

IRRADIANCE AND WATER DEFICIT EFFECTS ON GAS EXCHANGE BEHAVIOR OF TWO C₃ AMAZONIAN WEEDS¹

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ABSTRACT - The gas exchange behavior of two perennial weed species, a vine *Ipomoea asarifolia* (Desr.) Roem. & Schultz and a shrub *Stachytarpheta cayennensis* (L.C. Rich) Vahl., both common in the Brazilian Amazonia, was compared for plants grown under well watered and water limited conditions. Under well-watered conditions, light saturated rates of photosynthesis (A) and stomatal conductance (g) in *I. asarifolia* were, respectively, 15 and 83% higher than in *S. cayennensis*. When water stress was imposed, A and g in *I. asarifolia* declined, respectively, by 29 and 57% in relation to *S. cayennensis*. Dark respiration and light compensation point were similar on well-watered plants. Under water limited conditions, *S. cayennensis* had 60% higher dark respiration and 35% higher light compensation point than *I. asarifolia*. The observed responses are in accord with the known distribution of the species in the field and may provide important information for designing differential management strategies for controlling these weeds.

Index terms: Amazon, *Ipomoea asarifolia*, photosynthesis, stomatal conductance, *Stachytarpheta cayennensis*, water stress, tropical pasture.

LUZ E ESTRESSE HÍDRICO NO COMPORTAMENTO FOTOSSINTÉTICO DE DUAS PLANTAS INVASORAS C₃ DA AMAZÔNIA

RESUMO - O comportamento fotossintético de duas plantas invasoras perenes, *Ipomoea asarifolia* (Desr.) Roem. & Schultz e *Stachytarpheta cayennensis* (L.C. Rich) Vahl., ambas encontradas na Amazônia brasileira, foi comparado em plantas cultivadas em condições ótimas e subótimas de irrigação (estresse hídrico). Em condições ótimas de irrigação, a fotossíntese (A) e condutividade estomatal (g) em *I. asarifolia* foram, respectivamente, 15 e 83 % maiores que em *S. cayennensis*. Sob estresse hídrico, A e g em *I. asarifolia* decresceram, respectivamente, em 29 e 57 % em relação a *S. cayennensis*. A respiração e o ponto de compensação de luz foram similares em plantas em condições ótimas de irrigação. Sob estresse hídrico, *S. cayennensis* apresentou um aumento de 60 % na respiração e de 35 % no ponto de compensação de luz em relação a *I. asarifolia*. O comportamento fotossintético observado está de acordo com a distribuição destas espécies no campo e poderá ser utilizado para gerar informações de grande utilidade para o desenvolvimento de estratégias de controle e manejo das mesmas.

Termos para indexação: Amazônia, *Ipomoea asarifolia*, fotossíntese, *Stachytarpheta cayennensis*, pastagem tropical, condutividade estomatal.

INTRODUCTION

Little is known about the ecophysiological characteristics of weeds that invade tropical pastures, yet

understanding their ecological and physiological behavior is critical in helping to devise improved weed management strategies. Managing tropical pasture weeds through an improved understanding of their ecophysiology will not only help in their management but could also help in understanding what limits growth and productivity of the pasture plant they co-occur with. This is particularly important for the Brazilian Amazonia, where ecologically sound weed management strategies could decrease

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further deforestation by helping increase the agricultural sustainability of pastures.

Tropical pastures within the Brazilian Amazonia are subjected to marked variation in light and water stress levels. It is unknown how these stress may limit growth or distribution, however, improving our understanding of how tropical pasture weeds respond to variation in light, water, and other resource limitations will enhance the proper management and maintenance of such pastures.

Ipomoea asarifolia (Desr.) Roem. & Schultz and *Stachytarpheta cayennensis* (L.C. Rich) Vahl are noxious perennial C₃ weeds of crop and pasture areas in the Brazilian Amazonia (Albuquerque, 1980; Dias Filho, 1990; 1994). Although native to tropical America, *S. cayennensis* is also known to occur as a pasture invader in Australia (Kleinschmidt & Johnson, 1987) and Hawaii (Haselwood & Motter, 1983). In pasture areas, in the Brazilian Amazonia, *I. asarifolia* is most common in areas with a higher soil moisture content (Dias Filho, 1990), whereas *S. cayennensis* seems to be more common in drier areas. Such observations suggest that soil water content may be an important environmental factor determining the species' distribution and their ability to compete with cultivated species. Furthermore, as pastures grow, light quantity and quality will change and this could also play an important role in limiting performance. Because photosynthesis and stomatal behavior are intimately associated with water use and dry matter accumulation, and because light is known to limit carbon assimilation, understanding these processes in weeds may provide insight as to their effects on crop growth, help predict their occurrence, and ultimately provide the needed information to manage pastures successfully.

Although various aspects of photosynthetic productivity and stomatal behavior have been extensively studied for temperate weeds (Regnier et al., 1988; Gealy, 1989; Geber & Dawson, 1990; Gealy et al., 1991; Zimdahl et al., 1991), few similar studies can be found for tropical weeds (Rajendrudu et al., 1987). No previous work on the gas exchange behavior exists for Amazonian weeds (but see Dias Filho 1994) and inferences about their physiology are based on related species from regions other than tropical America (Dias Filho, 1990).

The objective of the present study was to describe the light-response of photosynthesis of *I. asarifolia* and *S. cayennensis* as a function of soil moisture deficit. We relate this information to its possible ecological significance and to its management implications.

MATERIALS AND METHODS

Plant material

Seeds of *Ipomoea asarifolia* (Convolvulaceae, herbaceous vine) and *Stachytarpheta cayennensis* (Verbenaceae, woody shrub) were collected from pasture areas near Paragominas (3° 05' S) in the Brazilian Amazonia. Seeds were cleaned and stored in low humidity until used.

Growing conditions

Seeds were germinated on filter paper in petri dishes and then planted individually in 15-cm-diam plastic pots filled with a mixture of peat:vermiculite:perlite (1:1:1) plus a slow release fertilizer (Osmocote, 20:20:20; N:P:K). Plants were grown in a greenhouse at temperatures of 21 ± 2.2 °C (night) to 33 ± 2.1 °C (day) and a maximum photosynthetic photon flux density (PPFD) of approximately 1000 μmol m⁻²s⁻¹. Photoperiod was extended to 12 hours by 400 W high-pressure sodium vapor lamps. Plants received ample water and were fertilized once a week with 50 ml of a water soluble fertilizer solution (15:30:15; N:P₂O₅:K₂O; 3.5 g L⁻¹).

Response of gas exchange to irradiance

A photosynthesis (A) versus irradiance (PPFD) response curve (starting at ca. 1700 μmol m⁻² s⁻¹ and decreasing in five steps to 0), was measured in the laboratory on the most recent, fully expanded intact leaf of all plants using a portable photosynthesis system (LI-6200, LI-COR, inc., Lincoln, Nebraska, USA). The light levels were obtained by combining neutral-density filters between the leaf chamber and the light source, a high-pressure sodium vapor lamp (1000 W). Gas exchange measurements were made after an adjustment period of about 30 min to each new light level. To absorb long-wave radiation and reduce the heat load on the leaves, a 10 cm deep Plexiglas circulating bath of cool water was suspended between the light source and the leaf chamber. This procedure allowed for uniform leaf temperatures over

the different light levels. After exposure to the lowest PPFD, the plants were left for 30 min in the dark and measurements were made to obtain dark respiration values. Six replicate plants of each species per experiment and one leaf per plant were sampled.

Response of gas exchange to water deficit

Six replicate plants of each species grown in the greenhouse (as described above) received, for five days, 30% as much water as they had been receiving previously. On the fifth day, A vs. PPFD response curves were determined for the youngest fully-expanded intact leaf of each plant following the same procedures described above. Leaf water potential of water limited and well watered plants was assessed by a Scholander-type pressure chamber (PMS Inc., Corvallis, OR).

The light compensation point for both water limited and well watered plants was determined according to Gealy (1987); a linear interpolation between 0 and the second lowest PPFD level.

Statistical analysis

Differences in net photosynthesis and stomatal conductance response curves for species and watering treatments were analyzed by analysis of variance with repeated measures (von Ende, 1993). The between-subject main effects were species and watering regimes, and the within-subjects or repeated measures effect was light level. Homoscedastic residuals were obtained with untransformed values for photosynthesis and log-transformed values for stomatal conductance. Compound symmetry of the covariance matrix of each analysis was tested by the Mauchly's sphericity test. The Huynh-Feldt (Huynh & Feldt, 1970) correction was considered for both analysis. *Post hoc* contrasts comparing species and watering regimes differences in photosynthesis and stomatal conductance was calculated. The statistical package STATISTICA for Windows release 4.5 (STATISTICA for Windows, 1994) was used for all computations of the data..

species achieved light saturation at approximately $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1). Upon rejection of the compound symmetry of the repeated measures ANOVA for the net photosynthesis data (Mauchly's sphericity test, $p < 0.001$), the Huynh-Feldt ($\epsilon = 0.93$) corrected significance levels were considered. There were significant watering regime and species by watering regime main effects differences on photosynthesis (Table 1). Similarly, the effect of light and its interaction with all other effects were also significant (Table 1). *Post hoc* contrasts showed significant differences in the average photosynthesis between the two species; *I. asarifolia* had a higher ($F_{1,20} = 5.4, p = 0.03$) mean rate ($10.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) than *S. cayennensis* ($9.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) under the well watered regime, but a lower ($F_{1,20} = 6.08, p = 0.02$) mean photosynthetic rate (8.02 vs. $9.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) under

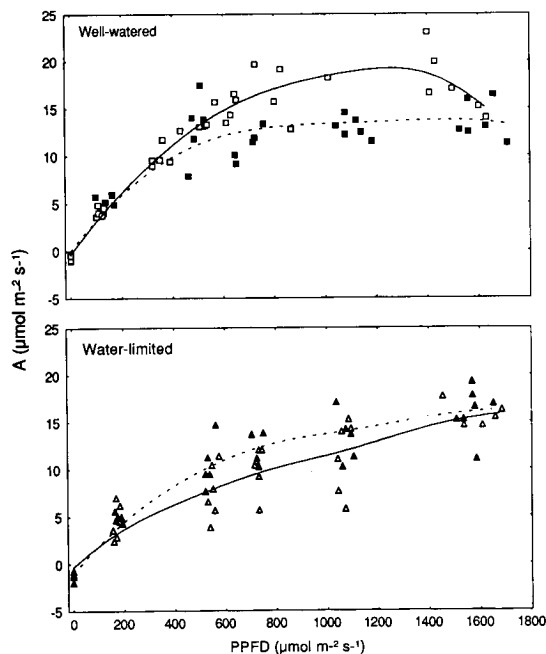


FIG. 1. Light-response curves of the youngest-fully-expanded leaves of *I. asarifolia* (open symbol, solid line) and *S. cayennensis* (closed symbol, dashed line) under well watered and water limited conditions. A = rate of net photosynthesis, PPFD = Photon flux density. Curves fitted according to the distance-weighted least squares smoothing procedure.

RESULTS AND DISCUSSION

Interspecific differences

The shape of the light response curves for *Ipomoea asarifolia* and *Stachytarpheta cayennensis* was similar when plants were well watered; each

TABLE 1. Analysis of variance of net photosynthesis with repeated measurement on light levels. Species (*I. asarifolia* and *S. cayennensis*) and watering regimes (well watered and water limited) are the fixed main effects.

Sources	df	MS	F	P	H-F
Between-subjects					
Species (Sp)	1	0.054	0.01	0.917	—
Regime (Re)	1	47.18	9.72	0.005	—
Sp x Re	1	55.47	11.43	0.002	—
Error	20	4.85			
Within subjects					
Light	5	937.36	239.87	—	0.001
Light x Sp	5	15.66	4.01	—	0.002
Light x Re	5	9.7	2.48	—	0.04
Light x Sp x Re	5	14.88	3.81	—	0.003
Error	100	3.91			

H-F, Huynh-Feldt corrected significance levels (see Materials and Methods).

water limited conditions (Fig. 1). The observed maximal photosynthetic rates of well watered *I. asarifolia* were up to 23 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while *S. cayennensis* attained a maximum of only 17 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Under drought stress conditions these values were 17 and 19 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively for *I. asarifolia* and *S. cayennensis* (Fig. 1), suggesting that *I. asarifolia* was more affected by water stress than *S. cayennensis*.

The compound symmetry for the stomatal conductance data was not rejected by the Mauchly's sphericity test ($p = 0.46$), however, the Huynh-Feldt adjusted significance levels are presented in Table 2 because the epsilon for this test was equal to one, which gives identical adjusted and unadjusted significance levels. Among the between-subject effects, only species was not significant (Table 2). The analysis of the within-subject effects revealed that just light and the interaction light by species by regime were significant (Table 2). Well watered *I. asarifolia* had an average maximal conductance over all light levels of $0.291 \pm 0.21 \text{ mol m}^{-2} \text{s}^{-1}$, significantly higher ($F_{1,20} = 34.1$, $p < 0.001$) than that of *S. cayennensis* which was $0.159 \pm 0.10 \text{ mol m}^{-2} \text{s}^{-1}$. Under the water limited regime, *Ipomoea*, however, had significantly lower ($F_{1,20} = 45.8$, $p < 0.001$) conductance, averaging $0.105 \pm 0.08 \text{ mol m}^{-2} \text{s}^{-1}$ against $0.165 \pm 0.11 \text{ mol m}^{-2} \text{s}^{-1}$ of *S. cayennensis* (Fig. 2). Consistent with

what has been found for other tropical species (Ramos & Grace, 1990; Riddoch et al., 1991), stomata did not close completely in the dark for either stressed or well watered plants (Fig. 3); for plants under water limited conditions this could further increase water stress effects.

Dark respiration and light compensation point of well watered plants showed no differences between species (Table 3). Under drought stress, however, *I. asarifolia* had dark respiration and light compensation point, respectively, 60 and 35% lower than *S. cayennensis* (Table 3).

TABLE 2. Analysis of variance of stomatal conductance with repeated measurement on light levels. Species (*I. asarifolia* and *S. cayennensis*) and watering regimes (well watered and water limited) are the fixed main effects.

Sources	df	MS	F	P	H-F
Between-subjects					
Species (Sp)	1	0.057	0.44	0.51	—
Regime (Re)	1	6.24	47.8	0.001	—
Sp x Re	1	10.38	79.48	0.001	—
Error	20	2.61			
Within subjects					
Light	5	22.25	129.89	—	0.001
Light x Sp	5	0.28	1.68	—	0.146
Light x Re	5	0.34	1.99	—	0.08
Light x Sp x Re	5	0.46	2.69	—	0.02
Error	100	0.171			

H-F, Huynh-Feldt corrected significance levels (see Materials and Methods)

TABLE 3. Effect of water regime on photosynthetic parameters of *Ipomoea asarifolia* and *Stachytarpheta cayennensis*. Means (s.d.)¹. n=6.

Moisture regimes	<i>I. asarifolia</i>	
	Dark respiration	Light compensation point
	$\mu\text{mol m}^{-2} \text{s}^{-1}$	
Water limited	0.86 (0.17)a B	29.13 (11.59)a B
Well watered	0.70 (0.29)a A	16.85 (6.35) b A
	<i>S. cayennensis</i>	
Water limited	1.38 (0.37)a A	39.20 (10.46)a A
Well watered	0.64 (0.23)b A	14.73 (5.88) b A

¹Means followed by different small letters indicate significant intraspecific differences between moisture regimes ($p < 0.05$). Means followed by different capital letters indicate interspecific differences within a moisture regime ($p < 0.05$), in the paired *t*-test.

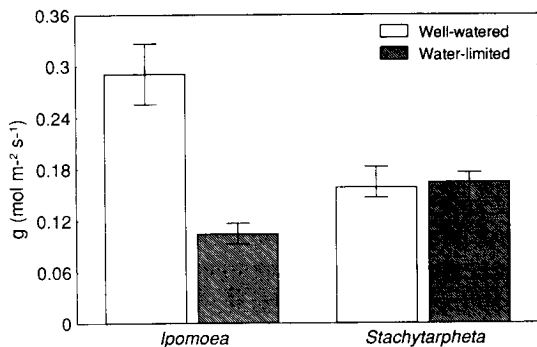


FIG. 2. Mean (\pm s.e.) stomatal conductance of *I. asarifolia* and *S. cayennensis* under two watering regimes. $n = 36$.

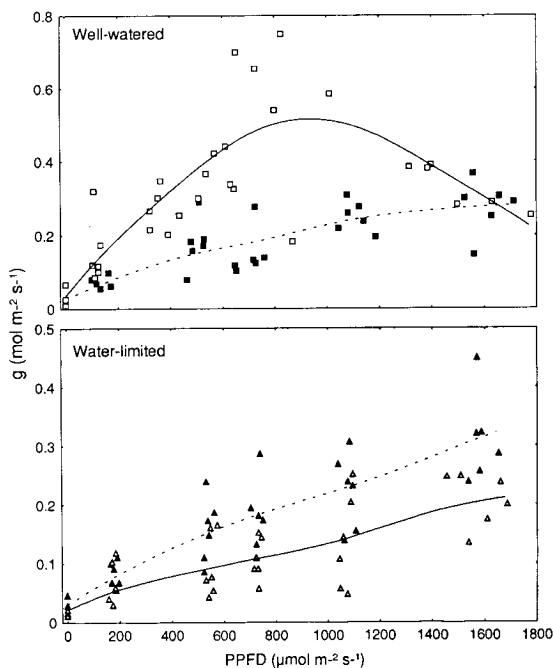


FIG. 3. Light-response of stomatal conductance of *I. asarifolia* (open symbol, solid line) and *S. cayennensis* (closed symbol, dashed line) under well watered and water limited conditions. g = stomatal conductance, $PPFD$ = Photon flux density. Curves fitted according to the distance-weighted least squares smoothing procedure.

Intraspecific differences

Short term moisture deficit reduced the average net photosynthesis of *I. asarifolia* by about 40% yet had no significant influence on *S. cayennensis* (Table 1, Fig. 1). Stomatal conductance also showed differences between species in relation to their sensitivity to water stress (Table 2, Fig. 2). *Post hoc* contrasts showed that stomatal conductance in *I. asarifolia* over all light levels was significantly reduced by the drought stress treatment ($F_{1,20} = 125.3$, $p < 0.001$), while that of *S. cayennensis* was unaffected ($F_{1,20} = 2.0$, $p = 0.17$) (Fig. 2). Leaf water potentials of water limited *I. asarifolia* and *S. cayennensis* plants averaged, $-0.53 (\pm 0.17)$ MPa and $-0.83 (\pm 0.09)$ MPa, respectively, while well watered plants averaged, respectively, $-0.06 (\pm 0.01)$ MPa and $-0.49 (\pm 0.08)$ MPa.

Dark respiration rate of *I. asarifolia* was little affected by watering regimes, while that of well-watered *S. cayennensis* was about two times higher on water limited plants (Table 3). Light compensation point provided a sensitive index of leaf response to watering regime. Drought stress always led to significantly higher values of light compensation point, being, respectively, 75 and 160% higher in water limited *I. asarifolia* and *S. cayennensis* (Table 3).

Availability of water and light is known to limit plant productivity and distribution throughout the world (Stephenson, 1990). Plant adaptation to limited water and light can extend the range of some species, allowing them to occupy a wide range of habitat types. Information about the physiological responses of weeds to variable light, water and other environmental conditions may help in understanding their field distribution and predict their invasive potential (Harper, 1977; Holt, 1988). Tropical pastures are typically disturbed agricultural environments, resulting in temperature extremes, and fluctuations in light and moisture levels. The best-adapted weeds in these environment would, therefore be tolerant of variable environmental conditions, such that they could grow and reproduce successfully.

Our results show that *I. asarifolia* has a limited ability compared with *S. cayennensis* to tolerate water limited conditions. These findings are in ac-

cord with the species distribution in the field, where, *I. asarifolia* is more abundant in more mesic areas (Dias Filho, 1990). Although these responses alone are not sufficient to explain what limits the distribution of these species in tropical pastures, they clearly are important contributing factors in either permitting or restricting these taxa from successfully inhabiting pasture habitats. Studies on tree seedling establishment in degraded pasture areas in the Brazilian Amazonia have shown that water stress, in the form of soil water deficits or high evaporative demand, can often be significant in these environments and may limit a tree's ability to invade pastures (Nepstad, 1989).

Ridloch et al. (1991) reported lower maximal rates of photosynthesis for the tropical weeds *Chromolaena odorata* and *Piper umbellatum* compared with the species studied here. These species were growing in forest gaps however, under low light and, perhaps, low nutrients and this may explain their low photosynthetic rates. Photosynthetic rates in *I. asarifolia* and *S. cayennensis* were comparable to those reported by Rajendrudu et al. (1987) for several tropical dicot C₃ weeds from India.

Stomatal behavior of both species showed the greatest differences in the present study, especially in response to limiting soil water (Fig. 2). *I. asarifolia* appears to have greater transpirational water loss than *S. cayennensis*. The plot of the stomatal conductance against PPFD (Fig. 3) shows that when PPFD is varied stomatal behavior is coordinated with photosynthetic capacity. Similar results have been found for *C. odorata* and *P. umbellatum* by Ridloch et al. (1991) and for tomato by Bolaños & Hsiao (1991).

The values of dark respiration for both water limited and well watered plants were in the same range as those of C₃ dicot weeds from India (Rajendrudu et al., 1987); similar to that reported for the tropical weed *C. odorata* (Ridloch et al., 1991) and the values measured for several early-successional species growing under full sunlight (Bazzaz & Carlson, 1982). Dark respiration and light compensation point of *S. cayennensis* were more affected by the water regimes than *I. asarifolia* (Table 3). The observed increase on the dark respiration and light compensation point of *S. cayennensis* under moisture stress

regime were significantly higher than for *I. asarifolia* and about twofold higher than rates reported by Gealy et al. (1991) in a similar study conducted with the temperate weed *Anthemis cotula*.

The response of *I. asarifolia* to the watering regimes indicates that, unlike *S. cayennensis*, this species could be more competitive in soils with high water-holding capacity or during periods of high soil water content and low evapotranspiration demand. It is not apparent, however, if under more natural conditions, due to a possibly more gradual soil drying in the field than in pots, a long-term water deficit would cause as pronounced a response in *I. asarifolia*. Yet the known distribution of this species in the field (Dias Filho, 1990) suggests that this might also be the case.

CONCLUSIONS

1. This research contributes to the basic understanding of the ecophysiology of *I. asarifolia* and *S. cayennensis*.
2. In addition, the knowledge of how these species respond differentially to soil water can be incorporated in weed management programs designed to take advantage of environmental interactions with plant performance and to improve control techniques and weed management strategies. For example, *I. asarifolia* might be more susceptible to control practices like mowing during periods of suspended rainfall in the wet season or during the dry season, because of reduced vigor as expressed by lower carbon gains, which could, in turn, restrict resprout ability.
3. Based on the observed stomatal response to soil moisture, the use of herbicides that require open stomata for improved absorption would be less effective on *I. asarifolia* under the above conditions.
4. Based on the known moisture regime of pasture areas in the Brazilian Amazonia (Nepstad, 1989), and the gas exchange response of *S. cayennensis* in relation to soil moisture, if left uncontrolled, this species appears to have the potential to become a more persistent and competitive weed than *I. asarifolia* in areas dominated by large fluctuations in light and water availability.

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