BIELEFELDER ÖKOLOGISCHE BEITRÄGE 11: 61-73, 1997

227

POPULATION STUDIES IN *ELAEAGIA AURICULATA* (RUBIACEAE) IN A PREMONTANE WET FOREST IN THE CORDILLERA DE TILARÁN, COSTA RICA

Sigrid Schroers & S.-W. Breckle
Dept. of Ecology, Faculty of Biology
University of Bielefeld, D-33501 Bielefeld, Germany
Fax: xx49-521-106-2963

INTRODUCTION

This study is part of the Schwerpunktprogramm "Mechanismen der Aufrechterhaltung tropischer Diversität" of the Deutsche Forschungsgemeinschaft (DFG). It is a population ecological study of the tree species *Elaeagia auriculata* (E.a.), which belongs to the family Rubiaceae. The study has been carried out on two different plots in the premontane wet forest of the Reserva Biológica Alberto Brenes (RBAB), Costa Rica. Former population ecological studies in the RBAB have considered the endemic tree *Plinia salticola* (Myrtaceae) (SPRENGER 1992), two palm species (LEYERS 1993), and two emergent trees (RÖMICH 1993). The palms and *Plinia salticola* are found frequently in the Reserva. C. Leyers, B. Römich, A. Sprenger and I. Wattenberg have already arranged the two plots. In contrast to the previous studies, the main interest of this investigation is the population structure, and the differences between the two plots, for a less frequent species. The species *Elaeagia auriculata* has been chosen since it is of major ecological importance in the RBAB (ORTIZ 1985).

STUDY AREA

The study was carried out during October 1994 and April 1995 in the Reserva Biológica Alberto Brenes (RBAB). The RBAB is located in the province of Alajuela in north-central Costa Rica (10°13'N, 84°37'W). It is part of the Caribbean slope of the Cordillera de Tilarán. 7800 ha of almost undisturbed primary forest cover this protected area. The relief is very mountainous with inclinations of up to 25-30 degrees over more than 80 % of the whole area (CRUZ 1989; ORTIZ 1991). With altitudes ranging between 800 and 1500 m, and an average rainfall up to 4000 mm, the RBAB can be classified as part of the Orobiome I (WALTER & BRECKLE 1983, 1991; WATTENBERG & BRECKLE 1995), forming a premontane wet forest following the life-zone system of HOLDRIGE ET AL. (1971).

Two sites near the biological station have been studied. The first one (Plot 1) is located along the line of the southern ridge of the Río San Lorencito valley. The altitude ranges between 1000 and 1040 m. The second site is on the south-eastern slope of the valley. Here the altitude ranges between 910 and 960 m with a mean inclination of 14 degrees (WATTENBERG & BRECKLE 1995).

STUDIED SPECIES

Elaeagia auriculata Hemsley (Rubiaceae) are trees of evergreen lower montane cloud forest and rain forest formations. The species ranges from Guatemala and Honduras to eastern Panama. In Costa Rica, it is found along the central highlands, from Volcán Tenorio in the Cordillera de Guanacaste to San Vito de Coto Brus, and on the Caribbean slope, in altitudes ranging from 350 to 1700 metres. The trees are up to 15 metres tall. They flower between November and March, and fruit between February and June (BURGER & TAYLOR 1993). The capsules open at the top, so that the up to 1 mm long seeds that have thin membranous wings at opposite ends (BURGER & TAYLOR 1993) can be distributed by the wind (anemochory). *Elaeagia auriculata* is also reproduced vegetatively, in particular by sprouting from fallen sticks (SCHROERS ET AL. 1996).

METHODS

Two hectars of forest area have been selected, marked out (LEYERS 1993; RÖMICH 1993; SPRENGER 1992; WATTENBERG & BRECKLE 1995), and subdivided into 100 squares of 10 x 10 m. On both plots the diameters at breast hight (DBH) of all trees, palms and tree ferns with DBH greater than 10 cm have been determined. For individuals with several trunks at the height of 1.30 m, the thickest trunk has been measured. The abundance and dominance values (total and proportional) of each group were calculated. The total abundance is the number of trunks per hectare of each group, the proportional abundance is the percentage with respect to the total trunk number per hectare. The basal area of trees provides a more reliable instrument for biomass estimation than do trunk numbers, therefore group dominance values are represented by their basal area, calculated from DBH (LAMPRECHT 1986; WATTENBERG & BRECKLE 1995). The proportional dominance is the percentage of each group value with respect to the total basal areas in the two study plots. The frequencies of *Elaeagia auriculata* have been examined by evaluation of the tree position within the 100 subplots on both study areas.

The position of all *Elaeagia auriculata* plants has been determined. For the sexual respectively vegetative juveniles of E.a. the following measurements have been carried out:

a) **Sexual juveniles**: The diameter of the stem (DS) has been measured with a sliding rule at the internode below the first leaf. Moreover, the height of the plants, i.e. the distance between the ground and the highest leaf, has been measured. All leaves have been counted.

With a spherical densiometer (Model A from LEMMON 1957) the shading has been determined. The densiometer has been held directly above the plants, which were not taller than one metre. It has been counted how many of the 96 quarter quadrats were at least half covered by higher vegetation. The resulting number has been multiplied by 1.04 to obtain a value for the percentage of shading, see (SCHROERS 1996) for details.

The calibration curve for the ideal leaf area (ILA) of E.a., i.e. including feeding on leaves, has been determined by measuring length, width and area of a limited number of leaves. It is given by

$$\mathrm{ILA} = 0.59\ x + 2.21\ e^{-6}\ x^2 - 1.96\ e^{-11}\ x^3 + 6.21\ e^{-17}\ x^4$$

where x = length x width, r = 0.999, see (SCHROERS 1996).

Then the length and width of the largest leaf of each plant smaller than one metre have been measured, and the corresponding ILA has been calculated.

b) **Vegetative juveniles**: For each sprout from a (fallen) stick the same parameters as for the sexual juveniles have been measured. The height has now been measured from the beginning of the sprout. Shadowing and ILA have been determined whenever possible. Here no height limit of one metre has been set.

RESULTS AND DISCUSSION

Abundances and Dominances

A registration of the total standing of trees with DBH ≥ 10 cm on both plots had the following results (Table 1):

On Plot 1 there are 617 trunks, on Plot 2 only 469. The total abundance of Plot 1 coincides with the abundances of other tropical forest regions, see e.g. (GENTRY 1990; LIEBERMAN & LIEBERMAN 1987; MABBERLEY 1992), but the abundance of Plot 2 is smaller. In particular, the number of trunks that are neither palms nor tree ferns is much higher on Plot 1, whereas on Plot 2 there are more tree ferns than on Plot 1. The numbers of palms on both plots do not differ essentially, the numbers of E.a. trees is low on both plots. The frequency of E.a. is 7 % on Plot 1 and 5 % on Plot 2. The relative abundances of E.a. on both plots coincide, but because of the low total numbers of E.a. trees this is not a very significant statement.

WATTENBERG & BRECKLE (1995) showed that E.a. is only the 24th most frequent of the 93 tree species that are found on Plot 2. By the classification of HARTSHORN (1991), E.a. is *frequent* on this plot (WATTENBERG 1996), whereas in the near by montane region of Monteverde it only appears *occasionally* (HARTSHORN 1991).

The basal area is 37.5 m²/ha on Plot 1, and 3.2 m²/ha less on Plot 2. This is slightly higher than values from lowland rain forests that range between 28 and 33 m²/ha (LAMPRECHT 1986). Again, in particular the dominance of other trees is higher on Plot 1 than on Plot 2, whereas tree trunks and palms have a higher dominance on Plot 2. The palms on Plot 1 are hence thinner. Since E.a. trees usually have small DBH, the relative dominance of E.a. is even less than its relative abundance. Results of DI STEFANO AND OTHERS (1995) state similar relative abundances and dominances on an other hectare of the RBAB.

A comparison with the study by RÖMICH (1993) shows, that the total number of trunks (without tree ferns) with DBH ≥ 10 cm on Plot 1 decreased by 15 between 1991 and 1994. In the same time the basal area increased by 1.1 m^2/ha. The major causes for the observed decrease of the abundance seem to be tree falls and fungal pathogens. The dominance increased nevertheless, because trees grew larger. The abundance of E.a. with DBH ≥ 10 cm increased from 5 to 7.

Since 1992, the total number of trunks with DBH ≥ 10 cm on Plot 2 decreased considerably. Compared to the study of SPRENGER (1992; Table 1) there are now 72 trunks less. In particular, the abundance of trees was reduced heavily (57 trunks less). The major cause seem to be tree falls. The decrease of the number of tree ferns by 16 individuals may be caused by different ways of counting the trunks, since often several trunks have connections with each other. The abundance of palms remained almost equal, and the number of E.a. individuals was constant as well (cp. WATTENBERG & BRECKLE 1995).

The basal area decreased since the 1992 study by 17.1 m^2/ha, i.e. by one third. The dominance of trees decreased by 17 m^2/ha. However, different methods of measuring thick trees in the study by Sprenger and in this study have to be taken in account. The dominance of tree ferns and palms did not change much. This means that in particular thick trees have fallen during the three years. There are now two new gaps on Plot 2.

Table 1: Total and proportional abundance, total and proportional dominance of palms, tree ferns and trees with DBH ≥ 10 cm in the two one hectare study plots. N stands for the trunk number, m^2 for the basal area per group and hectare. E.a.: *Elaeagia auriculata*.

		total	palms		tree ferns		E.a.		others	
Plot 1										
N	%	617	65	10.6	32	5.2	7	1.1	513	83.2
m^2	%	37.5	1.8	4.8	0.6	1.6	0.1	0.3	35.0	93.3
Plot 2										
N	%	469	67	14.3	69	14.7	5	1.1	328	69.9
m^2	%	34.3	2.4	7.0	1.2	3.5	0.1	0.3	30.6	89.2
Sprenger (1992)										
N	%	541	66	12.2	85	15.7	----	----	390	72.1
m^2	%	51.4	2.4	4.7	1.3	2.5	----	----	47.7	92.8

Elaeagia auriculata population

The *Elaeagia auriculata* plants are divided into groups of trees with DBH ≥ 5 cm, young trees with height of more than one metre and DBH < 5 cm, saplings with height less than one metre, and sprouts of vegetative juveniles.

There are more E.a. individuals on Plot 2 than on Plot 1 (Table 2; SCHROERS ET AL. 1996). E.a. hemiepiphytes grow on *Miconia* (Melastomataceae) and *Ficus* (Moraceae). One E.a. hemiepiphyte takes root around *Rondeletia* (Rubiaceae), which itself grows on *Ocotea* (Lauraceae).

Table 2: Numbers of *Elaeagia auriculata* plants on both plots.

	Plot 1	Plot 2
trees with DBH ≥ 5 cm	14	10
young trees with height > 1 m	25	41
saplings wiht height < 1 m	28	52
vegetative juveniles (sprouts)	27 (58)	89 (259)

Diameter of stems (DS)

- About 20 % of the E.a. saplings on Plot 1 have a DS of 0.1, 0.2, 0.3, 0.4, 0.5 cm respectively (Fig. 1). In contrast to this, on Plot 2 there are no saplings with DS less than 0.2 cm, and only 83 % of the saplings have DS ≤ 0.5 cm (Fig. 2). However, there is no significant difference between the two plots (U-Test).
- About 71 % of the young trees on Plot 2 have DS between 0.6 and 2.4 cm, whereas on Plot 1, about 56 % have a DS between 2.5 and 4.6 cm.
- The E.a. sprouts on both plots have DS between 1.3 and 2.8 cm. The percentage of sprouts with DS between 0.1 and 0.4 cm is 74 % on Plot 1, and 8 % less on Plot 2. Nevertheless, there is no significant difference (U-Test).

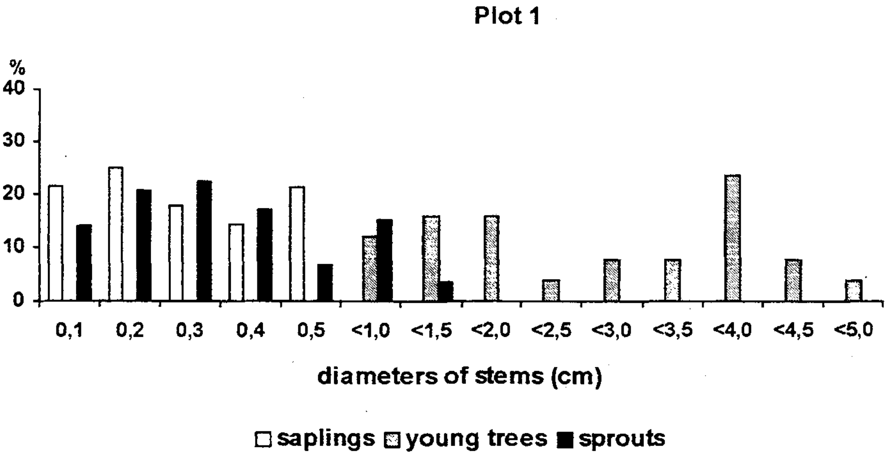
Plot 1

Fig. 1: Diameters of stems of *Elaeagia auriculata* juveniles on Plot 1.

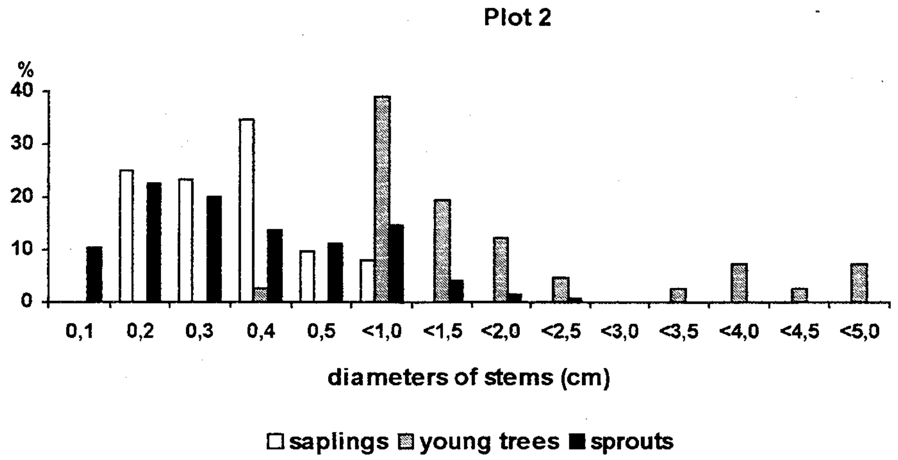

Fig. 2: Diameters of stems of *Elaeagia auriculata* juveniles on Plot 2.

Height

- The E.a. trees on both plots have heights less than 15 metres. Hence E.a. is part of the subcanopy.
- The E.a. saplings on Plot 1 have heights between 0.03 and 0.72 m (Fig. 3). The median is 0.25 m. About 40 % are smaller than 0.20 m. On Plot 2, the saplings have heights between 3 and 0.97 m, with a median of 0.39 m (Fig. 4). 37 % have heights between 0.20 and 0.40 m.
- The E.a. young trees on Plot 1 have heights between 1.0 and 7.5 m. The median is 3.19 m. 84 % of the trees have heights less than 5 metres, and between 1 and 5 m the heights are almost equally disributed. The situation is very different on Plot 2. Here 56 % (!) of the young trees have heights less than 2 metres. The heights vary between 1.07 and 8.00 m with a median of only 1.90 m.
- The E.a. sprouts on Plot 1 have heights between 0.02 and 2.0 m. Half of them are smaller than 0.2 m, and another quarter has heights between 0.2 and 0.4 m. The median is 0.2 m. The average sprout on Plot 2 is slightly higher. Here the heights range betweeen 0.01 and 3.70 m, only 36 % of the sprouts are smaller than 0.2 m, and another 20 % have heights between 0.2 and 0.4 m. The median is 0.33 m.

The difference between the heights of the young trees respectively the sprouts on both plots is significant, the corresponding difference between the heights of the saplings even highly significant (U-Test). On Plot 1 the young trees are higher than on Plot 2, whereas the saplings and the sprouts are higher on Plot 2. Moreover, the young trees on Plot 1 have larger DS than those on Plot 2. On Plot 1, there are more adult E.a. trees, and less young trees. Hence, the E.a. population on Plot 2 is probably "older" than that on Plot 1.

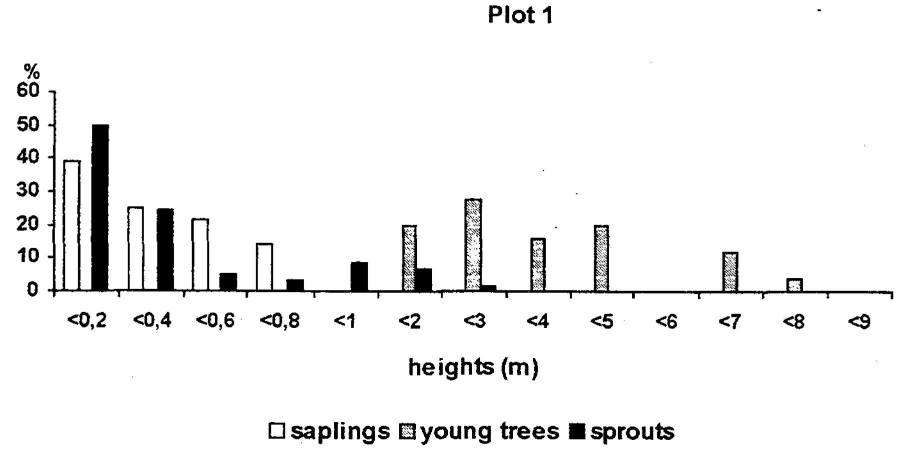

Fig. 3: Heights of *Elaeagia auriculata* juveniles on Plot 1.

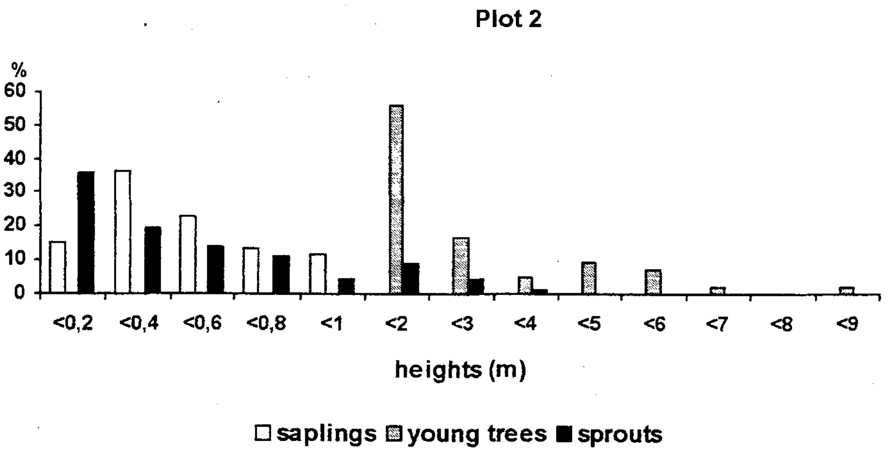

Fig. 4: Heights of *Elaeagia auriculata* juveniles on Plot 2.

Number of leaves

There is no significant difference concerning the number of leaves of the saplings, young trees respectively sprouts on both plots (U-Test). See SCHROERS (1996) for a description of the corresponding distributions.

Shading

- More than 80 % of the E.a. saplings on both plots are shaded for more than 95 %. There is no significant difference between the plots (U-Test). This fact, however, should not be overemphasized, since all the saplings on both plots are shaded for at least 85 %.
- More than 80 % of the sprouts on both plots are shaded for more than 95 %. Again there is no significant difference between the plots (U-Test).

- All the juveniles on both plots are shaded for the most part.

These results differ from those of WATTENBERG (1996). Wattenberg states that E.a. plants are found under relatively low crown roof densities. She concludes that E.a. prefers brighter places, although it is not a typical pioneer species in the sense of SWAINE & WHITMORE (1988). The regeneration of E.a. seems to be gap dependent.

Ideal leaf area (ILA)

- The E.a. saplings on Plot 1 have ILAs between 3 and 461 cm^2 (Fig. 5). Half of the leaves has an ILA of less than 50 cm^2. On Plot 2, only a third of the leaves has an ILA less than 50 cm^2. The ILAs range between 5 and 281 cm^2. However, there is no significant difference between the plots (U-Test).
- About half of the leaves of the sprouts on each plot have an ILA less than 50 cm^2. There is no significant difference between the plots (U-Test).

The leaves of higher or thicker saplings respectively sprouts have larger ILAs than those of smaller or thinner ones (SCHROERS 1996). Hence the leaves of "older" saplings and sprouts become larger. Moreover, the leaves of the sprouts tend to be larger for more shaded sprouts (SCHROERS 1996). Most of the higher E.a. plants have macrophyle leaf areas in the sense of RAUNKIAER (1934), i.e. leaf areas between 182 and 1640 cm^2. DOLPH & DIECHER (1980) showed that in Costa Rica there is a connection between macrophyle leaf areas and a mean annual biotemperature of 21-24° C. The RBAB has a mean annual temperature of about 20° C (BRECKLE 1996, unpublished data).

The large differences within the E.a. population with respect to the leaf areas of different plants cannot be explained by the used methods. Maybe the plant needs the different leaf areas in order to cope with the light anatomically and physiologically, and to use it for photosynthesis.

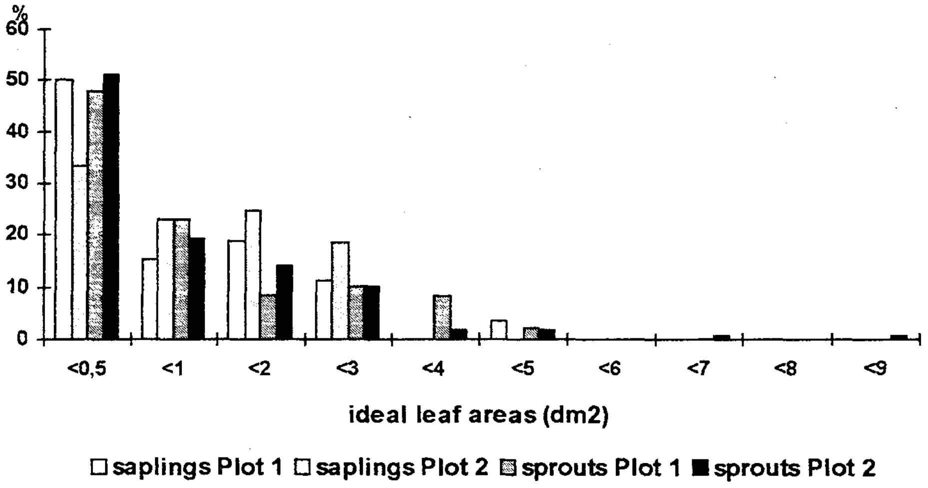

Fig. 5: Ideal leaf areas of *Elaeagia auriculata* juveniles on Plot 1 and 2.

Spatial distribution

There is a close connection between the pattern of spatial distribution of tropical tree species and the way the seeds are distributed (HUBBELL 1979). The pattern of population depends on the climatic conditions, since the winged E.a. seeds can be distributed by the wind. HAVEL (1971) shows that in a New Guinean forest winged seeds of a conifer are carried 60 metres in the direction of the monsoon wind but only 20 metres normal to the direction of the wind.

On the two plots studied here, the spatial distributions of E.a. are similar to each other. The whole population has a clumped pattern of distribution (χ^2-Test in the sense of FOWLER & COHEN 1990). *Plinia salticola* (- the most frequent tree species on Plot 2 -) and the two palm species *Iriatea deltoidea* and *Euterpe macrospadix* (- frequent on Plot 1 -) also have a clumped distribution (SPRENGER 1992; LEYERS 1993). Only the adult E.a. trees (DBH $\geq$ 7 cm) are randomly distributed, whereas E.a. saplings, young trees and vegetative juveniles have a clumped pattern of distribution. With increasing time the number of trees decreases, and the clumped distribution of the juveniles turns into the random distribution of the adult trees. This is consistent with results of WATTENBERG (1996) which state the high mortality of the E.a. juveniles. BARROS HENRIQUES AND GIRNOS DE SONSA (1989) also obtained a change from a clumped to a random distribution with increasing DBH.

The decrease of the number of individuals with growing age corresponds to the calculated minimal distances between neighbour E.a. plants (Fig. 6 and 7). On Plot 1, 71 % of the saplings have distances less than 2 metres from their nearest neighbour sapling. The median is 1.2 m. More than 60 % of the young trees have distances less than 6 m (median 4.6 m), whereas more than 80 % of the adult trees have distances between 8 and 12 m (median 8.5 m).

On Plot 2, 75 % of the saplings have distances less than 2 m (median 0.8 m), 75 % of the young trees have distances less than 6 m (median 2.8 m), whereas only 3 of the 8 adult trees on Plot 2 have distances less than 15 m (median 18.8 m).

The median of the distances between a sapling and the next adult tree (which is not necessarily the parent tree) is 11.4 m on Plot 1, and 4 metres more on Plot 2.

For *Plinia salticola*, SPRENGER (1992) also found the decrease of the number of individuals with growing age. However, here the mean distances of saplings are much larger (4.4 metres), whereas the mean distances of adults are smaller (7 metres).

Possible reasons for the decrease mentioned may be pathogens (AUGSPURGER 1983, 1984; AUGSPURGER & KELLY 1984), seed predation (JANZEN 1978; SCHUPP 1988; SCHUPP & FROST 1989), herbivores (JANZEN 1970; BAZZAZ 1987; CLARK & CLARK 1985), and competion for light and roots (BROKAW 1987; SCHMID 1991). For example, larvas of minierflies of the genus *Melanagromyza* can damage the epidermis of the leaves of E.a. juveniles.

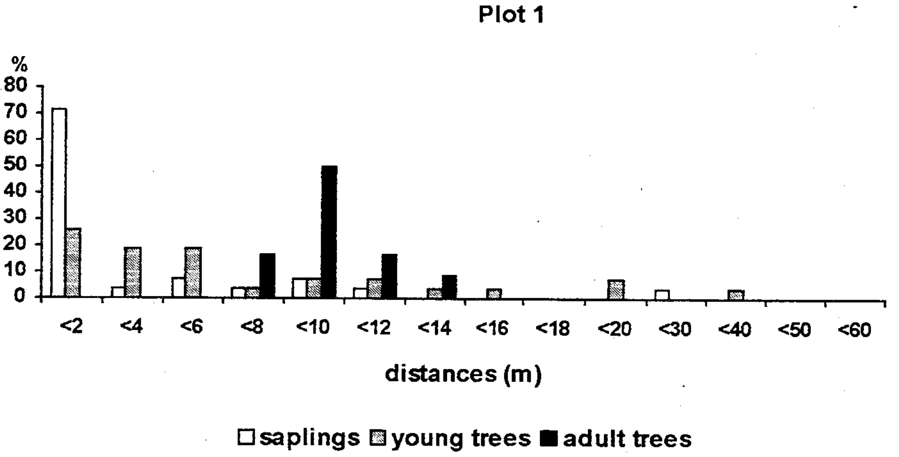

Fig. 6: Distances of *Elaeagia auriculata* plants on Plot 1.

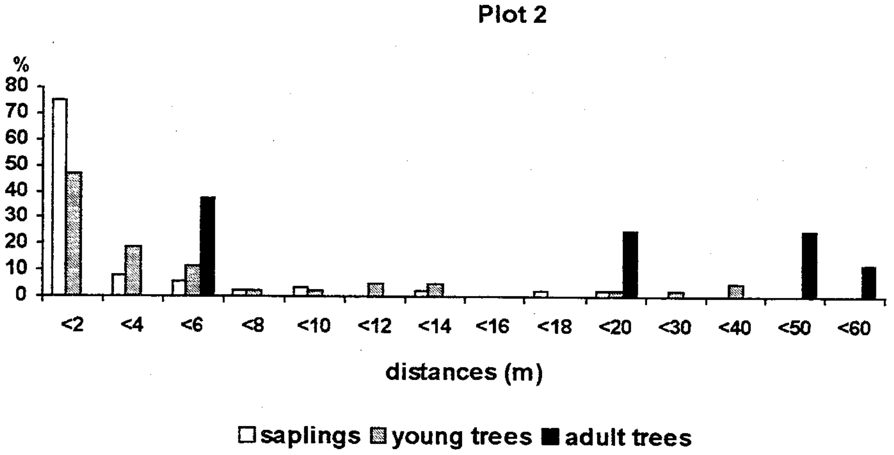

Fig. 7: Distances of *Elaeagia auriculata* plants on Plot 2.

Vegetative reproduction

The chance of survival of E.a. is increased by vegetative reproduction. A large part of the E.a. individuals is of vegetative origin. This part might be even larger, since it is not possible to distinguish the older young trees of vegetative origin from those of generative origin. This is confirmed by results of WATTENBERG (1996). In particular, in gaps in the RBAB, E.a. is the second most frequent species with sprouts from sticks, and the vegetative part is larger in gaps than in the closed stand of the forest. Furthermore, the height increase of vegetative juveniles is larger than that of generative juveniles (WATTENBERG 1996; HUNTER 1987). Hence the vegetative juveniles win the competion for light with the herbaceous vegetation at least during the first years (WATTENBERG 1996).

A crucial condition for a successful establishment of sprouts from sticks seem to be favourable climatic conditions. In the RBAB, there is less danger of dehydration by strong transpiration than in the lowlands. In fact, in the reserva there are few hours of sunshine and frequent fog, hence constantly high relative humidities and comparatively stable temperatures (WATTENBERG 1996). Experimental studies by BRENES & DI STEFANO (1996) confirm a high sensibility of *Elaeagia uxpanapensis* sprouts from sticks with respect to low relative humidity.

These researchers describe the advantages of vegetative reproduction in the following way:

In contrast to seed sources, there are permanently enough branches capable of reproduction. Once established, scions may grow very rapidly. In the case of extinction-prone tree species it is possible to increase the genetic pool in a comparatively short time.

ACKNOWLEDGEMENT

I would like to thank Andreas Eberle for assistance with the English translation. Financial support of the Deutsche Forschungsgemeinschaft (DFG) and the Deutscher Akademischer Auslandsdienst (DAAD) is gratefully acknowledged.

REFERENCES

AUGSPURGER, C.K. 1983. Seed dispersal of the tropical tree *Platypodium elegans* and the escape of its seedlings from fungal pathogens. Journal of Ecology 71: 759-771.

AUGSPURGER, C.K. 1984. Seedling survival of tropical tree species. Interactions of dispersal distance, light-gaps, and pathogens. Ecology 65 (6): 1705-1712.

AUGSPURGER, C.K. & C.K. KELLY 1984. Pathogen mortality of tropical tree seedlings. Experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia (Berlin) 61: 211-217.

BARROS HENRIQUES, R.P. & E.C. GIRNOS DE SONSA 1989. Population structure, dispersion and microhabitat regeneration of *Carapa guianensis* in northeastern Brazil. Biotropica 21 (3): 204-209.

BAZZAZ, F.A. 1984. Dynamics of wet tropical forests and their species strategies. In: Medina, E., Mooney, H.A. & C. Vazques-Yanes (eds). Physiological ecology of plants of the wet tropics. The Hague. Boston.

BRENES, L. & J.F. DI STEFANO G. 1996. Capacidad de propagación por estacas del árbol *Elaeagia uxpanapensis* D. Lorence, Rubiaceae. In: Revista de Biología Tropical Universidad de Costa Rica. In press.

BROKAW, N.V.L. 1987. Gap phase regeneration of three pioneer species in a tropical forest. Journal of Ecology 75: 9-19.

BURGER, Q. & C.M. TAYLOR 1993. Flora castaricensis. Fam. 202 Rubiaceae. In: Burger, W. Fieldiana Botany. Field Museum of Natural History. Chicago.

CLARK, D.B. & D.A. CLARK 1985. Seedling dynamics of a tropical tree. Impacts of herbivory and meristem damage. Ecology 66 (6): 1884-1892.

CRUZ, D.G. 1989. Nuestras Reservas Forestales y Zonas Protectoras. In: Ministerio de Recursos Naturales, Energía y Minas Costa Rica: 39-40.

DI STEFANO G., J.F., BRENES, L. & V. MORA 1995. Composición florística y estructura de un bosque primario del piso premontano pluvial, en San Ramón, Costa Rica. Rev. Biol. Trop. 43 (1-3): 67-73.

DOLPH, G.E. & D.L. DIECHER 1980. Variation in Leaf Size with Respect to Climate in Costa Rica. Biotropica 12 (2): 91-99.

FOWLER, J. & L. COHEN 1990. Practical Statistics for Field Biology. John Wiley & Sons. New York.

GENTRY, A. 1990. Four neotropical rainforests. Yale University. New Haven.

HARTSHORN, G.S. 1991. In: Janzen, D.H. (ed.). Historia Natural de Costa Rica. San José: 65-73.

HAVEL, J.J. 1971. The Araucaria forests of New Guines and their regenerative capacity. Journal of Ecology 59: 203-214.

HOLDRIDGE, L.R., GRENKE, W.C., HATHEWAY, W.H., LANG, T. & J.A.TOSI JR. 1971. Forest environments in tropical life zones. A pilot study.

HUBBELL, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299-1309.

HUNTER, R.J. 1987. Reforestation with *Bombacopsis quinatum* (Jaq.) Dugand (Bombacaceae) in Costa Rica by means of vegetative reproduction. In: Revista Biología Tropical Vol. 35 No. 2: 195-201.

JANZEN, D.H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104: 501-528.

JANZEN, D.H. 1978. Seeding patterns of tropical trees. In: Tomlinson, P.B. & M.H. Zimmermann. Tropical trees as living systems. Cambridge University Press. Cambridge: 83-128.

LAMPRECHT, H. 1986. Waldbau in den Tropen. Verlag Paul Parey. Hamburg.

LEMMON, P.E. 1957. A spherical densiometer for estimating forest overstory density. In: Forest Science Vol. 2 No. 1: 314-320.

LEYERS, C. 1993. Populationsökologische Untersuchung zweier Palmenarten im prämontanen Regenwald der Cordillera de Tilarán (Costa Rica). Diplomarbeit. Universität Bielefeld.

LIEBERMAN, D. & M. LIEBERMAN 1987. Forest tree growth and dynamica at La Selva, Costa Rica. Journal of Tropical Ecology 3: 347-358.

MABBERLEY, D.J. 1992. Tropical rain forest ecology. Chapman & Hall. New York.

ORTIZ, R. 1985. Analysis ecológico de un bosque premontano muy humedo en la Reserva Forestal de San Ramón, Alajuela, Costa Rica. Cienc. Tec. 9: 59-71.

ORTIZ V., R. 1991. Memoria de Investigación, Reserva Forestal de San Ramón. Serie Cátedra Universitaria. Sede de Ocidente.

RAUNKIAER, C. 1934. The life-forms of plants and statistical plant geography. Oxford University Press. Oxford.

RÖMICH, B. 1993. Anlayse der Populationsstruktur und der Vebreitungsstrategie der Baumarten *Pterocarpus hayesii* und *Inga leonis* im prämontanen Regenwald der Reserva Forestal de San Ramón, Costa Rica. Diplomarbeit. Universität Bielefeld.

SCHMID, B. 1991. Konkurrenz bei Pflanzen. In: Schmid, B. & J. Stöcking (eds). Populationsbiologie der Pflanzen, Birkhäuser. Basel.

SCHROERS, S. 1996. Populationsökologische Untersuchung von *Elaeagia auriculata* (Rubiaceae) im Regenwald von Costa Rica. Examensarbeit. Universität Bielefeld.

SCHROERS, S., ORTIZ, R. & S.-W. BRECKLE 1996. Apuntes sobre *Elaeagia auriculata* (Rubiaceae).In: M.Sc. R. Ortiz (ed.). Revista Pensamiento Actual Vol. 2. Memoria Investigación Reserva Biológica Alberto Ml. Brenes, San Ramon: 41-43.

SCHUPP, E.W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51: 71-78.

SCHUPP, E.W. & E.J. FROST 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and in the forest understory. Biotropica 21(3): 200-203.

SPRENGER, A. 1992. Populationsökologische Untersuchung von *Plinia salticola* (Myrtaceae) im prämontanen Regenwald der Cordillera de Tilarán (Costa Rica). Diplomarbeit. Universität Bielefeld.

SWAINE, M.D. &T.C. WHITMORE 1988. On the definition of ecological species groups in tropical rain forests. In: Vegetatio, Vol. 75: 81-86.

WALTER, H. & S.-W. BRECKLE 1983. Ökologie der Erde. Band 1: Ökologische Grundlagen in globaler Sicht. Stuttgart.

WALTER, H. & S.-W. BRECKLE 1991. Ökologie der Erde. Band 2 (2. Auflage): Spezielle Ökologie der Tropischen und Subtropischen Zonen. Stuttgart.

WATTENBERG, I. 1996. Struktur, Diversität und Verjüngungsdynamik eines prämontanen Regenwaldes in der Cordillera de Tilarán in Costa Rica. Dissertation. Universität Bielefeld.

WATTENBERG, I. & S.-W. BRECKLE 1995. Tree species diversity of a premontane rain forest in the Cordillera de Tilarán, Costa Rica. In: Ecotropica, Vol. 1: 21-30.