Rodriguésia 63(2): 419-427. 2012
http://rodriguesia.jbrj.gov.br

Does selective logging affect the leaf structure of a late successional species?

Como o corte seletivo de madeira pode afetar a estrutura foliar de uma secundária tardia?

Guilherme Rodrigues Rabelo[1], *Denise Espellet Klein*[1,2] & *Maura Da Cunha*[1,3]

Abstract

The anatomical characteristics of both sun and shade leaves of *Alseis pickelii* were investigated in order to evaluate the consequences of selective logging (in seasonally dry Atlantic Forest) on the leaf structure of this species. Fully expanded sun and shade leaves were collected in two distinct stands of *tabuleiro* forest; a stand of recently logged forest and an unlogged stand. Only leaves from the unlogged stand revealed significantly different magnitudes of response to light regimes, producing leaves with structural characteristics associated with different levels of irradiance. The sun leaves from this stand had a thicker adaxial surface, mesophyll, palisade and spongy parenchyma, a secondary cell wall of fibers and a lower leaf area compared with the shade leaves. However, in the logged stand, the leaf cuticles of sun and shade leaves showed no significant differences, although the leaf area of the sun leaves was higher than the shade leaves. According to these data, we concluded that the unlogged stand produced typical "sun" and "shade" leaves. In contrast, leaves from the logged stand showed a lower variation of types, where neither typical "sun" nor typical "shade" leaves were produced, suggesting lower leaf plasticity of this late successional tree in this area.

Key-words: selective logging, leaf plasticity, sun and shade leaves, leaf structure, *tabuleiro* forest.

Resumo

As características anatômicas de folhas de sol e sombra de *Alseis pickelii* foram investigadas a fim de se avaliar as consequências do corte seletivo de madeira sobre a estrutura foliar em uma floresta atlântica estacional semidecidual. Folhas expandidas de sol e de sombra foram coletadas em dois distintos setores da mata, setor explorado (área com recente atividade de corte seletivo), e setor preservado. Somente folhas do setor preservado revelaram significantes diferenças de resposta aos regimes de luz, produzindo folhas com características estruturais nitidamente associadas com diferentes níveis de irradiação. Folhas de sol deste setor apresentaram maiores espessuras da superfície adaxial, mesofilo, parênquima paliçádico e lacunoso, parede secundária das fibras e menor área foliar comparada às folhas de sombra. Entretanto, no setor explorado, as cutículas das folhas de sol e sombra não apresentaram diferenças significativas e as áreas foliares das folhas de sol foram maiores que a das folhas de sombra. De acordo com estes resultados, conclui-se que o setor preservado produziu árvores com típicas folhas de "sol" e "sombra". Em contraste, no setor explorado as árvores apresentaram menor variação nos tipos de folhas, onde nem típicas folhas de "sol" ou de "sombra" foram produzidas, sugerindo menor plasticidade desta espécie secundária tardia nesta área.

Palavras-chave: corte seletivo, plasticidade foliar, folhas de sol-sombra, estrutura foliar, floresta de tabuleiros.

Introduction

Selective logging is considered one of the main causes of treefall gaps in Brazilian forests (Rondon Neto *et al.* 2000). This type of disturbance causes widespread damage to surrounding trees, subcanopy vegetation, and soils; and also impacts the hydrological processes, erosion, fire, carbon storage, and animal species (Nepstad *et al.* 1995;

[1] Universidade Estadual do Norte Fluminense, Centro de Biociências e Biotecnologia, Lab. Biologia Celular e Tecidual, Av. Alberto Lamego 2000, 28013-602, Campos dos Goytacazes, RJ, Brazil. guilherme.rabelo@gmail.com
[2] Universidade Federal do Estado do Rio de Janeiro, Instituto de Biociências, Depto. Botânica, Av. Pasteur 458, 22290-240, Rio de Janeiro, RJ, Brazil. klein_d_e@yahoo.com.br
[3] Corresponding author: maurauenf@gmail.com

Veríssimo *et al.* 1992; Curran *et al.* 2004). Unlike deforestation, which can be observed from satellites, selective logging causes a spatially diffuse thinning of large trees, which is hard to monitor using satellite images (Asner *et al.* 2005). The most obvious impact of selective logging is the increase in canopy openness, which exposes organisms to changes in light, humidity, and temperature (Almeida 1989).

This process requires acclimation of shade plants, from the understory, to sunlight, and demonstrates the close association between the anatomical adaptation of leaves and the efficiency of photosynthesis when plants grow under different levels of light (Carpenter & Smith 1981; Ashton & Berlyn 1992). Although leaf anatomy should not be used solely as a basis for the prediction of a species' ability to acclimate, the variation found in the anatomy of leaves provides an indication of the ecological plasticity of a species (Strauss-Debenedetti & Berlyn 1994).

The ecological effects of variations in light, humidity, and temperature on leaf anatomy have been studied; however, most of these studies were carried out in greenhouses (e.g., Chabot *et al.* 1979; Tognetti *et al.* 1998; Lee *et al.* 2000; Paiva *et al.* 2003) compared to native tropical populations (Chazdon & Kaufmann 1993; Rôças *et al.* 1997, 2001; Hlwatika & Bhat 2002). The effects of microclimatic alterations caused by selective logging on the plasticity of leaf anatomy have not been studied. The present study proposes an analysis that can be used to determine the acclimation capacity of *Alseis pickelii* Pilger et Shmale.

Alseis pickelii (Rubiaceae, Cinchonoideae) is a late successional tree, 10 to 13 meters tall, which occurs in the understory of tropical deciduous forests, such as xeric shrublands and deciduous seasonal forests (Pereira Moura 2001). This type of forest has diminished over time due to deforestation for charcoal production, farming (e.g., pasture, sugar cane, and pineapple), and logging (Villela *et al.* 2006). The profile diagrams of unlogged and logged stands have shown differences in canopy structure, mainly in height and in crown connectivity (Villela *et al.* 2006).

Most plant species have the ability to develop distinct leaves when growing at different light levels (Chazdon & Kaufmann 1993; Lee *et al.* 2000), and a wide amount of leaf variation has been described in several species from the Brazilian Atlantic Forest that were subjected to extreme conditions of sun and shade (Scarano *et al.* 1999, 2002; Rôças *et al.* 2001; Mantuano *et al.* 2006; Pereira *et al.* 2009). The present investigation was carried out in order to identify the effects of light on the leaf structure of *A. pickelii*, by comparing sun and shade leaves from two stands (unlogged and logged) where this species is exposed to different light, humidity and temperature regimes. The study areas are in the most important remnant of *tabuleiro* forest (a type of lowland Atlantic forest) in the state of Rio de Janeiro, Brazil. Our hypothesis is that selective logging affects the leaf structure and consequently the leaf acclimation capacity of this species.

Material and Methods

Study area

The study areas are located in the Guaxindiba Ecological Reserve in the São Francisco do Itabapoana district (21°24'S, 41°04'W) of northern Rio de Janeiro, Brazil. This is the largest fragment of a lowland forest on Tertiary formations (ca. 1200 ha according Villela *et al.* 2006), known as *tabuleiro* forest (RadamBrasil 1983). The elevation of this region ranges from 20 m to 200 m, which distinguishes this lowland forest from other regions within the Atlantic Forest along the Brazilian coast. *Tabuleiro* forest is classified as seasonal, semideciduous, lowland forest due to its phytogeographic features (Veloso *et al.* 1991). The climate can be classified as Aw, according to Köppen (1948), and is seasonal, with an intense dry season from May to August (RadamBrasil 1983). Mean annual rainfall is ca. 1000 mm; the wettest month is December and the driest is August (Villela *et al.* 2006). The mean annual temperature is 23°C (RadamBrasil 1983). The soils are ultisols (USDA classification), with a low capacity of water retention and low levels of nutrients (Villela *et al.* 2006).

Leaf samples of *Alseis pickelii* were collected in two distinct stands at the Guaxindiba Ecological Station, during February to April of 2006". One stand, here referred to as the "logged stand" (LS), was part of an area of recently logged forest (less than five years ago). In the second stand, here referred to as the "unlogged stand" (US), selective logging has not occurred for the last 45 years and is, at this time, without traces of selective logging or forest fires (Souza 2005). The

noticeable differences between the two stands are canopy structure and crown connectivity. Climatic observations and canopy cover (Tab. 1) measurements were made over the summer and winter at each site, at the four cardinal points for each of five chosen individuals at both US and LS. All climate observations were made at breast height and measurements were carried out between 11:30h and 13:30h; additionally, open fields were measured to provide a better comparison among the forest stands. Photosynthetic active radiation (PAR) was measured with a LI-190SA quantum sensor adapted to a LI-250A Light Meter (Li-Cor Inc.). Air temperature (°C) and air humidity (%) were measured with HT-300 thermo-hygrometer (Instrutherm), and canopy cover (%) was measured using a 1 × 1 meter quadrat (Freitas *et al*. 2002).

Sampling, measurements and statistical analyses

For the anatomical analysis, seven fully expanded leaves growing in the sun and seven in the shade were collected from five adults randomly chosen in each of the two stands. The leaves were classified according to the amount of canopy light they were exposed to.

Fragments of the middle third of the leaf blade were fixed for two hours in solutions of 2.5% glutaraldehyde and 4.0% formaldehyde in a 0.05 M sodium cacodylate buffer, to pH 7.2, at room temperature. After being rinsed with the same buffer, the samples were post-fixed with 1.0% osmium tetroxide in a 0.05 M sodium cacodylate buffer (pH 7.2) for one hour. Subsequently, the samples were dehydrated in a graded series of acetone solutions. The material was infiltrated and embedded in epoxy resin. Transverse sections of approximately 0.70 µm were obtained and stained with toluidine blue (0.1% aqueous solution) (Johansen 1940). The slides were mounted in appropriate resin. Anatomical descriptions and measurements of the epidermis, mesophyll, and vascular bundles were made with image analysis software (analySIS®) using an Axioplan Zeiss microscope. For scanning electron microscopy, the samples were fixed, post-fixed, dehydrated the same way as used for light microscopy, rinsed in the same buffer, and dehydrated in an ascendant acetone series. Afterwards, the samples were CO_2 critical-point-dried (CPD 030 – Baltec). Dried samples were adhered to stubs with carbon adhesive tape (3M) and sputter coated with 20 nm gold (SCD 050 – Baltec). The material was observed using a ZEISS DSM962 operating at 25 kV. Stomatal density was estimated from fragments of the leaf blades that were cleared by dipping the samples in 80% lactic acid and then autoclaved at 1 atm and 120 °C, for 25 minutes, to separate the epidermis (O'Brien & McCully 1981). Counting and measurements were obtained using a sample size of 25 fields that were 0.24 mm^2. To test for phenolic compounds, a ferric chloride histochemical test was carried out for free-hand sections of newly collected material (Johansen 1940). Differences among leaf types and stands were tested by one-way analysis of variance (ANOVA), followed by Tukey's multiple comparison test (Zar 1996), and differences in microclimatic observations and canopy cover measurements were analyzed using the T-test (Zar 1996). The statistical analyses were performed using the statistical software package STATISTICA (StatSoft, USA).

Table 1 – Climate observations and canopy cover measurements for each site where *Alseis pickelii* was sampled in the Guaxindiba Ecological Station, Rio de Janeiro State – Brazil. US – Unlogged stand; LS – Logged stand. Values representing the average of two seasons (summer and winter), measured between 11:30h and 13:30h.

Parameters	**US**	**LS**
Air temperature (°C)†	(-) 3.3	(-)1.0 *
Air humidity (%)†	(+)13.5	(+)12.0 *
Canopy cover (%)	95	70 *
Photosynthetic active radiation (µmol m^{-2} s^{-1})	15 ± 19	340 ± 570 *

† Air temperatures were lower (-) and humidity was higher (+) than in open fields.

* Statistically different parameters (T-test $p < 0.05$).

Results

Despite phenotypic variations, *Alseis pickelii* shared some anatomical features irrespective of site and microhabitat (Fig 1). These features included: an adaxial and abaxial surface with a single cell layer, sinuous anticlinal cell walls only in the adaxial epidermis, paracytic stomata only on abaxial surfaces, dorsiventral mesophyll, a collateral arrangement in the vascular system, parenchymatic and fibrous bundle sheath cells, bundle sheath extension prolonged to the adaxial epidermis, and presence of phenols in the cells of spongy parenchyma.

Figure 1 and Table 2 compare the leaf anatomical structure of individuals from the logged and unlogged stands. When comparing sun and shade leaves from the unlogged stand, the adaxial surface was thicker in the former. No significant difference was found in the adaxial surface of sun and shade leaves from the logged stand (Fig. 1a–d). The abaxial surface showed no significant difference between sun and shade leaves from both stands (Tab. 2). The hypostomatic leaves of *A. pickelii* showed significantly different density of stomata in the sun and shade leaves of both stands, and higher occurrence in the sun leaves of both stands (Tab. 2). The thickness of the adaxial cuticle in sun and shade leaves of the logged stand was greater than the width in leaves of the unlogged stand; however, no significant difference was found in the sun and shade leaves from the logged stand (Tab. 2).

The dorsiventral mesophyll in the sun leaves of the unlogged stand had 2–4 cell layers of palisade parenchyma and 3–5 layers of spongy parenchyma. In contrast, shade leaves from the unlogged stand and both leaf types from the logged stand had significantly fewer cells and thinner tissues (Fig. 1 a-d; Tab. 2); 2–3 cell layers of palisade parenchyma and 3–4 layers of spongy parenchyma. Phenolic compounds were found in the spongy parenchyma mainly in the sun leaves from the unlogged stand and both leaves from the logged stand (Fig. 1 e–h).

The vascular system of *A. pickelii* presented a collateral arrangement, with parenchymatic and fibrous bundle sheath cells (Fig. 1 i) and a bundle sheath extension (Fig. 1 j). The secondary cell wall thickness of the perivascular fibers was wider in the sun leaves compared to the shade leaves from the unlogged stand, and no significant difference was found in the logged stand (Tab. 2). The leaf area was significantly different between sun and shade leaves from both stands. Sun leaves from the unlogged stand had lower area compared to shade leaves. However, this did not occur in leaves from the logged stand, where sun leaves had higher leaf area compared to shade leaves (Tab. 2).

Discussion

In spite of the microclimatic differences between the unlogged and logged stands, *Alseis pickelii* did not produce leaves with structural characteristics associated with different levels of irradiance in the same way in both stands. Only leaves from the unlogged stand revealed different magnitudes of response to light regimes, producing typical "sun" and "shade" leaves. In contrast, leaves from the logged stand showed lower phenotypic plasticity, which means that it was not possible to structurally distinguish sun leaves from shade leaves in this stand.

The occurrence of a thicker adaxial surface in the sun leaves of the unlogged stand appears to have had a greater role in protecting the leaves from excess irradiance (Strauss-Debenedetti & Berlyn 1994). Stomata density has already been cited for other species as being directly related to the amount of exposure to both light and water (Bastos *et al.* 1993; Rôças *et al.* 1997, 2001), and a greater number of stomata were found in the sun leaves of *A. pickelii* from both stands, allowing for efficient gas exchange (Lleras 1977), better control of transpiration, and possibly the avoidance of excessive water loss (Weyers & Meidner 1990). There was no significant difference in the width of the cuticles of the sun and shade leaves from the logged stand but the values were higher than for the leaves from the unlogged stand. This was probably a response to higher exposure to light (Cutler *et al.* 1982) and suggests a homogeneous environment in the logged stand.

The typical sun and shade leaves observed in the unlogged stand showed a classic pattern of response and adaptation to light exposure in the leaf tissues (Björkman 1981). The thicker palisade and spongy parenchyma from the sun leaves in this stand represents leaf tissue that maximizes light absorption and carbon fixation. Tubular palisade cells facilitate the penetration of direct sunlight, and thicker spongy parenchyma helps scatter the light, thus increasing the chance that light will be absorbed for photosynthesis

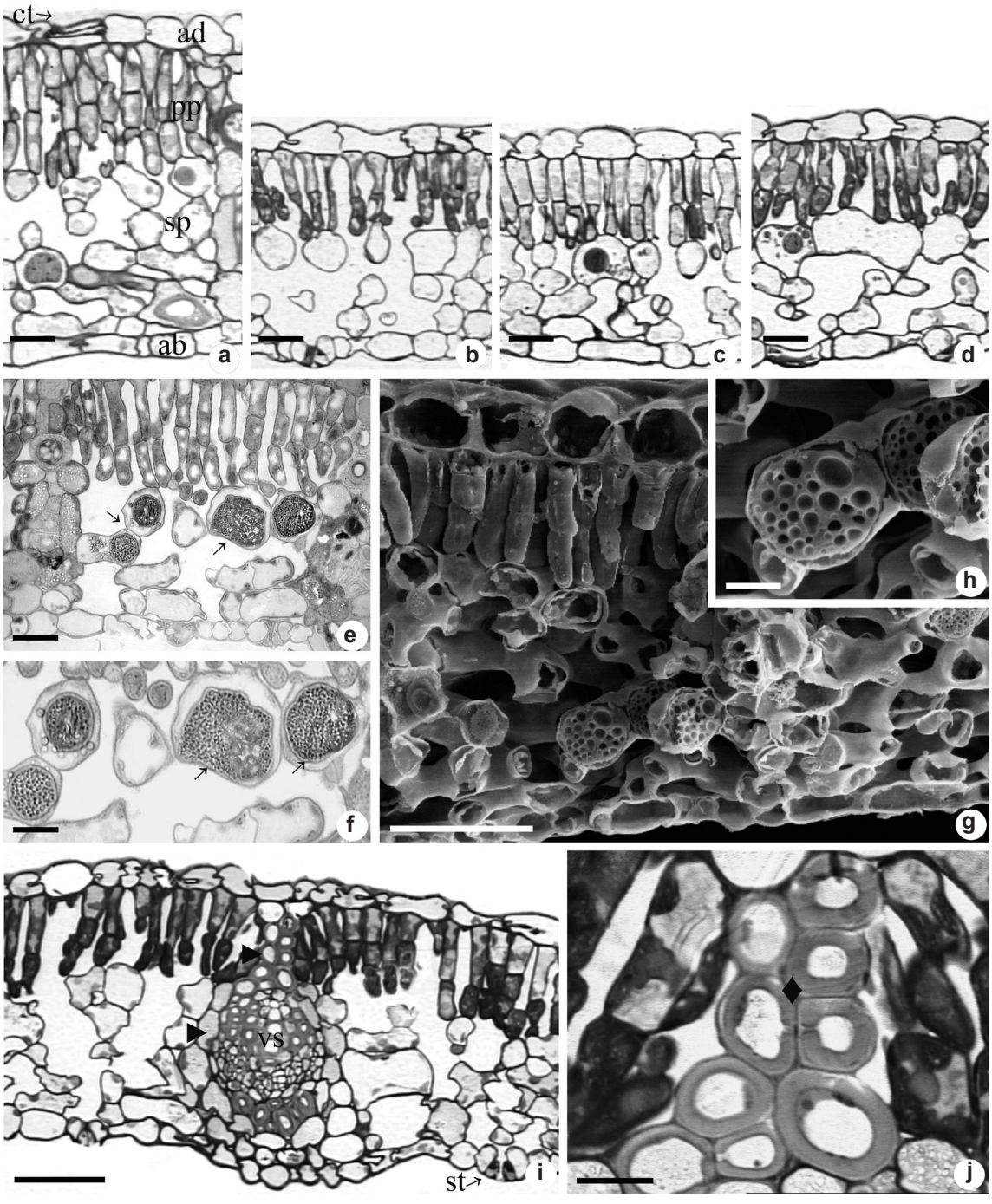

Figure 1 –Transverse sections of the sun (a) and shade (b) leaves of *A. pickelii* from the unlogged stand (UL) and sun (c) and shade (d) leaves from the logged stand (LS). Arrow indicates phenolic substances (e, f) in the cells of spongy parenchyma. Scanning electron microscopy of leaf blade (g). Detail of phenolic substances (h) in spongy parenchyma. Leaf transverse section showed a collateral arrangement in the vascular system and stomata in the abaxial surface, with parenchymatic and fibrous bundle sheath cells (i) and bundle sheath extension (j). ct - cuticle; ad - adaxial surface; pp - palisade parenchyma; sp - spongy parenchyma; ab - abaxial suface; st - stomata; vs - vascular system; ▶ - parenchymatic and fibrous bundle sheath; ♦ - bundle sheath extension. Bars: Figs. a-d and e = 25 µm; Fig. f = 15µm; Fig. g and i = 50µm; Fig. h and j = 10 µm.

Table 2 – Anatomical and morphological traits of sun and shade leaves of *Alseis pickelii* from both unlogged (US) and logged (LS) stands. (N) - Number of measures; (Mean ± S.D) – Mean ± standard deviations.

Parameters	Stands	Leaf	N	Mean ± S.D.	F
Adaxial surface thickness (µm)	US	Sun	75	18 ± 5 a	12.97
		Shade	75	14 ± 4 b	
	LS	Sun	60	15 ± 4 b	
		Shade	60	13 ± 4 b	
Abaxial surface thickness (µm)	US	Sun	75	14 ± 3 a	7.14
		Shade	75	12 ± 3 ab	
	LS	Sun	60	12 ± 3 b	
		Shade	60	11 ± 3 b	
Stomata/0.01mm^2	US	Sun	387	3.6 ± 1.5 a	16.07
		Shade	516	2.7 ± 1.3 b	
	LS	Sun	273	3.6 ± 1.3 a	
		Shade	376	2.4 ± 1.2 b	
Cuticle thickness (µm)	US	Sun	125	2.1 ± 0.9 a	37.98
		Shade	124	1.2 ± 0.8 b	
	LS	Sun	177	3.3 ± 2.3 c	
		Shade	149	3.3 ± 2.7 c	
Mesophyll thickness (µm)	US	Sun	75	152 ± 13 a	89.47
		Shade	75	127 ± 32 b	
	LS	Sun	60	102 ± 19 c	
		Shade	60	99 ± 16 c	
Palisade thickness (µm)	US	Sun	75	57 ± 7 a	47.81
		Shade	75	46 ± 14 b	
	LS	Sun	60	40 ± 8 c	
		Shade	60	41 ± 6 c	
Spongy thickness (µm)	US	Sun	75	95 ± 14 a	73.12
		Shade	75	81 ± 21 b	
	LS	Sun	60	62 ± 15 c	
		Shade	60	59 ± 13 c	
Secondary cell wall thickness of perivascular fibers (µm)	US	Sun	142	7 ± 1 a	26.66
		Shade	158	6 ± 2 b	
	LS	Sun	144	6 ± 1 b	
		Shade	132	6 ± 1 b	
Leaf area (cm^2)	US	Sun	99	32 ± 19 a	51.49
		Shade	100	71 ± 21 b	
	LS	Sun	78	61 ± 30 c	
		Shade	79	50 ± 21 d	

Means with the same letter are not significantly different (ANOVA, $p < 0.05$).

(Vogelmann & Martin 1993; Vogelmann *et al.* 1996). The thicker mesophyll in sun leaves also facilitates CO_2 dissolution into the water within the cell wall, which decreases the resistance to CO_2 diffusion from the intercellular space to the chloroplast stroma (Evans 1999; Terashima *et al.* 2001). Furthermore, sun leaves from the unlogged stand also had a higher amount of lignified tissues, which possibly enhance durability and promote greater mechanical resistance, for example,

against herbivory (Lee *et al.* 2000). An increase in defense mechanisms is supported by the phenolic compounds (Feeny 1976; Mantuano *et al.* 2006) that were frequently observed in the sun leaves from both stands, and the shade leaves from the logged stand.

The reduction of leaf area of the sun leaves from the unlogged stand is similar to that observed in many other species growing at different levels of light (Abrams & Kubiske 1990; Niinemets & Kull 1998; Klich 2000; Mendes *et al.* 2001). This adaptation could generate an increase in convective heat dissipation that could counteract the negative effects of overheating and high transpiration rates (Gates 1980).

The incapacity of *A. pickelii* to produce typical shade leaves in the logged stand is clearly related to high amounts of light caused by a greater amount of open space in the canopy. However, if sun leaves from both stands were collected at the same light exposure at the canopy level, why didn't the sun leaves from the logged stand produced typical sun leaves? It seems that this species needs stimulus from both low and high regimes of light to be able to develop different types of leaves. Although acclimation cannot be predicted from leaf anatomy alone (Strauss-Debenedetti & Berlyn 1994) the variation in the spectrum of leaf types found within the logged stand suggests lower leaf plasticity of this late successional tree and, consequently, that selective logging represents a clear threat to the conservation of this species. Further studies are necessary to better understand the acclimation and fitness mechanisms in this species.

Acknowledgements

The authors are indebted to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), the Fundação de Amparo a Pesquisa do Rio de Janeiro (FAPERJ), and Coordenação de Aperfeiçoando de Pessoal de Nível Superior (CAPES) for their financial support. We thank Dr. J.S. Souza for suggesting the study area, the technicians B.F. Ribeiro and G.A. de Moraes of LBCT/CBB/UENF for helping with laboratory tasks, and the biologists D.O. dos Santos and G.M. Gonçalves for their help with collecting plants. This study was part of the Master's thesis of the first author, presented to the Programa de Pós-Graduação em Biociências e Biotecnologia.

References

Abrams, M.D. & Kubiske, M.E. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in Central Wisconsin: influence of light regime and shade tolerance rank. Forest Ecology and Management 31: 245-253.

Almeida, S.S. 1989. Clareiras naturais na Amazônia Central: abundância, distribuição, estrutura e aspectos da colonização vegetal. Master's Dissertation. INPA, Manaus. 125p.

Ashton, P.M.S. & Berlyn, G.P. 1992. Leaf adaptations of some *Shorea* species to sun and shade. New Physiologist 121: 587-596.

Asner, G.P.; Knapp, D.E.; Broadbent, E. N.; Oliveira, P.J.C.; Keller, M. & Silva, J.N. 2005. Selective logging in the Brazilian Amazon. Science 310: 480-482.

Bastos, E.O.; Perazzolo, M. & Baptista, J.M.R. 1993. Variação do número de estômatos e micropêlos em *Paspalum vaginatum* SW. em relação às condições abióticas numa marisma do estuário da Lagoa dos Patos, Rs-Brasil. Acta Botanica Brasilica 6: 105-117.

Björkman, O. 1981. Responses to different quantum-flux density. *In*: Lange, O.L.; Nobel, P.S.; Osmond C.B. & Ziegler, H. (eds.). Encyclopedia of plant physiology 12 A. Springer, Berlin. Pp.57-107.

Carpenter, S.B. & Smith, N.D. 1981. A comparative study of leaf thickness among southern Appalachian hardwoods. Canadian Journal of Botany 59: 1393-1396.

Chabot, B.F.; Jurik, T.W. & Chabot, J.F. 1979. Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. American Journal of Botany 66: 940-945.

Chazdon, R.L. & Kaufmann, S. 1993. Plasticity of leaf anatomy of two rain forest shrubs in relation to photosynthetic light acclimation. Functional Ecology 7: 385-394.

Curran, L.M.; Trigg, S.N.; McDonald, A.K.; Astiani, D.; Hardiono, Y.M.; Siregar, P.; Caniago, I. & Kasischke, E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. Science 303: 1000-1003.

Cutler, D.S.; Alvin, K.L. & Price, C.E. 1982. The plant cuticles. Academic Press, London. 462p.

Evans, J.R. 1999. Leaf anatomy enables more equal access to light and CO_2 between chloroplasts. New Phytologist 143: 93-104.

Feeny, P.P. 1976. Plant appearance and chemical defense. Recent Advances in Phytochemistry 10: 1-40.

Freitas, S.R.; Cerqueira, R. & Vieira, M.V. 2002. A device and standard variables to describe microhabitat structure of small mammals

based on plant cover. Brazilian Journal of Biology 62: 795-800.

Gates, D.M. 1980. Biophysical ecology. Springer-Verlag, New York. 611p.

Gratani, L.; Covone, F. & Larcher, W. 2006. Leaf plasticity in response to light of three evergreen species of the Mediterranean maquis. Trees 20: 549-558.

Hlwatika, C.N.M. & Bhat, R.B. 2002. An ecological interpretation of the difference in leaf anatomy and its plasticity in contrasting tree species in Orange Kloof, Table Mountain, South Africa. Annals of Botany 89: 109-114.

Johansen, D. 1940. Plant microtechnique. McGraw-Hill, New York. 523p.

Klich, M.G. 2000. Leaf variations in *Elaeagnus angustifolia* related to environmental heterogeneity. Environmental and Experimental Botany 44: 171-183.

Köppen, W. 1948. Climatologia con un estudio de los climas de la tierra. Fondo de Cultura Economica, México. 479p.

Lee, D.W.; Oberbauer, S.F.; Johnson, P.; Krishnapilay, B.; Mansor, M.; Mohamad, H. & Yap, S.K. 2000. Effects of irradiance and spectral quality on leaf structure and function in seedlings of two southeast asian *Hopea* (Dipterocarpaceae) species. American Journal of Botany 87: 447-455.

Lleras, E. 1977. Differences in stomatal number per unit area within the same species under different micro-environmental conditions: a working hypothesis. Acta Amazonica 7: 473-476.

Mantuano, D.G.; Barros, C.F. & Scarano, F.R. 2006. Leaf anatomy variation within and between three "restinga" populations of *Erythroxylum ovalifolium* Peyr. (Erythroxylaceae) in Southeast Brazil. Revista Brasileira Botânica 29: 209-215.

Mendes, M.M.; Gazarini, L.C. & Rodrigues, M.L. 2001. Acclimation of *Myrtus communis* to contrasting Mediterranean light environments-effects on structure and chemical composition of foliage and plant water relations. Environmental and Experimental Botany 45: 165-178.

Nepstad, D.C.; Jipp, P.; Moutinho, P.R.d.S.; Negreiros, G.H. & Vieira, S. 1995. Forest recovery following pasture abandonment in Amazonia: canopy seasonality, fire resistance, and ants. *In*: Rapport, D. (ed.). Evaluating and monitoring the health of large-scale ecosystems. 2nd ed. Springer-Verlag. Pp. 333-349.

Niinemets, Ü. & Kull, O. 1998. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiology 18: 467-479.

O'Brien, T.P. & Mccully, Y.E. 1981. The study of plants structure: principles and selected methods. 2nd ed. Termercarphy, Melbourne. 344p.

Paiva, E.A.S.; Isaias R.M.S.; Vale, F.H.A. & Queiroz, C.G.S. 2003. The influence of light intensity on anatomical structure and pigment contents of *Tradescantia pallida* (rose) hunt. *cv purpurea* Boom (Commelinaceae) leaves. Brazilian Archives of Biology and Technology 46: 617-624.

Pereira, D.C.; Barros, C.F. & Scarano, F.R. 2009. *In situ* variation in leaf anatomy and morphology of *Andira legalis* (Leguminosae) in two neighbouring but contrasting light environments in a Brazilian sandy coastal plain. Acta Botanica Brasilica 23: 267-273.

Pereira-Moura, M.V.L. 2001. Revisão taxonômica do gênero *Alseis* Schott (Rubiaceae, Cinchonoideae). PhD Thesis. Instituto de Biociências da Universidade de São Paulo, São Paulo. 141p.

RadamBrasil. 1983. Levantamento de recursos naturais. Rio de Janeiro/Vitória. Ministério das Minas e Energia, Rio de Janeiro. 780p.

Rôças, G.; Scarano, F.R. & Barros, C.F. 1997. Leaf anatomy plasticity of *Alchornea triplinervia* (Euphorbiaceae) under distinct light regimes in a Brazilian montane Atlantic rain forest. Trees 11: 469-473.

Rôças, G.; Scarano, F.R. & Barros, C.F. 2001. Leaf anatomical variation in *Alchornea triplinervia* (Spreng) Müll. Arg. (Euphorbiaceae) under distinct light and soil water regimes. The Botanical Journal of the Linnean Society 136: 231-238.

Rondon Neto, R.M.; Botelho, S.A.; Fontes, M.A.L.; Davide, A.C. & Faria, J.M.R. 2000. Estrutura e composição florística da comunidade arbustiva-arbórea de uma clareira de origem antrópica, em uma floresta estacional semidecidual montana, Lavras-MG, Brasil. Cerne 6: 79-94.

Scarano, F.R.; Mattos, E.A.; Franco, A.C.; Herzog, B.; Ball, E.; Grams, T.E.E.; Mantovani, A.; Barreto, S.; Haag-Kerwer, A. & Lüttge, U. 1999. Habitat segregation of C3 and CAM *Nidularium* (Bromeliaceae) in response to different light regimes in the understory of a swamp forest in southeastern Brazil. Flora 194: 281-288.

Scarano, F.R.; Duarte, H.M.; Rôças, G.; Barreto, S.M.B.; Amado, E.F.; Reinert, F.; Wendt, T.; Mantovani, A.; Lima, H.R.P. & Barros, C.F., 2002. Acclimation or stress symptom? An integrated study of intraspecific variation in the clonal plant *Aechmea bromeliifolia*, a widespread CAM tank-bromeliad. Botanical Journal of the Linnean Society 140: 391-401.

Souza, J.S. 2005. Efeito do corte seletivo de madeira na dinâmica de uma Mata Atlântica de Tabuleiro

no Norte Fluminense, Campos dos Goytacazes, RJ. Tese de Doutorado. Universidade Estadual do Norte Fluminense-UENF, RJ. 177p.

Strauss-Debenedetti, S. & Berlyn, G.P. 1994. Leaf anatomical responses to light in five tropical Moraceae of different successional status. American Journal of Botany 81: 1582-1591.

Terashima, I.; Miyazawa, S. & Hanba, Y.T. 2001. Why are sun leaves thicker than shade leaves? Consideration based on analyses of CO, diffusion in the leaf. Journal of Plant Research 114: 93-105.

Tognetti, R.; Minotta, G.; Pinzauti, S.; Michelozzi, M. & Borghetti, M. 1998. Acclimation to changing light conditions of long-term shade-grown beech (*Fagus sylvatica* L.) seedlings of different geographic origins. Trees 12: 326-333.

Veloso, H.P.; Rangel Filho, A.L.R. & Lima, J.C.A. 1991. Classificação da vegetação brasileira adaptada a um sistema universal. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro. 123p.

Veríssimo, A.; Barreto, P.; Mattos, M.; Tarifa, R. & Uhl, C. 1992. Logging impacts and prospects for sustainable forest management in an old Amazon frontier: the case of Paragominas. Forest Ecology and Management 55: 169-199.

Villela, D.M.; Nascimento, M.T.; Aragão, L.E.O.C. & Gama, D.M. 2006. Effect of selective logging on forest structure and cycling in seasonally dry Brazilian forest. Journal of Biogeography 33: 506-516.

Vogelmann, T.C. & Martin, G. 1993. The functional significance of palisade tissue: penetration of directional vs. diffuse light. Plant, Cell & Environment 16: 65-72.

Vogelmann, T.C; Nishio, J.N. & Smith,W.K. 1996. Leaves and light capture: light propagation and gradients of carbon fixation within leaves. Trends in Plant Science 1: 65-70.

Weyers, J.D.B. & Meidner, H. 1990. Methods in stomatal research. Longman Scientific & Technical, Lynn. 233p.

Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, New Jersey. 663p.

Artigo recebido em 24/08/2010. Aceito para publicação em 16/03/2011.