Diurnal and seasonal patterns of leaf water relations in spontaneous and enriched secondary vegetation components

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ABSTRACT

Stomatal conductance g_s, and leaf water potential P, are being monitored in chronosequences of secondary vegetation under fallow and on enriched fallow in Northeastern Pará. Controlled environment studies have just started to understand indigenous and planted species response to water stress. The results from the chronosequence survey indicated that: i) most of the species show a tendency for decreasing g_s and ≥ along the time under fallow; ii) the diversity of responses of g_s and P found under a range of meteorological conditions suggests that these species adopt different physiological mechanisms to couple with limiting environmental conditions; iii) g_{smax} values found in enriching species exceeded those found in the indigenous species; and iv) in most of the species P stayed ≥ -1.5 MPa. The results from the enriched fallow reveal that among the fast growing trees *Acacia mangium* exhibited higher g_s values than the other planted and indigenous species, suggesting that enriching fallow with that species may result in changes in water vapour regimes in this vegetation.

Key words: stomatal conductance, leaf water potential, enriched fallow vegetation.

RESUMO

Condutância estomática g_s, e potencial hídrico foliar P, vêm sendo monitorados em cronoseqüências de capoeiras e em capoeiras enriquecidas no nordeste do Pará. Estudos em ambiente controlado avaliando a resposta de espécies endêmicas e plantadas a défice hídrico tiveram início. As avaliações em cronoseqüências de capoeiras indicam que: i) a maioria das espécies mostra tendência de decréscimo em g_s, e ψ com o tempo em pousio; ii) a diversidade de respostas de g_s, e de ψ sob diferentes condições meteorológicas sugere que estas espécies adotam diferentes mecanismos fisiológicos para fazer face a condições limitantes; iii) os valores de g_{smax} encontrados nas espécies de enriquecimento excederam em geral os encontrados nas espécies endêmicas; e iv) na maioria das espécies ψ manteve-se ≥ –1,5MPa, em especial em capoeiras jovens. Na capoeira enriquecida, *Acacia mangium* exibiu valores mais elevados de g_s, que as outras espécies plantadas e endêmicas, sugerindo que o enriquecimento com esta espécie, poderá modificar as trocas de vapor de água na vegetação.

Palavras chaves: condutência estomática; potencial hídrico foliar; capoeira enriquecida

ZUSAMMENFASSUNG

Stomataleitfähigkeiten g_s und Blattwasserpotentiale ψ wurden in einer Chronosequenz verschieden alter Brachevegetationen (Capoeira) und in angreichterten Brachen im Nordosten von Pará bestimmt. Diesbezügliche Studien unter kontrollierten Umweltbedingungen lieferten bereits ein erstes Verständnis für pflanzenphysiologische Reaktionen von nativen und angereicherten Brachearten auf Wasserstreß. Ergebnisse der vorliegenden Arbeit zeigen, i) daß g_s und ψ vieler Arten mit zunehmendem Alter der Capoeiras abnehmen; ii) daß diese Arten spezifische physiologische Anpassungsmechanismen entwickeln, um sich wechselnden, wachstumslimitierenden Umweltbedingungen anzupassen; iii) daß in angereicherten Brachen die $g_{s\text{-}max}$ -Werte über denen der natürlichen Brachevegetation liegen und iv) daß ψ der meisten untersuchten Arten stetig über 1.5 MPa liegen. *Acacia mangium* als eine der Anreicherungsarten lieferte höhere g_s-Werte als die restlichen Anreicherungsarten und die hier untersuchten Arten der natürlichen Brache, was auf ein verändertes Wasserdampfregime in den Beständen dieser Art hindeutet.
Key words: Stomataleitfähigkeit, Blattwasserpontential, angereicherte Brache.

INTRODUCTION

The understanding of daily and seasonal patterns of plant-water relations and of water vapour exchange in components of spontaneous and enriched secondary vegetation is crucial for reasons such as: to identify functional groups; to quantify water vapour pressure flux in the vegetation; to orient vegetation management; and to the assessment of the impact of land-use changes on water resources.

Since 1992, series of field campaigns have been carried out aiming to assess diurnal and seasonal patterns of leaf water potential P and stomatal conductance g_s in species commonly found in secondary vegetation (*capoeira*) in Northeastern Pará state, Brazil, and later (since 1995) also in fast growing leguminous trees (FGLTs) being tested to enrich fallow vegetation in this region, as an initiative of SHIFT "Capoeira" (Env-25), as described in this issue by Brienza Junior et al. (1998) and Vielhauer et al. (1998). More recently, environmental controlled studies have started aiming to characterise morpho-physiological responses of secondary vegetation key species and enriching woody species to water stress. Here we present a brief overview of the main features emerging from the analysis of the available data from the field studies.

MATERIAL AND METHODS

Field measurements were performed in smallholder plots located in Igarapé-Açu, Pará, in chronosequencies of natural *capoeiras* (Hölscher et al. 1997) and in *capoeiras* enriched with fast growing leguminous trees, planted under three spacings, as described by Brienza Junior et al. (1998).

The measurements of g_s were taken with a dynamic diffusion porometer (Model AP$, Delta-T Devices, Burwell, Cambs., UK), calibrated following the manufacturer's instructions. At the beginning of the study species behavior with respect to g_s was determined, measuring

both adaxial and abaxial leaf surfaces, to detect if the species had active stomata in both leaf surfaces.

ψ was monitored with a pressure chamber in leaves generally chosen from the same portion of the canopy on which leaf stomatal conductance was determined. For that purpose, leaves were cut with a sharp knife and promptly placed in the pressure chamber.

Measurements of g_s and ψ were taken under a wide range of environmental conditions, during field campaigns, as described in Table 1, covering wet, dry and transitional seasons. Daily courses of these variables were followed on most of the days of measurement, at 1 or 2 hour intervals, from about 8.00h until 16.00h. Measurements were taken on five randomly selected individuals of the studied species. Photosynthetic photon flux density (P) was measured simultaneously to g_s with a quantum sensor adjacent to the measurement. Air temperature (T) and specific humidity deficit (D) were also measured nearby.

RESULTS AND DISCUSSION

The general pattern of stomatal conductance varied substantially between the indigenous species of *capoeira* and the leguminous species used to enrich it, as well as among the species of each of these two groups, and even considering the four studied indigenous species growing in spontaneous *capoeira* as compared to the same species in enriched *capoeiras*, as it may clearly be observed in Table 2, where values of g_s found in a 6-year-old spontaneous *capoeira* are compared to those found in a group of 2-year-old *capoeiras* enriched with four fast growing leguminous trees.

Among the indigenous species, the highest g_s values were found in *Lacistema pubescens*, reaching g_{smax} even above 800 mmol m^{-2} s^{-1}. These values may be considered as relatively high, when compared to those found in species from primary and secondary forests in tropical regions (Schulze et al. 1994, Körner 1994, Sá et al. 1996). Generally g_s tended to be lower for the same indigenous species, in the older spontaneous *capoeira* when compared to them under the enriching trees, what may also be associated to the age of the vegetation.

The enriching leguminous tended to exhibit even higher g_s values than those found in the indigenous species. Among the leguminous species *Acacia mangium* was the one to present the higher values, what may be, at a certain extent, associated to the stomatal distribution peculiar to that species, characterised by containing almost equal number of stomata in both leaf surfaces (Atipanumpai 1989). The ratio between g_s on the two leaf surfaces found in *A. mangium* during the present study agrees with that, although a seasonal pattern is clear (Figure 1). Comparing the ratios of g_s on the abaxial (lower) and adaxial (upper) leaf surfaces observed in *A. mangium* with those found in the other enriching leguminous trees and in the indigenous species presenting active stomata on both leaf surfaces herein studied (Table 3), it is possible to have an idea of the peculiar feature of stomata distribution of that species. While the average value for this ratio for that species was 1.09 ($\pm$ 0.51), the values for the other enriching trees ranged between 17.0 ($\pm$ 12.10) and 26.23 ($\pm$ 14.82), and among the indigenous species, the ratio ranged from 9.18 ($\pm$ 1.79) to 31.85 ($\pm$ 15.21). Roberts et al. (1990) report ratios on average between 1.4 and 15.1, studying ten species in a terra firme Amazonian forest near Manaus, Brazil.

Table 1: Temporal distribution of field campaigns carried out in spontaneous and enriched capoeiras, in Igarapé-Açu, Pará. Numbers indicate month in the year.

Capoeira (start of fallow)	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**
Spontaneous:						
A (--/1984)	7-8-11	1-5—8-9	1-3-4-5-6-7-	1-2-5		
			8-10	1-2-5		
B (--/1989)	7-8-11	5-8	3-4-5-7-8-10	1-2-5		
C (08/1992)		5-8	1-4-5-6-7-8-			
			10			
D (08/1993)						3-5-7-8-9-
						10-11
Enriched:						
(11/1995)					3-4-5-7-9-11	5-7-8

The data suggest that fast growing leguminous trees, specially *A. mangium,* show a tendency to present higher rates of stomatal conductance than indigenous species, resulting that the adoption of the enriching fallow technique with these species may lead to substantial changes in water vapour exchange on these areas. Further in depth studies should be carried out to evaluate this possible impact.

The diurnal distribution of g_s exhibited also a seasonal pattern, as may be observed in Figure 2, suggesting also a possible influence of the phenological phase.

Daily courses of ψ exhibited also a seasonal pattern, with a tendency to higher magnitudes of differences between hourly values observed during the transitional period. Nevertheless, even during the dry season, ψ for all species did not reach values below 2.5MPa.

Table 2: Average and extreme values, and mean standard error (SE) of stomatal conductance, g_s (mmol m^{-2} s^{-1}), in leaves of four leguminous tree species (*C. racemosa=CR*, *I. edulis=Ie*, *A. mangium=Am* and *S. paniculatum=Sp*) and of four endemic species of capoeira (*P. guyannense=Pg*, *D. rugosa=Dr*, *L. pubescens=Lp* and *M. bracteata=Mb*), in a spontaneous capoeira after around six year under fallow, and in a fallow vegetation enriched with fast growing leguminous trees (*Cr, Ie, Am and Sp*).

Treatment\ species	*Cr*	Ie	Am	Sp	Pg	Dr	Lp	Mb
SPONTANEOUS CAPOEIRA								
average	-	-	-	-	157.9	277.3	302.9	334.3
maximum	-	-	-	-	184.3	597.7	721.7	508.3
minimum	-	-	-	-	115.7	113.0	84.0	155.0
SE	-	-	-	-	10.7	78.8	98.3	64.8
ENRICHED CAPOEIRAS								
C. racemosa								
average	639.0	-	-	-	309.3	468.4	521.7	453.8
maximum	803.3	-	-	-	370.0	676.7	833.3	716.7
minimum	458.3	-	-	-	229.0	250.7	287.3	262.7
SE	19.6	-	-	-	19.5	57.3	79.6	60.8
I. edulis								
average	-	528.4	-	-	327.0	309.0	451.1	335.1
maximum	-	740.0	-	-	631.7	536.7	780.0	633.3
minimum	-	189.0	-	-	124.3	153.0	222.7	170.7
SE	-	33.1	-	-	54.5	45.9	70.5	57.6
A. mangium								
average	-	-	769.9	-	337.6	368.6	471.0	419.7
maximum	-	-	1116.	-	566.7	743.3	631.7	780.0
minimum	-	-	454.0	-	183.3	190.0	292.0	223.3
SE	-	-	33.3	-	44.4	56.3	43.7	58.4
S. paniculatum								
average	-	-	-	618.3	288.6	319.7	477.8	418.9
maximum	-	-	-	776.7	336.7	398.7	571.5	526.7
minimum	-	-	-	550.0	228.3	277.7	345.0	355.0
SE	-	-	-	46.1	26.0	32.3	55.7	44.2

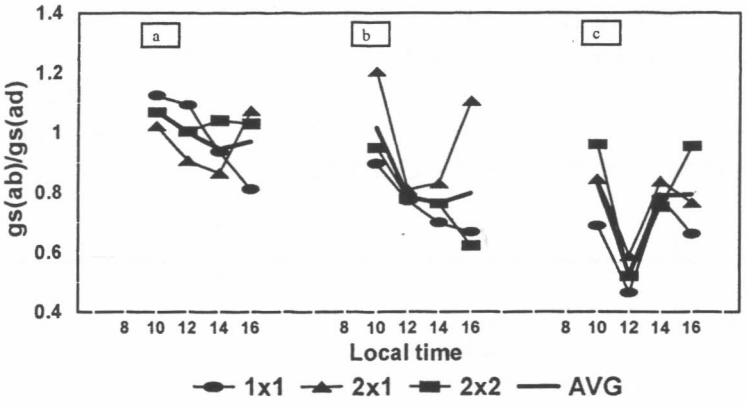

Figure 1: Ratio between stomatal conductance (g_s) on abaxial (ab) and adaxial (ad) phyllode surfaces of *A. mangium* during wet (a), transitional (b) and dry season (c) on fallow vegetation stands enriched at three densities (AVG= average of the three seasons).

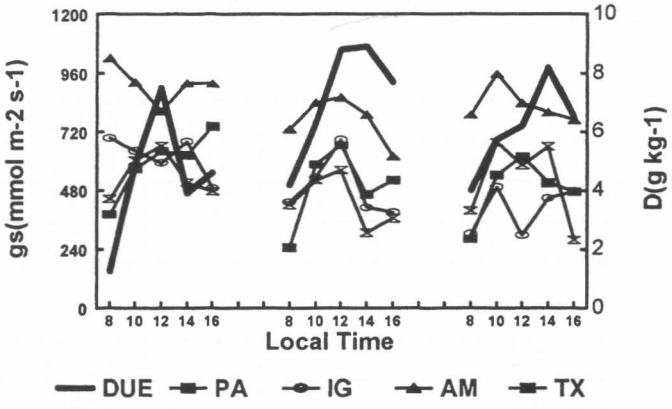

Figure 2: Daily courses of g_s on leaves of the four studied fast growing leguminous trees, associated to specific humidity deficit (D). (PA= *Clitoria racemosa*, IG= *Inga edulis*, AM= *Acacia mangium* and TX= *Sclerolobobium paniculatum).* From left to right: examples of days during the dry, transitional and wet seasons.

Figure 3 displays the relationship between ψ and g_s considering a chronosequency of three *capoeiras*, where it may be observed that during the early (≤ 3-year-old) and intermediate phases (from 4 to 7-year-old) g_s reaches considerably high values, and ψ values fall seldom below –1.5MPa, while during the late phase of the *capoeira,* (≥8-year-old) g_s values tend to be relatively lower, and ψ reaches values as low as –2.5MPa. These ψ values suggest that older capoeiras tend to have lower ψ and to reach lower g_s values.

Table 3: Mean and standard error (±) values of the ratio between stomatal conductance on abaxial and adaxial leaf surfaces of species of indigenous and enriching leguminous species, obtained in *capoeiras* in Igarapé-Açu, Pará.

Species	Mean ratio ± SE
INDIGENOUS SPECIES	
Davilla rugosa Poir.	31.85 (±15.11)
Banara guianensis Aubl.	13.52 (±8.81)
Lacistema pubescend Mart.	13.46 (±7.18)
Myrcia bracteata (Rich.) AC	9.18 (±4.23)
ENRICHING LEGUMINOUS SPECIES	
Clitoria racemosa Benth.	19.00 (±11.00)
Inga edulis Mart.	17.01 (± 12.10)
Acacia mangium Willd.	1.09 (±0.51)
Sclerolobium paniculatum Vog.	26.23 (± 14.82)

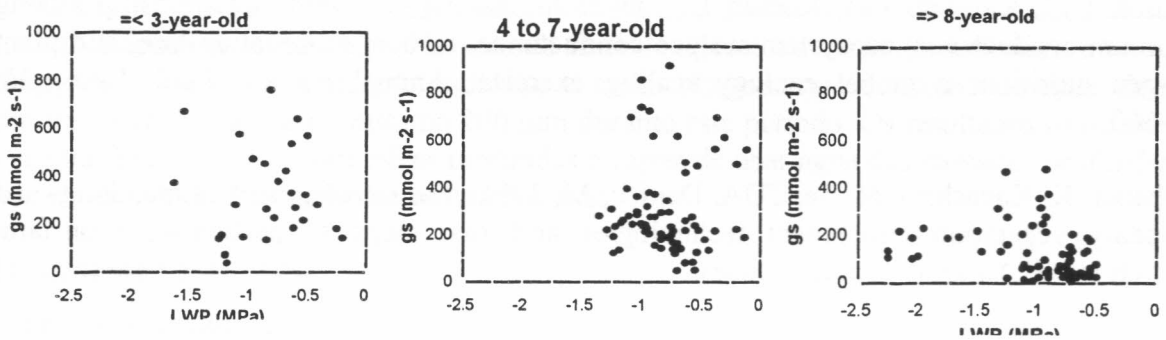

Figure 3: Relationship between ψ and g_s during three moments of a chronosequency of capoeiras found in Igarapé-Açu, Pará.

term of x-axis: I WP (MPa); of y-axis: g_s [mmol m^{-2} s^{-1})

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