Stand structure of Monocotyledons and Dicotyledons in different successional stages in Corcovado National Park, Costa Rica

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Photograph 1.
Primary forest.
Photograph S. Ayangma.

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RÉSUMÉ

STRUCTURE DES PEUPLEMENTS DE MONOCOTYLEDONES ET DICOTYLEDONES LORS DE DIFFERENTS STADES DE SUCCESSION DANS LE PARC NATIONAL DE CORCOVADO AU COSTA RICA

Les deux grands groupes d'angiospermes, monocotylédones et dicotylédones, diffèrent à plusieurs égards au niveau de leur cycle de vie. Malgré les différences évidentes entre ces deux groupes, peu d'études se sont penchées de façon approfondie sur la manière dont cela pourrait influencer leur succession écologique. L'étude compare les densités relatives de ces deux groupes fondamentaux à l'évolution contrastée, lors de deux stades de succession forestière à la station de Sirena dans le Parc national de Corcovado au Costa Rica, en Amérique centrale. Selon l'hypothèse de départ, le rapport monocotylédones/dicotylédones devrait diminuer aux stades plus avancés de la succession. L'échantillonnage a porté sur un ensemble de 40 placettes triangulaires à angle droit ($(5 \times 5$ m)/2), où les plantes ont été classées en quatre catégories selon la dimension des houppiers, ainsi qu'en monocotylédones et dicotylédones. Une analyse de la distribution des densités et des classes de dimension des houppiers a été effectuée par ANOVA selon la procédure de modélisation linéaire généralisée. La densité moyenne totale de la forêt secondaire apparaît significativement plus importante que celle de la forêt primaire (P < 0,001). Cependant, la structure de la distribution des classes de dimension des houppiers est proche entre monocotylédones et dicotylédones, mais aussi entre forêt primaire et secondaire. Il n'apparaît aucune différence significative entre les deux types de forêt dans le rapport monocotylédones / dicotylédones (P = 0,99). Les résultats concernant la distribution des classes de dimension des houppiers indiquent une tendance similaire dans la distribution des successions de monocotylédones et dicotylédones, même si les dicotylédones sont toujours plus nombreux. Ces résultats amènent à conclure qu'il est nécessaire d'avoir une importante différence entre les stades de succession avant de percevoir la différence anticipée dans cette étude.

Mots clé : forêt tropicale humide, forêt primaire, forêt secondaire, évolution floristique, tropiques humides, Amérique centrale.

ABSTRACT

STAND STRUCTURE OF MONOCOTYLEDONS AND DICOTYLEDONS IN DIFFERENT SUCCESSIONAL STAGES IN CORCOVADO NATIONAL PARK, COSTA RICA

The two major groups of angiosperms, monocotyledons and dicotyledons, differ in several of their life history traits. Despite the obvious differences between the two groups, there are few studies elaborating on how these may relate to their ecological succession. The study compares the relative densities of these two fundamental groups of plants with different evolutionary histories in forests in two different successional stages at the Sirena station in Costa Rica's Corcovado National Park, in Central America. The hypothesis was that the monocotyledons/dicotyledons ratio would decrease in later successional stages. A total of 40 right-angled triangular plots ($(5 \times 5$ m)/2) were sampled and the plants were divided into four crown size classes, as well as into monocotyledons and dicotyledons. Plant densities and crown size class distribution were analysed using ANOVA with the general linear model (GLM) procedure. The mean overall plant density in the secondary forest was significantly greater than in the primary forest (P < 0.001). The structure of the crown size class distribution, however, was similar for both monocotyledons and dicotyledons, and for the primary and secondary forest types. There was no significant difference between the two forests in the monocotyledons to dicotyledons ratio (P = 0.99). The crown size class distribution results indicate that there is a similar distribution trend in monocotyledon and dicotyledon succession, although there are always more dicotyledons than monocotyledons. These results led to conclude that a larger difference between successional stages is necessary to perceive the difference anticipated in this study.

Keywords: rain forest, primary forest, secondary forest, plant evolution, humid tropics, Central America.

RESUMEN

ESTRUCTURA DE LOS RODALES DE MONOCOTILEDÓNEAS Y DICOTILEDÓNEAS EN DIFERENTES ETAPAS DE SUCESIÓN EN EL PARQUE NACIONAL DE CORCOVADO EN COSTA RICA

Los dos principales grupos de angiospermas, monocotiledóneas y dicotiledóneas, difieren en varios aspectos de su ciclo vital. A pesar de las evidentes diferencias entre estos dos grupos, existen pocos estudios que hayan profundizado en cómo podría esto relacionarse con su sucesión ecológica. Éste estudio compara las densidades relativas de estos dos grupos fundamentales de plantas de distinta evolución, en dos etapas de sucesión forestal en la estación de Sirena en el Parque Nacional de Corcovado, en Costa Rica. Según ésta hipótesis, la relación monocotiledóneas/dicotiledóneas debería disminuir en las etapas más avanzadas de la sucesión. Se muestrearon un total de 40 parcelas triangulares de ángulo recto ($(5 \times 5$ m)/2), en las que se clasificaron las plantas en cuatro clases según el tamaño de las copas, así como en monocotiledóneas y dicotiledóneas. Se efectuó un análisis de la distribución de densidades y clases de tamaño de las copas mediante ANOVA (modelo lineal general). La densidad promedio total del bosque secundario fue significativamente mayor que la del bosque primario (P < 0.001). Sin embargo, la estructura de distribución de las clases de tamaño de las copas fue similar entre monocotiledóneas y dicotiledóneas, y también entre bosque primario y secundario. No aparece ninguna diferencia significativa entre los dos tipos de bosque en la relación monocotiledóneas/dicotiledóneas (P = 0.99). Los resultados de la distribución de clases de tamaño de las copas indican una tendencia similar en la distribución de sucesiones de monocotiledóneas y dicotiledóneas, aunque las dicotiledóneas sean siempre más numerosas. Estos resultados llevan a la conclusión de que las diferencias entre etapas de sucesión deben ser mayores para percibir la diferencia anticipada en éste estudio.

Palabras clave: bosque tropical húmedo, bosque primario, bosque secundario, evolución florística, trópicos húmedos, América Central.

INTRODUCTION

Flowering plants are conventionally, divided into two major classes: Dicotyledons (Magnoliopsida) and Monocotyledons (Liliopsida). This separation into two classes is commonly taken for granted, because it is "patently obvious", but botanists have not always recognized these as the two fundamental groups of angiosperms (Barabé, Brouillet, 1982). Despite the problems with recognizing basal angiosperm taxa, the conventional distinctions between dicotyledons and monocotyledons are still quite useful. The main morphological differences between monocotyledons and dicotyledons are, respectively, embryo with a single cotyledon vs. embryo with two cotyledons; pollen with a single furrow or pore vs. pollen with three furrows or pores; flower parts in multiples of three vs. flower parts in multiples of four or five; parallel major leaf veins vs. reticulated major leaf vein; scattered vs. ring-shaped pattern of stem vascular bundles; adventitious roots vs. roots developing from radicles; secondary growth absent vs. secondary growth often present. It is thanks to the extreme plasticity of their vegetative and reproductive organs that angiosperms have become so widely and successfully established; their genesis was the ultimate link in the ongoing chain of evolution of our planet's plant kingdom (Takhtajan, 1953). It is universally agreed that monocotyledons are derived from primitive dicotyledons, and that monocotyledons must follow rather than precede dicotyledons in any proper linear sequence (Cronquist, 1965). Few conclusions have been published by botanists as to which traits are more advanced or more primitive. Looking beyond the ongoing debate on Angiosperm classification (Agp II, 2003), there is also the question of how the life-histories of monocotyledons and dicotyledons relate to their ecological succession in different ecosystems. Most studies of plant diversity have dealt with species richness and the family importance value index (Gentry, Dodson, 1987; Oosterhoorn, Kappelle, 2000; Macía, 2008). Very few studies have investigated plant diversity in relation to life-history traits, although the primitive or advanced character of a plant's life-history influences its ability to become established in different ecosystems.

The Corcovado National Park is an appropriate site for investigating stand structure in relation to plant life-history traits. The park was created in 1975 to preserve 35,000 hectares of humid tropical forest with outstanding biological diversity. After declaring the area a national park, the government evicted 330 subsistence farmers living in the coastal lowlands, offering land or money in compensation. Fewer than 200 subsistence farmers lived on the peninsula until the 1940s (Lewis, 1984). By the 1960s, extensive cattle ranching and rice production had been established on the peninsula. These agro-export activities expanded to occupy the most fertile land available. The area was first logged in the 1970s, by a North American company. Corcovado National Park and its adjacent areas cover the largest tract of extant lowland tropical humid forest on the Pacific side of Central America (Hartshorn, 1983), and the park contains

Photograph 2.
Secondary forest.
Photograph F. Bognounou.

the largest remaining tract of rainforest on the Pacific coast of Central America (Janzen *et al.*, 1985; Vaughan, 1981). So far, over 1,510 vascular plant species in 707 genera and 154 families have been documented (Fnt, 1992). Based on successional stages, the park was divided into two different forest types, primary and secondary forests. The primary forest has never been logged, and has reached its climax species composition stage, with the typical structure of lowland tropical rainforest. The secondary forest, on the other hand, is still in an earlier succession stage, with pioneer species such as balsa trees and others that are generally not found in primary forest. This study investigated the stand structure of monocotyledons and dicotyledons in the two succession stages and compared their ratios.

The objective of the study was to assess the process of monocotyledon and dicotyledon succession in Corcovado National Park. In the early stages of secondary succession in fields left fallow, annual plants are replaced by perennial plants. Weed communities (monocotyledons) on arable land are then the earliest stages of succession. How then do the successional stages of vegetation affect stand structure and the ratio of monocotyledons to dicotyledons? Our hypothesis was that the abundance ratio of monocotyledons to dicotyledons would, based on their life-histories, be lower in primary than the secondary forest. The first reason for this expectation is that because monocotyledons derive from primitive dicotyledons, they are usually found as pioneer species in disturbed areas. Another reason is that the early successional stage of vegetation in disturbed areas is characterized by the replacement of annual plants by perennial plants. Consequently, a decrease in monocotyledons and an increase in dicotyledons might be expected (Uhl, Jordan, 1984). Therefore, from the colonization stage to the climax (primary forest) stage, the ratio of monocotyledons to dicotyledons may be expected to decline.

METHODOLOGY

Study site

The study was conducted at the Sirena station in Corcovado National Park in Costa Rica, Central America (figure 1). Costa Rica is located in the humid tropics where only minimal seasonal water shortages occur, if any. Mean monthly temperatures do not fall much below +25 °C and rarely exceed +35 °C. Radiation levels are high; the air is always humid and seasonal temperature variations are usually smaller than diurnal variations, which may vary by as much as +10 °C. Some thirteen ecosystems have been identified within Corcovado National Park (TOSI, 1975; BOZA, MENDOZA, 1981; VAUGHAN, 1981). The vegetation is characterized by:
1. Mangrove swamps, where up to five tree species occur, including *Pelliciera rhizophorae, Rhizophora racemosa, Crinum erubescens* and *C. brevilobatum*;
2. Lagoon, replenished in each rainy season by up to 1 m of standing fresh water, and supporting a floating central mat of abundant herbaceous vegetation including *Eichhornia crassipes, Pistia stratiotes, Salvinia* sp. and *Utricularia* spp.;
3. Herbaceous marshland bordering the lagoon, with *Hymenachne* sp., *Panicum maximum*, *Ludwigia* sp., *Polygonum* sp. and *Aeschynomene* sp.;
4. A strip of palm swamp (jolillo forest) around the marsh, dominated by virtually pure stands of *Raphia taedigera*, which has leaves nearly 15 m in length.;
5. A variety of swamp forests, peripheral to the palm swamp at first, with *Andira inermis, Carapa guianensis, Crateva tapia* and *Luehea seemannii*, then with large well-buttressed canopy trees, stilt-rooted sub-canopy trees and a fairly open palm under-storey further inland (*Crysophila guagara, Prestoea decurrens*), commonly including *Carapa guianensis, Erythrina lanceolata, Grias fendleri, Mouriri* sp., *Pterocarpus officinalis* and *Virola koschnyi*. Lower forests are found on particularly poorly drained alluvial soils and estuaries, with, for example, *Mora oleifera* (which has the largest dicotyledon seed, averaging c. 500 g), *Pterocarpus officinalis, Hasseltia* sp. and *Pachira aquatica*.

6. Gallery forest on well-drained alluvial flats and terraces, with giant *Anacardium excelsum* and other large trees including *Caryocar costaricense, Hernandia didymantha, Pterygota excelsa, Terminalia oblonga* and an epiphyte-rich emergent of *Ceiba pentandra* in low-lying areas;
7. Plateau forest: an awe-inspiring environment with a very high density of large trees such as *Vantanea barbourii*. Other common trees include *Anaxagorea costaricensis, Aspidosperma spruceanum, Brosimum utile, Calophyllum longifolium, Carapa guianensis, Caryocar costaricense, Chrysochlamys* sp., *Couratari guianensis, Minquartia guianensis, Qualea paraense, Symphonia globulifera, Tetragastris panamensis, Trichilia* sp. and *Welfia georgii*;
8. Mountain or upland forest: this extensive, 5-stratum ecosystem has a high diversity of species, featuring very tall canopy trees sometimes with no branches up to a height of 35 m or with spectacular buttresses, and abundant palms (*Iriartea deltoidea, Socratea exorrhiza*), lianas and vines. An absence of dominance is characteristic among the common tree species, which include *Ardisia cutteri, Aspidosperma spruceanum, Brosimum utile, Heisteria longipes, Poulsenia armata* and *Sorocea cufodontisii*;
9. Cloud forest, with many epiphytes, tree ferns (possibly *Cnemidaria choricarpa, Cyathea trichiata*), *Quercus* spp. (e.g. *Q. insignis, Q. rapurahuensis*), *Alfaroa guanacastensis, Oreomunnea pterocarpa* and *Ticodendron incognitum*.

Data collection

The vegetation survey was conducted in November 2008 in the primary and secondary forests using a balanced, completely randomized design. The plots were right-angled triangles with sides of 5 × 5m. The use of small triangles as plots provided an easy and accurate method for counting all the plants in an area. By working inwards from the corners, individuals were sorted into four plant crown diameter classes: class 1 = 0-30 cm, class 2 = 30-100 cm, class 3 = 100-300 cm and class 4 = › 300 cm. This measure was chosen because it gives a good idea of how much sunlight a plant is able to capture and how far it succeeds in shading out other plants. In an environment where light is the limiting factor, this seemed to be a good approximate measure of plant abundance. For practical reasons, epiphytes and vines were excluded from this study. All other plants were counted into one of these four crown size classes as either monocotyledons or dicotyledons, based on leaf venation. The average amount of sky seen by looking up from the three corners of the triangle was also noted, as a percentage. A total of 40 plots were sampled, 20 in the primary forest (photo 1) and 20 in the secondary forest (photo 2).

Figure 1.
Corcovado National Park in Costa Rica, Central America.

Data analysis

The composition of the plant classes in each plot was described by the following parameters.

$$\text{Density} = \frac{\text{Individuals number of a plant class in a plot}}{\text{Plot surface area}}$$

$$\text{Relative Density} = \frac{\text{Individuals number of a plant class in a plot}}{\text{Total individuals number in a plot}} \times 100$$

Statistical analyses were performed using the Minitab program. The data were checked whether they fulfilled the assumptions for the parametric tests and they were found not normally distributed. So, a logarithmic transformation was performed on the data before analysis. Plant densities, light transmittance and crown size class distribution were analysed using ANOVA. The forest type, plant life-history and crown size class were set as categorical factors.

Results

Densities: all plants

The mean density of plants was significantly higher in the secondary than the primary forest ($F_{1,\,78}$ = 29.64, P < 0.001), at 50,380 and 23,360 individuals/ha, respectively. Size class distributions were similar in both forests. The distribution patterns formed a reverse "J" shaped curve: the majority of plants were found in the first crown size class and the density of individuals diminished as the size class increased (figure 2). The number of class 1 individuals in the secondary forest was twice as high as in the primary forest.

Light transmittance differed significantly between the two forest types ($F_{1,\,68}$ = 10.76, P < 0.001). The mean percentages of visible sky were 8±2 (mean ± SE %) in the primary forest and 18±2 in the secondary forest.

Densities: monocotyledons vs. dicotyledons

There were significantly more monocotyledon and dicotyledon individuals in the secondary forest than in the primary forest ($F_{1,\,304}$ = 19.57, P < 0.001). The mean density of dicotyledons in both forest types was significantly greater than the mean density of monocotyledons (Figure 3, $F_{1,\,304}$ = 5.71, P = 0.017). There was no significant difference in the monocotyledon/dicotyledon ratio between the two forests (Figure 4, $F_{1,\,76}$ < 0.001, P = 0.99).

Stand structure of monocotyledons and dicotyledons

The structure of the crown size class distribution was similar for both monocotyledons and dicotyledons, and for both primary and secondary forest (figure 5, figure 6). There was a significant difference in plant abundance between different class sizes, depending on the type of forest (table I). Within each plant group, the number of individuals in each size class also differed significantly (table I). The number of individuals in a given size class varied significantly in terms
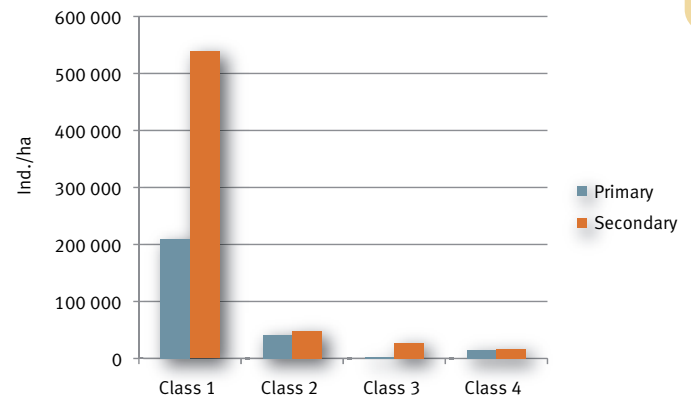

Figure 2.
Size class distribution of the total plant population in the primary and secondary forests.
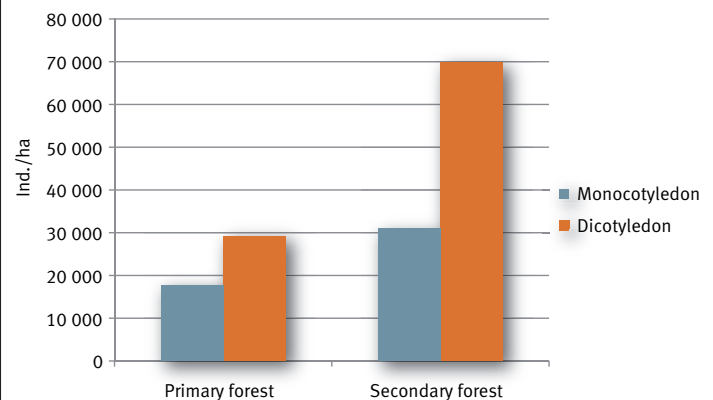

Figure 3.
Mean density of monocotyledons and dicotyledons in the primary and secondary forests.
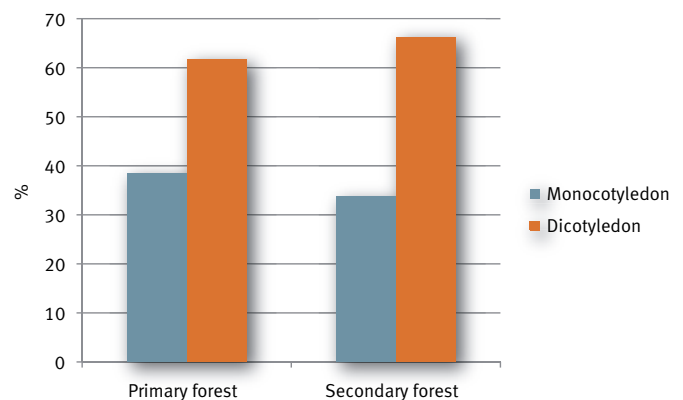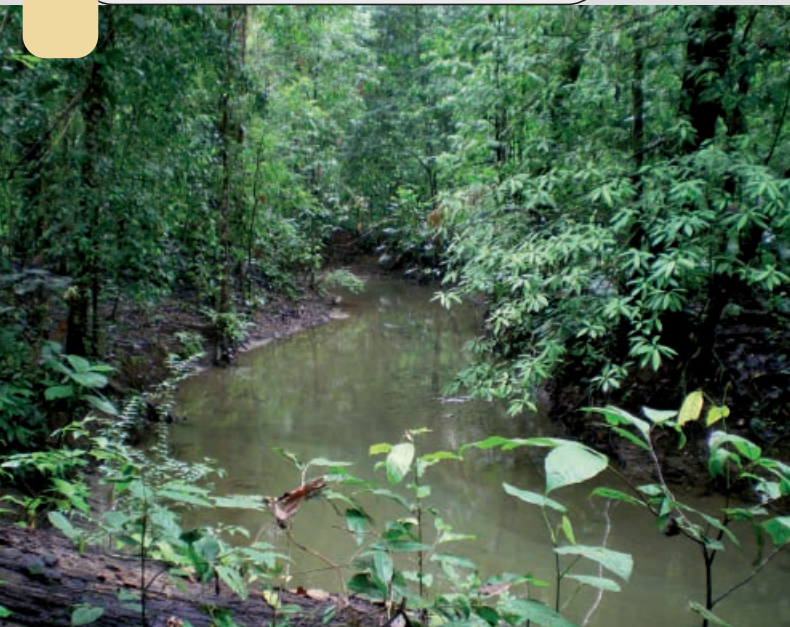

Figure 4.
Relative mean density by class in the primary and the secondary forests.

of plant groups and forest type (table I). This significant interaction indicates the differences in the contributions of monocotyledons and dicotyledons to the stratification of primary and secondary forest.

Photograph 3.
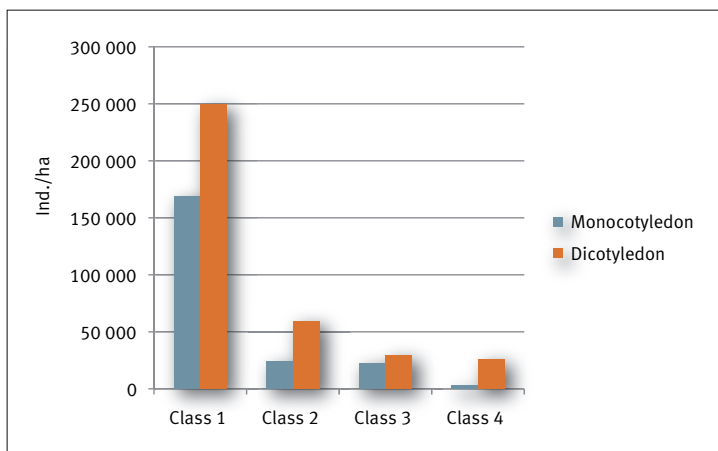River flowing through secondary forest.
Photograph C. González Aloson.

Figure 5.
Class distribution of monocotyledons and dicotyledons
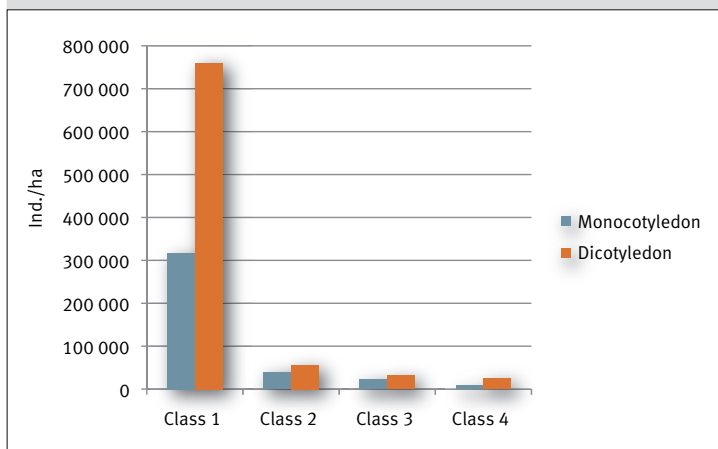in the primary forest.

Figure 6.
Class distribution of monocotyledons and dicotyledons
in the secondary forest.

Discussion

Our results show that the vegetation size class structure of the primary and secondary forests was similar. A reverse "J" shaped curve indicates excellent regeneration dynamics, with dead plants compensated by the growth of individuals in low size classes. Seedling establishment is an important part of vegetation dynamics, as the recruitment of seedlings determines the composition of the future population (VIEIRA, SCARIOT, 2006). Many authors regard this structure (reverse "J" shaped curve) as an ideally stable plant population because it is self-maintaining (PETER, 1997; ZEGEYE *et al.*, 2006). This is why tropical ecosystems are considered among the most stable in the world.

With regard to density, our results indicate that the secondary forest was denser than the primary forest and that it also had more seedlings and saplings. This is probably due to the canopy crown cover. More light transmittance in the secondary forest stimulates the germination and growth of pioneer species (BROKAW, 1985; OSBORNE, 2000). In the successional process, plant density rises in the secondary forest, reaches a peak, declines due to high seedling and sapling mortality, and eventually forms primary forest. Large-scale losses of seeds, seedlings and saplings are accounted for by seed aging, the quality of the seed germination medium (soil flooding and compaction), failure of seed to germinate, competition for light and nutrients, predators, pathogens and disturbances (KOZLOWSKI, 2002).

A further analysis revealed a greater difference between class one and class two densities in the secondary forest when compared to the primary forest, which may be partially explained by the fact that some herbivores, such as tapirs, prefer to feed in secondary forest (FOERSTER, VAUGHAN, 2002). Herbivores produce various effects on vegetation succession. By selectively removing biomass, grazing and browsing regulate interaction and competition between plants. Trampling and heavy browsing by herbivores may contribute to a steep decline in class one plants. The plants that survive towards the end of a successional sequence are those which compete well and are best suited to the particular local conditions.

The results show that the stand structure and the variation in monocotyledon and dicotyledon densities between the forest types were similar to the overall structure of the two forests. The explanations for similarities and differences in all plants are also valid for monocotyledons and dicotyledons. Moreover, within each forest type, more dicotyledon seedlings are lost than monocotyledon seedlings. This could be explained by a preference for dicotyledons among herbivores because of their toughness and leaf conformations (GRUBB *et al.*, 2007). By reducing dicotyledon biomass, grazing can reduce competition from the seedling layer, thereby increasing monocotyledon production and regeneration.

Within each forest, the results indicate that dicotyledons are denser than monocotyledons. This could be explained by the greater diversity of dicotyledons compared to monocotyledons in the plant kingdom (175,000 species vs. 50,000 species), by environmental factors (nutrient and light availability) and by their life-histories.

Because monocotyledons derive from the primitive dicotyledons (CRONQUIST, 1965), they are more apt to colonize harsh and barren areas, which is why their density is greater than that of dicotyledons in desert and savannah areas (OSBORNE, 2000). The early successional stage of tropical rainforest vegetation is characterized by the replacement of annual plants by perennial plants, and a corresponding decrease in monocotyledons and an increase in dicotyledons (UHL, JORDAN, 1984; BROKAW, 1985; OSBORNE, 2000; DE CAUWER *et al.*, 2006). As the succession from secondary forest to the primary forest proceeds, the ratio of monocotyledons to dicotyledons should accordingly decrease with time. However, our finding does not bear out this assumption.

The conclusion, therefore, is that from the colonisation of bare soil to the primary forest stage, the monocotyledon/dicotyledon ratio changes in three phases. The ratio is highest in the first phase. Shifting agriculture and cattle ranching cause forest clearing, litter burning, soil damage and erosion leading to bare soil. This plant succession stage is characterized by rapid colonisation of the bare soil by mainly herbaceous plants dominated by monocotyledons (grasses). In the second phase, the ratio decreases. This successional stage is characterized by the replacement of annual plants (monocotyledons) by perennial plants (monocotyledons and dicotyledons), with a corresponding decrease in monocotyledons and an increase in dicotyledons. Succession takes place because the environmental conditions in a particular place change over time. Each species is adapted to thrive and compete best against other species under a very specific set of environmental conditions. If these conditions change, then the existing species will be replaced by a new set of species that are better adapted to the new conditions. In the third phase, the ratio reaches its lowest level and then remains more or less constant. This plant succession stage is characterized by positive interactions and interdependence among plant communities. A high frequency of minor disturbances at this stage may serve to homogenize growing conditions. Frequent disturbances such as tree fall offer more opportunity for different growth strategies to be effective, thus minimizing the success of monocotyledons over dicotyledons.

Photograph 4.
Two successional stages in colonisation
(first and third phase).
Photograph S. Ayangma.

Table I.
Summary of the three-way ANOVA for the effects of plant group and forest type on plant contribution in the Sirena station rainforest.

Factors	d.f.	F	P
Forest type	1	22.47	‹ 0.001
Plant group	1	19.57	‹ 0.001
Size class	3	94.16	‹ 0.001
Forest × plant group	1	5.71	0.017
Forest × size class	3	20.99	‹ 0.001
Plant group × size class	3	11.76	‹ 0.001
Forest × plant group × size class	3	6.75	‹ 0.001
Residual	304		

References

APG II, 2003. An update of Angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society, 141: 399-436.

BARABÉ D., BROUILLET L., 1982. Commentaires sur le système de classification des Angiospermes de Takhtajan. Acta Biotheoretica, 31 : 127-141.

BOZA M. A., MENDOZA R., 1981. National Parks of Costa Rica. Madrid: INCAFO.

BROKAW N. V. L., 1985. Gap-phase regeneration in a tropical forest. Ecology, 66: 682-687.

CRONQUIST A., 1965. The status of the general system of classification of flowering plants. Annals of the Missouri Botanical Garden, 52 (3): 281-303.

DE CAUWER B., REHEU D., D'HOOGHE K., NIJS I., MILBAU A., 2006. Disturbance effects on early succession of field margins along the shaded and unshaded side of a tree lane. Agriculture, Ecosystems and Environment, 112: 78-86.

FNT, 1992. Evaluación ecológica rápida þ Península de Osa. Programa BOSCOSA, con la asistencia de WWF-US. Fundación Neotrópica (FNT), San José, Costa Rica, 136 p. + annexes.

FOERSTER C. R., VAUGHAN C., 2002. Home Range, Habitat Use, and Activity of Baird's Tapir in Costa Rica. Biotropica, 34 (3): 423-437.

GRUBB P. J., JACKSON R. V., BARBERIS I. M., BEE J. N., COOMES D. A., DOMINY N. J., DE LA FUENTE M. A. S., LUCAS P. W., METCALFE D. J., SVENNING J. C., TURNER I. M., VARGAS O., 2007. Monocot Leaves are Eaten Less Than Dicot Leaves in Tropical Lowland Rain Forests: Correlations with Toughness and Leaf Presentation. Annals of Botany, doi:10.1093/aob/mcn047.

GENTRY A. H., DODSON C., 1987. Contribution of nontrees to species richness of a tropical rein-forest. Biotropica, 19 (2): 149-156.

HARTSHORN G. S., 1983. Plants: introduction. Site descriptions: La Selva. In Janzen D. H. (Ed.), Costa Rican natural history. University Chicago Press, Chicago: 136-140.

JANZEN D. H., DIRZO R., GREEN G. C., ROMERO J. C., STILES S. G., VEGA G., WILSON D. E., 1985. Corcovado National Park: a perturbed rainforest ecosystem. A Report to the World Wildlife Fund. San José: World Wildlife Fund, 79 p.

KOZLOWSKI T. T., 2002. Physiological ecological of natural regeneration of harvested and disturbed forest stands: implications for forest management. Forest Ecology and Management 158: 195-221.

LEWIS B., 1984. El uso de los recursos naturales en la Peninsula de Osa. San José: Consejo Nacional de Investigaciones Científicas y Tecnológicas.

MACÍA M. J., 2008. Woody plants diversity, floristic composition and land use history in the Amazonian rain forests of Maladi National Park, Bolivia. Biodiversity Conservation, 17: 2671-2690.

OOSTERHOORN M., KAPPELLE M., 2000. Vegetation structure and composition along interior-edge-exterior gradient in Costa Rican mountain cloud forest. Forest Ecology and Management, 126: 291-307.

OSBORNE P. L., 2000. Tropical ecosystems and ecological concepts. University press, Cambridge, 464 p.

Photograph 5.
Secondary forest.
Photograph F. Massiot.

PETERS C. M., 1997. Exploitation soutenue de produits forestiers autres que le bois en forêt tropicale humide : Manuel d'information d'écologie. Programme d'appui à la biodiversité, n° 2, Corporate press. Inc. Landover, M.D., 49 p.

TAKHTAJAN A. L., 1953. Phylogenetic principles of the system of higher plants. Botanical Review, 19 (1): 1-45.

TOSI J. A., 1975. The Corcovado Basin on the Osa Peninsula. In Tosi J. A., Jr., Potential national parks, nature reserves, and wildlife sanctuary areas in Costa Rica: a survey of priorities. Centro Científico Trop., San José, Separate, 12 p.

UHL C., JORDAN C. F., 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology, 65: 1476-1490.

VAUGHAN C., 1981. Parque Nacional Corcovado, Plan de manejo y desarrollo. Heredia, Costa Rica, Editorial de la Universidad Nacional.

VIEIRA D. L. M., SCARIOT A., 2006. Principle of natural regeneration of tropical dry forests restoration. Restoration Ecology, 14: 11-20.

ZEGEYE H. L., TEKETAY D., KELBESSA E., 2006. Diversity, regeneration status and socio-economic importance of the vegetation in the islands of Lake Ziway, south-central Ethiopia. Flora, 201: 483-498.