.6% $year^{-1}$) occurred in the FW use group.

3.2.2.3. Median diameter increment. The Kolmoroz–Smirrnov test showed that the annual stem diameter increment did not have a normal distribution ($Z = 2.757$, $N = 586$, $p = 0.00$). The median increment was 0.24 cm $year^{-1}$ with a range of 0.71 cm $year^{-1}$. The lowest increments (0.23 cm $year^{-1}$) were found in the two smallest diameter classes (Table 4). *C. pachaca* had the highest diameter increment rate (0.28 cm $year^{-1}$) whereas *Stemmadenia obovata* and *Trichilia hirta* had the lowest (0.16 cm $year^{-1}$) (Table 5). The UN use group showed the highest annual diameter increment rate with 0.29 cm $year^{-1}$ (Table 6).

4. Discussion

4.1. Stand dynamics

Annual mortality rates reported for tropical forests vary considerable; 0.9% in a dry forest in Ghana (Swaine et al., 1990); 2.03% in a rain forest in Costa Rica (Lieberman and Lieberman, 1987); 2.91% in a mixed deciduous forest in Thailand (Marod et al., 1999); 1.06% in a humid forest in Panama (Swaine et al., 1987). In comparison the rates recorded in this study in Chacocente (4.5% in the dry deciduous forest and 4.2% in the gallery forest) were considerably higher. Mortality rates in our study corroborated results reported by Sabogal and Valerio (1998) in the gallery forest whereas the mortality rate in the deciduous forest of 4.0% in our study was almost twice higher the result of 2.1% reported by Sabogal and Valerio (1998) on the same plots in Chacocente from 1990 to 1993. Our results were based on data for a 7-year-period and calculated with a logarithmic model whereas their study period was shorter, with 4 years for the deciduous and 2 years for the gallery forest type and their calculations was not based on logarithmic values. In the deciduous forest the recruitment in our study (2.5% year^{-1}) was in the same order of magnitude (1.6% year^{-1}) as Sabogal and Valerio (1998) whereas in the gallery forest they had one-tenth (0.4% year^{-1}) of what we have found. In our study the recruitment by use group in the deciduous forest was highest in the UN with 5.4% year^{-1} whereas Sabogal and Valerio (1998) had the highest recruitment in the FW use group with 11.6% year^{-1}. *S. ovovata* was the most frequently recruited species in both studies. The annual mortality rates were irregular for the three largest diameter classes in the studied forest types due to few stems in these classes. In the other diameter classes there was no obvious tendency between diameter class and mortality rate. This finding is comparable to data reported by Lieberman et al. (1985) and Finegan and Camacho (1999) who point out that there is no evidence that annual mortality rate is dependent on tree size in most tropical forests. There was an anthropogenic influence from villages surrounding the wildlife reserve in terms of recurrent fires, grazing livestock, collection of firewood and poles as well as harvesting of non-timber products (Gillespie et al, 2000; Anon., 2002). In fact Larson (2002) pointed out that the local governments do not have neither economic nor technical capacity to protect the reserve areas. In most cases trees recorded as dead has not been possible to confirm by dead standing stems or existing stumps without or with coppice growth. Dead, but still standing stems were likely to be used as woodfuel or burnt on the spot during the annual fires. Strong winds could brake part of the trees or eventually uproot trees making them more exposed to fires as well as easy to cut and transport. An indication of human influence could be a higher than average mortality among economically valuable and useful species. In both forest types the NT use group actually had almost twice higher (7.2 and 7.4% year^{-1}) the average mortality rates. In the deciduous forest type four of the five most common species showed a higher than average mortality and all belonged to TW and NT use group. However the fifth species *(T. ochracea)* was a timber species with a low mortality rate of 1.9%. In the gallery forest the mortality rates for the two timber species among the five most common species had a lower (3.7 and 2.3%) than average mortality rate (4.2%).

Contrary to the deciduous forest, the gallery forest maintained the same stand density during the study period. There was about the same mortality rate in both forest types but the recruitment rate in the gallery forest of almost twice that of the deciduous forest may be attributed to lack of recurrent fires. Strong winds may cause fewer windfalls due to the deeper soils allowing deeper root systems. In addition, the gallery forest does not have some of the economically most valuable species such as *T. ochraceae, L. minimiflorus and Caesalpinia exostema,* which grow in the deciduous forest (Anon., 2002).

4.2. Basal area growth and diameter increment

Stand density and basal area in this study were lower than reported in other studies (Murphy and Lugo, 1986; Tercero and Urrutia, 1994; Gillespie et al., 2000). For six dry forests in Nicaragua and Costa Rica of which one was Chacocente Wildlife

Reserve, Gillespie et al. (2000) reported on average 22.03 and 21.2 m^2 ha^{-1} for the Chacocente forest. In a review of dry forests across the world Murphy and Lugo (1986) reported basal areas between 17 and 40 m^2 ha^{-1}. In Thailand in a natural mixed deciduous forest a basal area of 17.25 m^2 ha^{-1} was recorded (Marod et al., 1999). Tercero and Urrutia (1994) made a forest inventory in 1993 in the Chacocente gallery forest and reported 328 trees ha^{-1} and a basal area of 27 m^2 ha^{-1}, while Gentry (1995) recorded 41.6 m^2 ha^{-1} in a similar gallery forest in Guanacaste in Costa Rica. It is important to point out that in Chacocente selective timber harvesting has been ongoing since the beginning of the last century until 1983 when the forest was declared wildlife reserve prohibiting legal cutting (Sabogal, 1992). This means that there might be historical reasons for the present low basal area although similar harvesting has been reported from most other deciduous forests. The changes in basal area were not equal among the different use groups and not linked to increased stand density (Table 3).

The median of the periodic annual diameter increment recorded in this study was in the same order of magnitude as in other studies from tropical dry forests (Murphy and Lugo, 1986; Swaine et al., 1990), whereas twice as high values (0.45 cm $year^{-1}$) were reported for the humid forest in Nicaragua (Sabogal et al., 2001). In our study the annual median increment was higher in the gallery than in the deciduous forest type for all diameter classes (Table 4) as well as overall for all species included (0.24 cm $year^{-1}$ versus 0.14 cm $year^{-1}$), which could be attributed to better soil and moisture conditions (Tercero and Urrutia, 1994; Navarrete and Téllez, 1996). In the gallery forest the variation in median diameter increment rates among species was less (0.16–0.28 cm $year^{-1}$) than in the deciduous forest (0.04–0.26 cm $year^{-1}$) (Table 6). At the species level median increment calculated in this study was less for 8 out of 12 species reported by Sabogal and Valerio (1998). In the deciduous forest type our average median increment was less than half the value (0.34 cm $year^{-1}$) reported by Sabogal and Valerio (1998). For the gallery forest they calculated with 0.0 cm $year^{-1}$. To make reliable estimations of annual median diameter increments, we have only considered species with at least 27 measurements (Table 5). In this study only five species from the gallery and seven from the deciduous forest fulfilled the criteria. For these species it appeared like the variation in median diameter growth rates among species was less in the gallery forest (0.16–0.28 cm $year^{-1}$) than in the deciduous forest (0.04–0.26 cm $year^{-1}$) (Table 5).

The pattern of variation between use groups in the two forest types was not the same (Table 6). For instance the UN use group had the largest diameter increment in the gallery forest type (0.29 cm $year^{-1}$) but it was among the lowest (0.13 cm $year^{-1}$) in the deciduous forest type. The opposite pattern was found for the FW. In the deciduous forest the non-timber use group had a higher than average median diameter increment (0.17 cm $year^{-1}$) but it had a lower than average recruitment rate (Table 3).

5. Conclusions

In this study in the Chacocente Wildlife Reserve in Nicaragua we found that there were differences among species use groups with regard to stand dynamics and growth, which indicated that there was an anthropogenic influence. All species included the stand density and basal area decreased in the deciduous forest type whereas there was no change in the gallery forest type. Species with no local use increased at the expense of other use groups in both forest types. In the deciduous forest type the non-timber species as a group decreased whereas the pattern was less clear in the gallery forest.

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Appendix A

Stand density (stems ha^{-1}) and basal area (m^2 ha^{-1}) of stems $\geq$10 cm dbh per species classified in four use groups 1993 and 2000 in a deciduous forest type in a dry forest in Nicaragua.

Latin name	Stand density (stems ha^{-1})		Basal area (m^2 ha^{-1})		Use group
	1993	2000	1993	2000	
Lonchocarpus minimiflorus	52.5	39	0.82	0.59	TW
Caesalpinia exostema	40	31.5	1.10	1.04	TW
Tabebuia ochracea	38.5	41	1.04	1.11	TW
Myrospermun frutesncens	30.5	28.5	0.72	0.78	TW
Achotocarpus nigrican	30	27.5	0.71	0.61	TW
Luehea candida	19.5	18.5	0.47	0.44	TW
Lysiloma divaricatum	16.5	17.5	1.13	1.45	TW
Gliricidia sepium	14	11.5	0.98	0.99	TW
Alophyllus psilospermus	13	10	0.35	0.27	TW
Guazuma ulmifolia	11	8.5	0.36	0.24	TW
Senna atomaria	9.5	8	0.26	0.24	TW
Cordia alliodora	8.5	6.5	0.29	0.25	TW
Other species	57.5	56	2.79	2.71	TW
Subtotal	341	304	11.00	10.72	TW
Thounidium decandrum	7	7.5	0.11	0.13	FW
Sapranthus nicaraguensis	3	2	0.04	0.02	FW
Lysiloma demostachys	2.5	3	0.08	0.11	FW
Diospyros nicaraguensis	2.5	3	0.03	0.05	FW
Other species	4	4	0.05	0.05	FW
Subtotal	19	19.5	0.30	0.37	FW
Gyrocarpus americanus	63	38.5	3.00	1.84	NT
Stemmadenia ovovata	43.5	30.5	0.70	0.52	NT
Caesalpinia coriaria	8	8.5	0.16	0.21	NT
Bursera simaruba	5.5	6	0.22	0.26	NT
Spondia purpurea	4	4	0.80	0.87	NT
Other species	5.5	5	0.19	0.17	NT
Subtotal	129.5	92.5	5.06	3.87	NT
Esenbeckia litoralis	11	10	0.15	0.14	UN
Caseaha tremula	7.5	9	0.16	0.18	UN
Trichilia glabra	3.5	3.5	0.20	0.17	UN
Other species	7	11	0.14	0.17	UN
Subtotal	29	33.5	0.65	0.66	UN
Total	518.5	449.5	17.00	15.62	

Use group: TW, timber; FW, firewood; NT, non timber forest products; UN, use not known locally.

Appendix B

Stand density (stems ha^{-1}) and basal area (m^2 ha^{-1}) of stems $\geq$10 cm dbh per species classified in four use groups 1993 and 2000 in a gallery forest type in a dry forest in Nicaragua.

Latin name	Stand density (stems $ha^{-}1$)		Basal area (m^2 ha^{-1})		Use group
	1993	2000	1993	2000	
Thrichilia hirta	28	27.5	1.13	1.18	TW
Guarea glabra	18	17.5	0.49	0.62	TW
Simaruba glauca	18	16.5	0.80	1.02	TW
Thrichilia moschata	11.5	9	0.44	0.41	TW
Astronium graveolen	10	10.5	0.44	0.60	TW
Ziziphus guatemalensis	7.5	7.5	0.54	0.56	TW
Thrichilia martiana	6.5	5.5	0.66	0.58	TW
Guazuma ulmifolia	6	7	1.36	1.17	TW
Other species	35	32	11.08	11.12	TW
Subtotal	140.5	133	16.95	17.27	TW
Thounidium decandrum	32.5	31.5	1.10	1.08	FW
Pisonia macranthocarpa	6	4.5	0.12	0.08	FW
Coccoloba caracasana	4.5	4.5	0.17	0.18	FW
Other species	5	4.5	0.10	0.07	FW
Subtotal	48	45	1.48	1.42	FW
Stemmadenia obovata	24	23	0.38	0.45	NT
Gyrocarpus americanus	13.5	13	1.21	1.16	NT
Annona sp.	12	13.5	0.29	0.32	NT
Bixa orellana	6	2.5	0.08	0.04	NT
Other species	4.5	5	0.23	0.26	NT
Subtotal	60	57	2.19	2.23	NT
Capparis pachaca	27.5	44	0.41	0.69	UN
Trichilia sp.	19.5	19	0.72	0.66	UN
Other species	11	8.5	0.82	0.82	UN
Subtotal	58	71.5	1.95	2.17	UN
Total	310.5	308	22.68	23.14	

Use group: TW, timber; FW, firewood; NT, non timber forest products; UN, use not known locally.

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