

ECOPHYSIOLOGICAL STUDIES OF FOUR AMAZONIAN WEEDY
SPECIES: IMPLICATIONS FOR THEIR INVASIVE POTENTIAL

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Moacyr B. Dias-Filho

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ECOPHYSIOLOGICAL STUDIES OF FOUR AMAZONIAN WEEDY SPECIES: IMPLICATIONS FOR THEIR INVASIVE POTENTIAL

Moacyr B. Dias-Filho, Ph.D.

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Very little is known about the biology of the weed flora that invade Amazonian agroecosystems. Such information could help determine their potential for occurrence and abundance in certain microhabitats and also help predict if such species are on the verge of massive range extensions. Ultimately this information may also aid in the development of ecologically sound weed management and control strategies that could help slow further deforestation by enhancing agricultural productivity.

This research focused on a comparative study of four important perennial weedy species from pastures and crop areas in eastern Brazilian Amazonia: *Ipomoea asarifolia* (Desr.) Roem. & Schultz (Convolvulaceae), *Stachytarpheta cayennensis* (Rich) Vahl. (Verbenaceae), *Solanum crinitum* Lam. (Solanaceae) and *Vismia guianensis* (Aubl.) Choisy (Guttiferae). Two major lines of experiments were conducted. The first investigated some aspects of the seed ecology of the species: longevity in the soil, germination responses to light, nitrate and osmotic stress and the effect of planting depth on seedling emergence. The second line of experiments evaluated the effect of limited soil moisture or of contrasting light environments on physiological and morphological responses of the

species. In addition, the effect of a simulated mowing regime on the fecundity of *S. cayennensis* was evaluated.

The results from this research have identified ecophysiological characteristics which indicate that all four species studied are equipped with traits that can render them noxious weedy species in tropical regions. However, based on the environmental and management conditions known to exist in cultivated pastures and certain crop areas in eastern Brazilian Amazonia, the potential of these species to become persistent weeds and extend their ranges could be tentatively classified in the following sequence: *Stachytarpheta* \geq *Vismia* > *Solanum* > *Ipomoea*.

The species' ecophysiological responses to environmental conditions, together with additional aspects of their biology identified in this research or previously known, should provide the basis for planning ecologically sound weed management control strategies and predicting the potential of occurrence of these and other species with similar characteristics.

BIOGRAPHICAL SKETCH

Moacyr B. Dias-Filho was born on July 9, 1955 in Castanhal, Pará, Brazilian Amazonia. He graduated in 1978 from *Faculdade de Ciências Agrárias do Pará* – the oldest agronomy, forestry and veterinary medicine university in Amazonia – with a B.S. in Agronomy. In 1979, he started working as a research scientist for the Brazilian Agricultural Research Organization in Belém (EMBRAPA-CPATU). At EMBRAPA, he first started collaborating in on-going field research on low input technology for the reclamation of degraded pasture areas in forest ecosystem in Paragominas, eastern Brazilian Amazonia, and also on field research for increasing the productivity of native pastures in savanna ecosystems on Marajó Island, in the Amazon river delta. By the end of 1979, at a time when conducting scientific research in forest ecosystems in Amazonia was not yet a “fad,” he decided to dedicate his full research time to doing field work in Paragominas. In 1986, he received an M.S. in Agronomy with honors and distinction from *Escola Superior de Agricultura “Luiz de Queiroz”* (Universidade de São Paulo), in Piracicaba, Brazil.

For the past 15 years, Moacyr has been working on many aspects of low input technology for the reclamation of degraded pasture areas in forest ecosystems in Amazonia. During this period, his major lines of research have been: evaluation of new forage legume and grass germplasm, soil fertility and plant nutrition, forage legume seed production, and weed management and control. Based on this research, he has written several

papers, and, in 1990, a book on weed management and control in pastures. Besides doing formal research, he has done consultant work for farmers in eastern Brazilian Amazonia. He has also done consultant work for the Peruvian government in Peruvian Amazonia, and visited the International Center of Tropical Agriculture (CIAT) in Colombia to do collaborative research work on forage germplasm evaluation (in 1982) and on forage seed production (in 1988). In December 1987 he was nominated Chairman of the Section of Pasture and Animal Science at EMBRAPA-CPATU, a position he resigned in February 1989, after realizing that his administrative duties were leaving little time to conduct and write about scientific research. In 1989, he received an award for outstanding agronomic research for Brazilian Amazonia, given by the Agronomy Society of the State of Pará, Brazil.

Moacyr enrolled in the Ph.D. program of Cornell University in the fall of 1990 and received his degree in the summer of 1994. He then returned to his position as a research scientist at EMBRAPA-CPATU in Brazil.

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INTRODUCTION

During the past 30 years large areas of forest in the Amazonian humid tropics of Brazil have been cleared for agricultural activities. Due to the extreme shifts in the environmental conditions (e.g., increases in irradiance, greater diurnal variability in soil and air temperatures, and marked changes in soil moisture regimes) in these cleared areas, some plant species that were originally restricted to forest margins and gaps have increased in abundance. As a consequence their ecological and agronomic importance for Brazilian Amazonia has also changed significantly. For example, many of these species have become important weeds in active agricultural areas or have flourished in abandoned ones (see Albuquerque 1980, Dantas 1989, Dias Filho 1990).

The weed problem in Brazilian Amazonia is especially evident in cultivated pastures which, after a few years of utilization, are usually abandoned due to weed invasion (Dias Filho 1990). To slow down land-use pressure on Amazonian forests, due to pasture and agricultural development, there is a need to improve economic and environmentally feasible technologies that enhance the productivity of these areas and thus slow further deforestation.

In a sustainable agricultural system, it is both economically and environmentally desirable to develop management strategies based on a more detailed understanding of the weeds' ecology and physiology. Also,

it is critical to know the factors, resources and means that regulate changes in the population size and dynamics of an individual weed species. Such knowledge can add important information to help determine their potential for occurrence and abundance in certain microhabitats and also could help predict if such species are on the verge of massive range extensions. Ultimately this information may also aid in the improvement of weed management strategies and the development of novel control practices.

Very little information has been published on the biology of the weed flora that invade different Amazonian agroecosystems (for a review on the biology of some pasture weed species see Dias Filho 1990). Most studies on this matter are observational ones, related to aspects such as dispersal mechanisms of seeds and fruits, and composition and size of the soil seed bank (e.g., Charles Dominique 1986, Nepstad 1989, Staver 1991, Uhl et al. 1981, 1982). However, the practical use of such data for weed management strategies and to determine their potential of occurrence is limited by lack of information on seed longevity, germination biology and the resultant patterns of seedling emergence and the physiological attributes that enable seedling development of those species.

Since very little is known not only about the weed species, but the environmental parameters that trigger seed germination and promote seedling growth and development of the weeds common to the Amazon region, basic studies are needed if ecologically sound management strategies are to succeed, and if we hope to understand the adaptive capabilities of these plants.

Often the recommended weed control for tropical pastures and agricultural areas is based on an indiscriminate approach; disregarding

unique characteristics of distinct weed taxa that could be important in understanding their population dynamics and how to manage them. In this situation, the entire weed community is treated as biologically equivalent and little regard is given to the factors and processes that may determine an individual species' colonizing ability, or ability to "hold" a site once established.

In tropical pastures and agricultural areas, weeds are often seen as "by-products" of mismanagement and environmental factors that, by negatively interfering with the pasture or crop vigor and competitive ability, open suitable "spaces" for the establishment and development of weeds (Dias Filho 1990). The degree to which these open spaces will be colonized by a certain weed species, or reclaimed by the desirable plant, usually will depend on the weed's ability to exploit favorable conditions through rapid germination and development.

It has long been recognized that by knowing the appropriate conditions provided by the environment for seed germination and seedling development, a better understanding of the causes governing the density and composition of a plant population could be acquired (Harper 1977). As these conditions vary among different weed species (see Holt 1988, Wilson 1988 and references therein), information about requirements for successful germination, emergence and seedling growth and development could be a valuable tool for predicting weed occurrence and to manage strategically the environment to promote weed control (Radosevich & Holt 1984). For example, unlike dormant seeds that are often protected from weed control measures, germinating seeds are often vulnerable to most

control techniques. Thus, knowledge of the factors that favor seed germination is vital to weed control programs.

The weed flora of Brazilian Amazonian pastures is composed of both native and alien species (Dias Filho 1990). Weed seed dispersal into and within a pasture commonly occurs by biological agents such as bats and birds, or by wind and rain water (e.g., Dias Filho 1990, M. B. Dias Filho personal observation). Also, seeds are known to be carried from one pasture or ranch to another inside the gut or adhered to the coats and hooves of cattle and horses (Dias Filho 1990). It is also hypothesized (see Dias Filho 1986) that many weed seeds have been, and still are, introduced from other regions of Brazil into pasture areas in Amazonia as contaminants of grass seed (mainly *Panicum maximum* and *Brachiaria brizantha*, which usually have their seeds harvested after they fall on the soil).

The relative importance of reproduction by seed, and vegetative regeneration or spread, on weed invasion of agricultural areas seems to be dependent on the prevailing conditions of management (Kigel & Koller 1985). *Solanum crinitum*, a major pasture-invader small tree in eastern Brazilian Amazonia (see Dias Filho 1990), is thought to be apparently dependent on seed germination and seedling growth that take place when the pasture is still active (Nepstad 1989). Once established, this species persists in pasture areas following abandonment mostly through vegetative reproduction from root sprouts (Nepstad 1989).

In Peruvian Amazonia, Staver (1991) observed that only with a decline in weeding frequency (i.e., a decrease in vegetation disturbance), vegetative spread began to play a more important role than seed

germination in the weed build up of a bush fallow agricultural area. As active pastures in eastern Brazilian Amazonia are agroecosystems characterized by a high degree of disturbance (e.g., grazing, burning, weeding), it is expected that seed germination and seedling establishment may play a critical role in the weed build up in those systems.

Because the current trend among pasture scientists in Brazilian Amazonia is to recommend any further pasture establishment be made on abandoned pasture areas (i.e., pasture renovation or reclamation), as opposed to areas of primary forest (see Dias Filho 1986, Serrão & Toledo 1990), the relative importance of weed invasion by seed germination can be further increased. On these areas, the weed soil seed bank is known to be much bigger than on recently deforested areas (e.g., Nepstad 1989, Uhl et al. 1981).

The primary objective of the experiments described in this dissertation was to obtain a better understanding about the ecophysiological attributes that enable some weedy species from Brazilian Amazonia to be particularly successful under certain husbandry practices and environmental conditions. Also, this information may aid in the planning of weed control strategies; however, identification of methods for the management of weeds *per se* was not a primary concern of this thesis.

Four perennial weedy species common to eastern Brazilian Amazonia (Table 1.1) were studied comparatively. The selection of these species was made largely on the basis of their ecological and agronomic importance for Brazilian Amazonia (see Albuquerque 1980, Dantas 1989, Dias Filho 1990, Nepstad 1989). Also, the diversity of their growth forms was taken into account. Even though all four selected species are known

to be native to tropical America, *Stachytarpheta cayennensis* is also reported as a weed in Australia (Kleinschmidt & Johnson 1987), India (Nair et al. 1982) and Hawaii (Haselwood & Motter 1983). To date, the occurrence of *Ipomoea asarifolia*, *Vismia guianensis* and *Solanum crinitum* outside tropical South America has not been reported.

Table 1.1. Features of the species studied.

Species	Family	Growth form	Seed mass (mg) ¹
<i>Ipomoea asarifolia</i> (Desr.) Roem. & Schultz	Convolvulaceae	herbaceous vine	64.31 (1.49)
<i>Stachytarpheta cayennensis</i> (Rich) Vahl.	Verbenaceae	woody shrub	1.22 (0.04)
<i>Solanum crinitum</i> Lam.	Solanaceae	small tree	4.16 (0.10)
<i>Vismia guianensis</i> (Aubl.) Choisy	Guttiferae	medium tree	0.50 (0.01)

¹ Values are means (\pm s.e.), n = 52.

Although, during a certain time, all the species selected can co-occur as established individuals in a certain area, they show marked distinctions in their population dynamics (Figure 1.1).

Ipomoea asarifolia and *S. cayennensis* are typical “agricultural weeds.” They seem to benefit from agricultural activities for dispersal, probably invading new areas as contaminants of pasture and crop seeds or

carried on footwear and agricultural machinery. *Stachytarpheta cayennensis* is mostly common in overgrazed pastures and in agricultural areas with a poor vegetation cover. Once the area becomes highly invaded

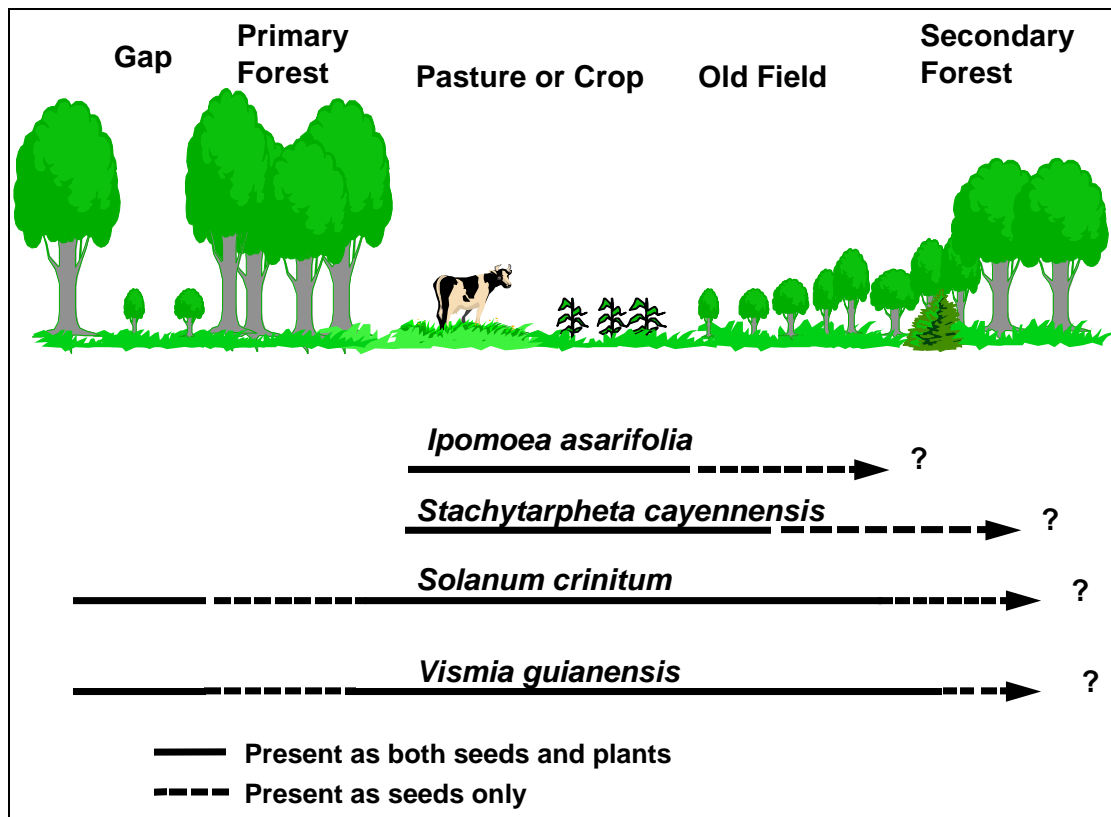


Figure 1.1. A simplified diagram of the population dynamics of the species studied.

by shrubs and trees *S. cayennensis* tends to disappear. *Ipomoea asarifolia* more commonly originates from areas along fences and slash where it seems to benefit from the relatively higher humidity and nutrient content on these sites. Unlike *S. cayennensis*, this species is usually not found in areas lacking vegetation cover. However, once the area becomes increasingly invaded by other species, *I. asarifolia* also tends to disappear.

Solanum crinitum and *V. guianensis* are typical forest gap-invader species that have benefited from agricultural and cattle ranching activities in Brazilian Amazonia to become “weedy” species. Both species are dispersed by bats (Charles-Dominique 1986, Whalen 1984) and, in pasture areas, *S. crinitum* fruits are also known to be eaten by cattle that further help to disperse this species. Although both species tend to appear at about the same period, *S. crinitum* does not persist as an adult individual for a period as long as *V. guianensis*, which is still able to survive at the initial stages of the formation of a secondary forest.

Two major lines of experiments are described in this dissertation. The first (Chapters 2 and 3) investigated some aspects of the seed ecology (i.e., longevity in the soil, germination and emergence in response to selected factors) of the species. The major research question asked in this line of experiment was: *What germination and emergence responses to chemical and physical environmental variables (and other aspects of seed ecology) would help predict and/or explain the occurrence and/or potential for spread of the species under specific management practices or environmental conditions ?* I hypothesized that the studied species display different key aspects of their seed ecology (e.g., longevity, germination behavior). These different characteristics are useful tools in helping to understand their ecological role, to determine their patterns of occurrence under natural and managed conditions, to explain and predict their infestation potential, and plan sound management strategies for their control or conservation. The goal of the seed ecology experiments was not to find the optimum germination or emergence conditions for each species, but to determine the way in which certain physical and chemical factors, to

which the seeds of these species are naturally exposed in the field, affect their patterns of survival, germination, and emergence.

The second line of experiments (Chapters 4 to 9) investigated the effect of soil moisture or light environment on selected physiological and morphological responses of the species. Also, the effect of simulated mowing on the fecundity of *S. cayennensis* was studied (Chapter 10). The major research question of these experiments was: *What physiological and morphological attributes may help explain the colonizing ability of the species studied under specific environmental and management conditions ?* I hypothesized that variations in the responses to physical environmental variables would be useful indicators of how the studied species (and other related species) could become successful invaders in active and abandoned agricultural areas in Brazilian Amazonia.

In addition to the experiments described in this thesis, other “exploratory” experiments were conducted on the species studied in order to identify basic aspects of their biology. These experiments are not formally described on this thesis; however, part of their results is mentioned in Chapter 11 (see Table 11.1) or in the other chapters of this thesis.

Due to similarities in their population biology and/or growth form, in most experiments *I. asarifolia* was compared with *S. cayennensis*, while *S. crinitum* was compared with *V. guianensis*.

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SOME ASPECTS OF THE SEED ECOLOGY OF *IPOMOEA ASARIFOLIA* AND *STACHYTARPHETA* *CAYENNENSIS*

Introduction

Knowledge of the seed germination requirements of weed species can be relevant to both agronomic and ecological perspectives. For example, much of the loss of seeds from the soil (decline in soil seed bank) seems to be attributable to germination (Schafer & Chilcote 1970); therefore decline in the soil seed bank would be greatest under conditions favoring germination of specific species. The significance of seed germination to weed control programs is indicated by the fact that, unlike dormant seeds that are often unaffected by most methods of weed control, germinating seeds are usually vulnerable. Thus, knowledge of germination patterns and the influence of environmental factors on seed germination is essential for development of preventive weed control programs.

Ipomoea asarifolia, a member of the Convolvulaceae, and *Stachytarpheta cayennensis*, in the Verbenaceae, are important perennial weedy species from pastures and crop areas in Brazil (Albuquerque 1980, Dias Filho 1990, Lorenzi 1982). Although native to tropical America, *S. cayennensis* also occurs as a weed in Australia (Kleinschmidt & Johnson 1987), Hawaii (Haselwood & Motter 1983) and India (Nair et al. 1982).

In addition, many *Ipomoea* species are considered as troublesome weeds in warm temperate zones (for a review see Elmore et al. 1990).

No biological or ecological information is available on the environmental factors influencing seed germination and emergence of these species. Also, no information on the seed longevity in the soil exists for these species. Such information would enable the understanding of these species' adaptive capabilities and their potential for infestation, and could also aid in the development of effective control practices. Because in tropical pasture and agricultural areas soil water potential and nitrate levels can vary due to temporal changes in soil water availability, and the light environment can be extremely variable due to vegetation cover, it is important to know the germination response of tropical weed seeds to these factors. Also, in these environments livestock trampling, soil cultivation and other physical and biotic agents may often change the position of weed seeds in the soil profile; hence, it is important to know the emergence response of weed seedlings from different seed depths. Emergence responses from different depths can also be useful for determining the ability of species, immediately after germination, to elongate their hypocotyl to overcome physical barriers for light capture by the developing seedling. In addition, knowledge of the survival ability of seed buried in the field may provide important information about the persistence and depletion patterns of seeds in the soil seed bank.

The objectives of this research were to assess the effects of light, nitrate and water stress on seed germination of *Ipomoea* and *Stachytarpheta*, and to determine the effect of planting depth on seedling emergence and biomass allocation of the two species. Furthermore, I

determined the influence of burial depth and duration on seed longevity in the field of these species. This information could aid in understanding and predicting their occurrence patterns under natural conditions, and also help provide a basis for the development of management control strategies of these species.

Materials and methods

Seed of both species were collected from pasture areas near Paragominas, PA (3° 05' S, 47° 21' W) in eastern Brazilian Amazonia. After collection, seed were cleaned and stored at low humidity at room temperature until initiation of the experiments 6-10 months later.

Experiment 1: Germination response to osmotic stress

Soil water stress for germinating seeds is imposed by osmotic and matric forces in the soil matrix. As such, the effect of osmotic stress on germination was assessed in water solutions with osmotic potentials of -0.2, -0.4, -0.6, -0.8 and -1.0 MPa, prepared by dissolving appropriate amounts of polyethylene glycol (PEG 8000) in deionized water (Smith et al. 1992). Deionized water alone was used for the 0 MPa standard in the experiment. Seeds were incubated in 9-cm glass petri dishes with two sheets of filter paper (Whatman No. 1. Whatman International Ltd. Maidstone, England) in a growth chamber (Percival, Model PT-80, Boone, IA) set at 12-h photoperiod and 31/24°C temperature regime. Each petri dish had 20 seeds and received 7 ml of the appropriate solution. Solutions and filter papers were renewed every other day to minimize water potential

changes through time (Emmerich & Hardegree 1990). All petri dishes were sealed with a strip of Parafilm (Laboratory film, American National Can, Greenwich, CT). Prior to incubation, *Ipomoea* seeds were scarified with sulfuric acid for 20 min. Germination counts were made every two days for eight days for *Ipomoea* and for 18 days for *Stachytarpheta*.

Experiment 2: Germination response to light and nitrate

The effects of nitrate and light were determined in a growth chamber with temperature set at 31°C (day) and 24°C (night), and a photoperiod of 12h. Fluorescent lighting provided a mean photosynthetic photon flux density (PPFD) of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Two sets of 9-cm glass petri dishes lined with two filter papers received 7 ml of either 0, 5 or 10 mM of KNO_3 . Deionized water alone was used for the 0 mM standard. One set of petri dishes was wrapped in two layers of aluminum foil to exclude light. All petri dishes were sealed with a strip of Parafilm. The experiment was concluded after seven days for *Ipomoea* and after 14 days for *Stachytarpheta* when germination was determined.

Experiment 3: Emergence response to planting depth

Seed from each species were planted in 15-cm-diam plastic pots on the soil surface and at depths of 1, 2, 4, 6, 8, and 10 cm. Pots were filled with 250 g (air dry weight) of a potting soil mixture (peat:vermiculite:perlite, 1:1:1) and placed in a greenhouse with temperatures ranging from $33 \pm 2.1^\circ\text{C}$ during the day to $24 \pm 2.2^\circ\text{C}$ at night. In addition to natural light, 400 W lamps extended day length to 12 h and maintained PPFD, measured at the soil surface, at about $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. The soil was initially subirrigated to saturation, then watered daily from the top. Ten or five seeds per pot

were planted, respectively for *Stachytarpheta* and *Ipomoea*. Prior to planting, *Ipomoea* seeds were scarified with sulfuric acid for 20 min. Emergence counts were recorded daily for 12 (*Ipomoea*) or 42 (*Stachytarpheta*) days. Preliminary trials indicated that these periods were at least twice as long as the ones required for maximum germination of these species in the greenhouse. Seedlings were considered to have emerged after they had broken the soil surface. At the end of the experimental period, the leaf, stem and root dry weights of all emerged seedlings were recorded. These data were used for the calculations of biomass allocation patterns: leaf, stem and root weight ratios (respectively, leaf, stem or root weight per unit of weight of whole plant, LWR, SWR and RWR).

Experiment 4: Depth of burial on seed longevity

The influence of burial depth on seed longevity in the field was evaluated in an experiment established in August 1992, on a clayey yellow Latosol (Oxisol) at an abandoned pasture area near Paragominas, in Eastern Brazilian Amazonia. The area has an annual rainfall of 1750 mm with distinct wet (December to June) and dry (July to November) seasons (Dias Filho et al. 1992). Freshly collected seed from a local field population were cleaned, dried in the shade at ambient temperature (ca. 27°C) for two days, and stored in paper bags at ambient temperature until the beginning of the experiment, one day later. The initial viability of the seeds, determined in the laboratory by germination test, was 95 % for *Ipomoea* and 90 % for *Stachytarpheta*. Lots of 100 (*Stachytarpheta*) or 50 (*Ipomoea*) seed each were enclosed in small (ca. 15 cm² for

Stachytarpheta or ca. 30 cm² for *Ipomoea*) nylon mesh packets and placed at the soil surface (slightly covered by soil) or buried at 5 or 10 cm deep.

Packets were retrieved 6, 10, 14 and 18 months after burial. On each occasion seed were removed from the packets and the number of viable seeds determined. Seeds were considered to be viable if they were whole, undamaged and firm when pressed with the tip of a pair of forceps. Viability of *Ipomoea* seed was further confirmed by germinating on soaked rolls of germination paper seeds scarified with sulfuric acid for 20 min. Viability of *Stachytarpheta* was assessed by soaking seed retrieved from the packets (technically fruits with two seed each) in water for 30 min, slicing off seed coats of both seeds in each fruit at the narrowest seed extremity and put seed in 1 % tetrazolium solution. The seed were left in the dark at 40 °C for four to five hours. Seed with embryos that stained pink to red after incubation were considered viable.

Statistical analysis

For the germination experiments, each treatment was replicated five times in a completely randomized block design (osmotic stress) or a completely randomized design (light/nitrate). For the planting depth experiment, treatments were replicated four times in a completely randomized block design (each pot represented one replication of a given depth). The seed longevity experiment (Experiment 4) was a split-plot arrangement of a randomized complete block design with burial duration as main plots, burial depths as subplot, and three replications. All controlled-environment experiments were repeated once with similar results, but only one set of data is presented. Each data set was subjected to Levene's test for

homogeneity of variance and to residual plots to check for homoscedasticity. Normal probability plots were constructed to examine the assumption of normality. When necessary, germination and emergence data were transformed by $\arcsin(\sqrt{y})$; no transformation was required for the biomass allocation data. Transformed data were retransformed for presentation. Data from each experiment were subjected to analysis of variance. Within each species and experiment, treatment means were separated by single degree of freedom contrasts or by the Bonferroni's method of multiple comparison ($P= 0.05$). Means from Experiment 4 were separated by the LSD procedure according to Milliken & Johnson (1992, pg. 300). Statistical analyses were performed by STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994) or SYSTAT Version 5.03 (Wilkinson 1990).

Results and discussion

Experiment 1: Germination response to osmotic stress

Both *Ipomoea* and *Stachytarpheta* showed a similar response to increasing osmotic stress. Germination decreased linearly with decreasing osmotic potentials (Table 2.1). However, for *Ipomoea*, no germination was observed when osmotic stress exceeded -0.8 MPa, whereas *Stachytarpheta* seed germinated at -1.0 MPa (Table 2.1, Fig. 2.1). Related *Ipomoea* species have been shown to possess similar responses to increasing osmotic stress (Crowley & Buchanan 1980, Hoveland & Buchanan 1973).

Osmotic stress also affected germination timing of both species. Unstressed *Ipomoea* seed (0 MPa) germinated faster, showing a maximum value at day two (Fig. 2.1 A). Under osmotic stress, germination of

Ipomoea was delayed, being maximum at day four, for the -0.2 MPa treatment; at day six for the -0.4 MPa treatment, and at day eight for the -0.6 and -0.8 MPa treatments (Fig. 2.1 A). For *Stachytarpheta*, germination of unstressed seeds was maximum at day 14, decreasing sharply at day 18 (Fig 2.1 B). Seeds incubated at -0.2 and -0.4 MPa showed a plateau of maximum germination from day 10 to the end of the experiment, while germination of seeds from the -0.6 to -1.0 MPa treatments was maximum at day 14, decreasing slightly thereafter (Fig. 2.1 B).

Table 2.1. Percent germination for *Ipomoea*, at eight days after planting and for *Stachytarpheta*, at 18 days after planting, as influenced by changes in the osmotic potential of the germinating media.

Species	Osmotic potential (-MPa)					
	0	0.2	0.4	0.6	0.8	1.0
	%					
<i>Ipomoea</i>	70 a	60 ab	50 abc	37 c	11 d	0 e
<i>Stachytarpheta</i>	71 a	54 ab	55 ab	33 bc	20 c	4 d

Means within a row followed by the same letters do not differ at the 0.05 level of significance according to the Bonferroni's method of multiple comparison.

Stachytarpheta showed a remarkable capacity to germinate under low osmotic potentials. This characteristic may in part help to explain the occurrence of this and related species in overgrazed areas in pastures (Dias Filho 1990, Haselwood & Motter 1983, Kleinschmidt & Johnson 1987). In these exposed areas, moisture content of the soil surface is subjected to a greater variability, and is normally lower than in adjacent areas protected

Figure 2.2. Effect of osmotic stress on the proportion of *Ipomoea* (A) and *Stachytarpheta* (B) seed germinating at different days after planting. Surfaces fitted by a bicubic spline smoothing procedure.

by vegetation. Colonization of such areas is expected to be primarily by species capable to germinate over a wide range of osmotic pressures.

Experiment 2: Germination response to light and nitrate

Germination response to light indicated that *Ipomoea* seed was insensitive to light environment, while *Stachytarpheta* seed showed a positive photoblastic behavior (Fig. 2.2). This suggests that management practices that help prevent seeds from receiving light, such as soil cultivation and mulching, could drastically reduce the occurrence of *Stachytarpheta*, while no such effect would be observed for *Ipomoea*. *Stachytarpheta* seed that did not germinate in the dark were able to germinate normally once exposed to light (data not shown). This response suggests that the short term period (14 d) that the seed was deprived from light, under appropriate moisture and temperature regimes, did not stimulate dormancy.

Post hoc contrasts showed that nitrate had a negative effect on germination of *Ipomoea* seed under both light ($F_{1,24} = 5.38$; $P = 0.03$) and dark ($F_{1,24} = 8.71$; $P = 0.007$) conditions (Fig. 2.2A). For *Stachytarpheta*, no effect of nitrate could be detected on the final seed germination in the light. However, dark germination of this species was weakly, but significantly ($F_{1,24} = 6.37$; $P = 0.02$) stimulated by nitrate (Fig. 2.2). Germination stimulation by nitrate in the dark has been suggested to act like a “gap detection mechanism,” an ecologically important characteristic that may enable buried seeds to sense the presence of nearby plants (Pons 1989). The observed response of *Stachytarpheta* to nitrate in the dark may, to some extent, suggest the presence of such mechanism. This characteristic could be of a great adaptive significance for a small seeded

species, with a relatively small seedling size and growth rate like *Stachytarpheta*, by decreasing the risks of an early competition for external resources with other plants.

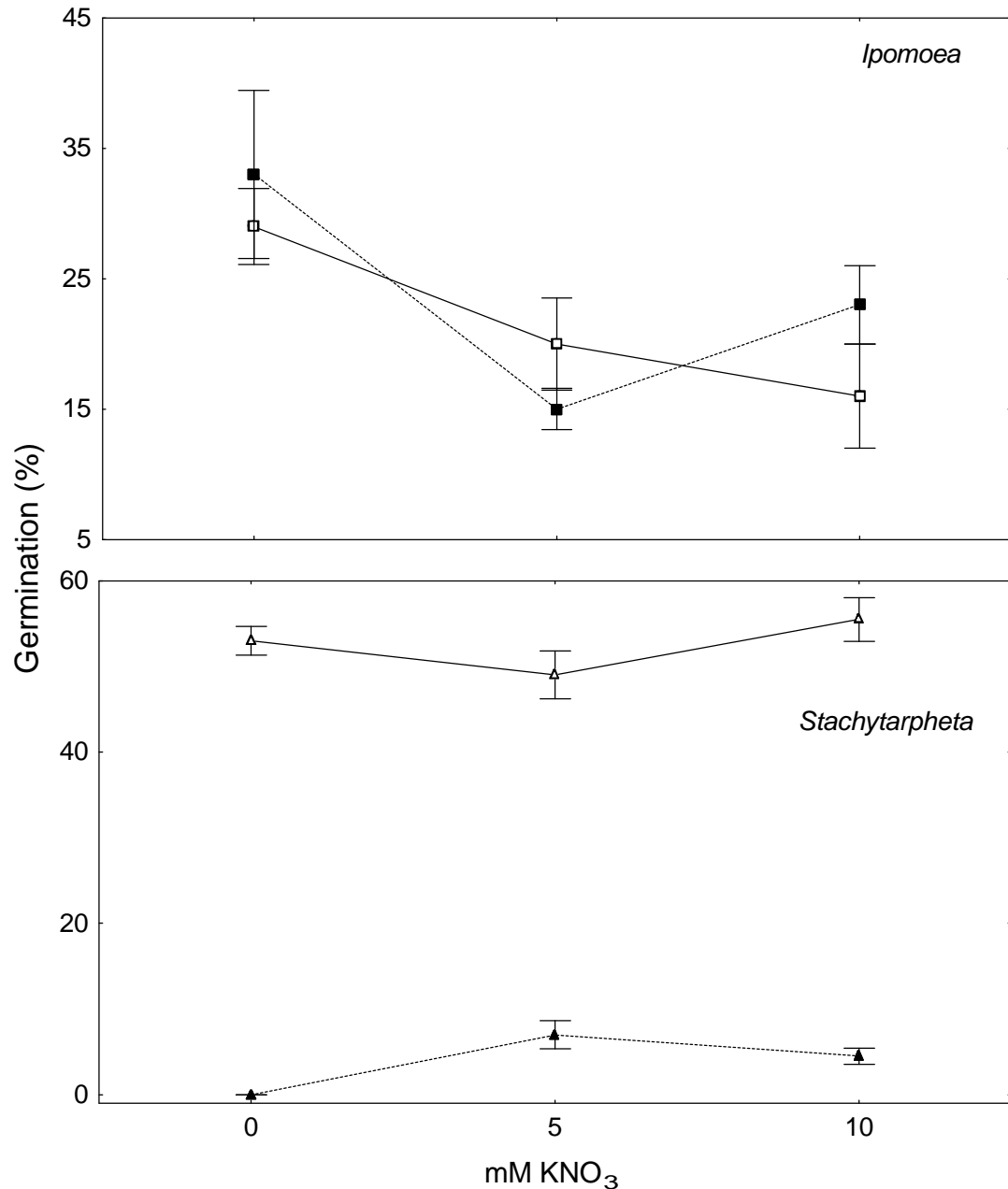


Figure 2.3. Effect of light and nitrate levels on percent germination of *Ipomoea* and *Stachytarpheta*, at seven (*Ipomoea*) or 14 (*Stachytarpheta*) days after planting. Each value is the mean of 20 seeds each, with five

replications. Vertical bars are ± 1 standard error of the mean. Light = open symbols and solid lines; dark = closed symbols and dashed lines.

Experiment 3: Emergence response to planting depth

No significant ($P > 0.05$) effect of planting depth could be detected on seedling emergence of *Ipomoea* (Fig. 2.3). However, a tendency for lower emergence was observed for seed placed on the soil surface (Fig. 2.3), probably due to poor seed-soil contact and desiccation. Results from the osmotic stress (Fig. 2.1A) and light (Fig. 2.2) trials corroborate the observed emergence response of *Ipomoea* to planting depth. Many *Ipomoea* species also have been reported to have the ability to emerge from relatively great depths (for a review see Elmore et al. 1990), a characteristic that, for the present species, is probably related to the lack of a light requirement for germination and to the relatively large seed size.

The observed emergence response of *Ipomoea* shows that this species has a great degree of plasticity with respect to hypocotyl extension when buried at different depths. Because in agricultural environments, conditions such as seed position in the soil profile may be constantly changing due to practices like cultivation and to biological agents, this characteristic may be of great adaptive significance for this species.

Unlike *Ipomoea*, emergence in *Stachytarpheta* was restricted to seeds planted at the soil surface (Fig 3). This result agrees with the positive photoblastic nature of the seed of this species shown in the light experiment (Fig 2) and correlates with the natural occurrence of this species mainly on disturbed open areas like overgrazed pastures and road sides.

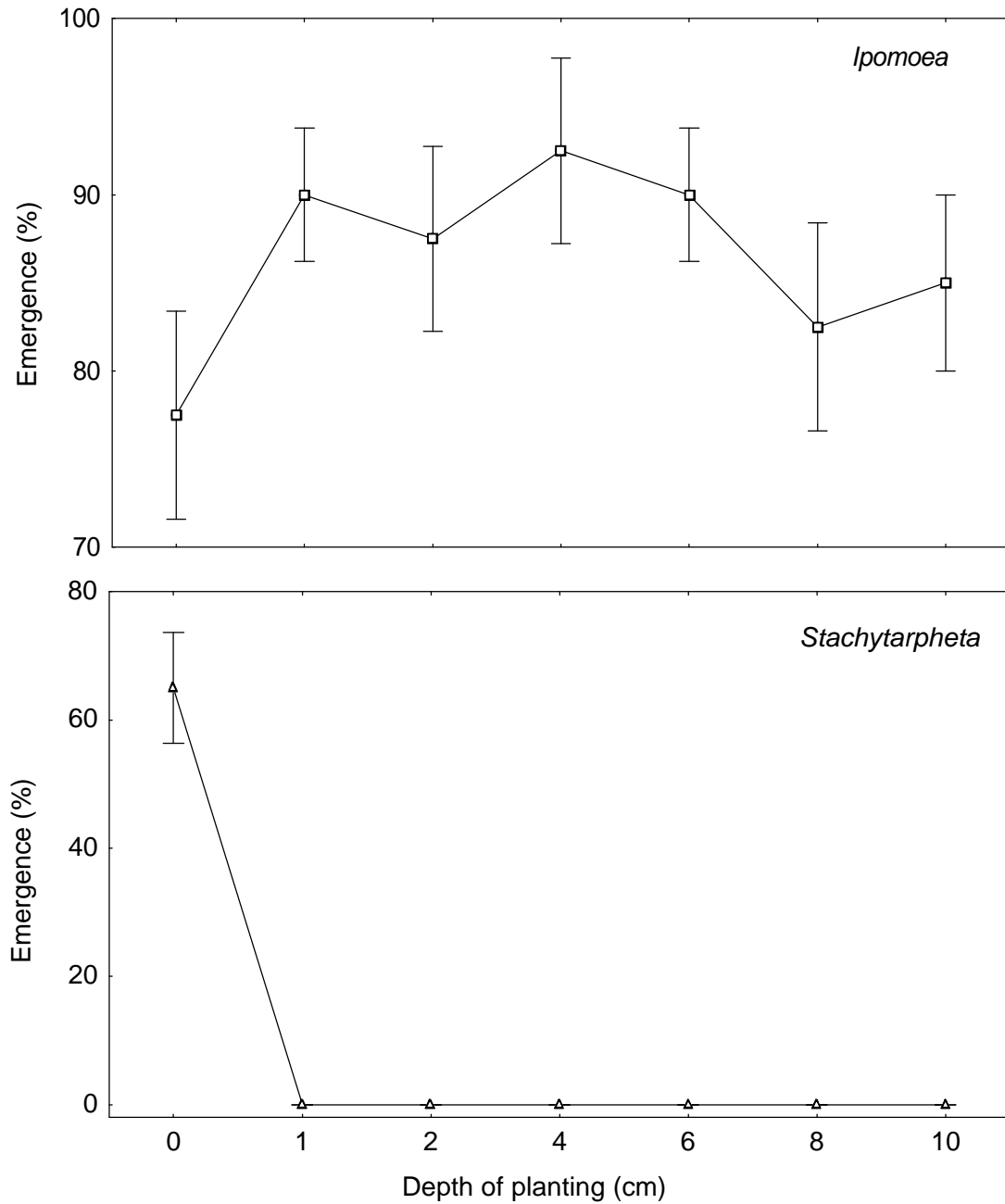


Figure 2.4. Effect of planting depth on percent emergence of *Ipomoea* and *Stachytarpheta*, at 12 (*Ipomoea*) or 42 (*Stachytarpheta*) days after planting. Each value is the mean of five (*Ipomoea*) or 10 (*Stachytarpheta*) seeds each, with four replications. Vertical bars are ± 1 standard error of the mean.

An important characteristic often overlooked in planting depth trials is the biomass allocation pattern of seedlings that emerge from different seeding depths. In the present study, the amount of biomass allocated to roots (RWR) by *Ipomoea* was significantly (Bonferroni's method, $P < 0.006$) higher for seedlings that emerged from depths up to 6 cm, and decreasing at greater depths (Fig. 2.4). Biomass allocated to stems (SWR) and leaves (LWR) had a tendency to be similar for depths up to 2 cm, respectively, increasing (SWR) or decreasing (LWR) at greater depths (Fig 2.4). These patterns suggest that emergence from greater depths compromises the ability of *Ipomoea* seedling to develop rapidly roots and leaves, as during the early phase of seedling development, greater amounts of stored seed reserves had to be allocated to hypocotyl elongation to enable the cotyledons to reach the soil surface.

As a fast and efficient capture of above and below ground resources can be key for the survival and competitive ability of establishing seedlings (e.g., Harper 1977, Fenner 1987), therefore, it could be speculated that emerging from increasing depths may compromise the survival ability of *Ipomoea* seedlings by reducing the relative amount of biomass invested to leaves and roots, thus making these plants less capable of competing for external resources and, as a consequence, to endure and recover from stresses such as drought, mowing or herbivory.

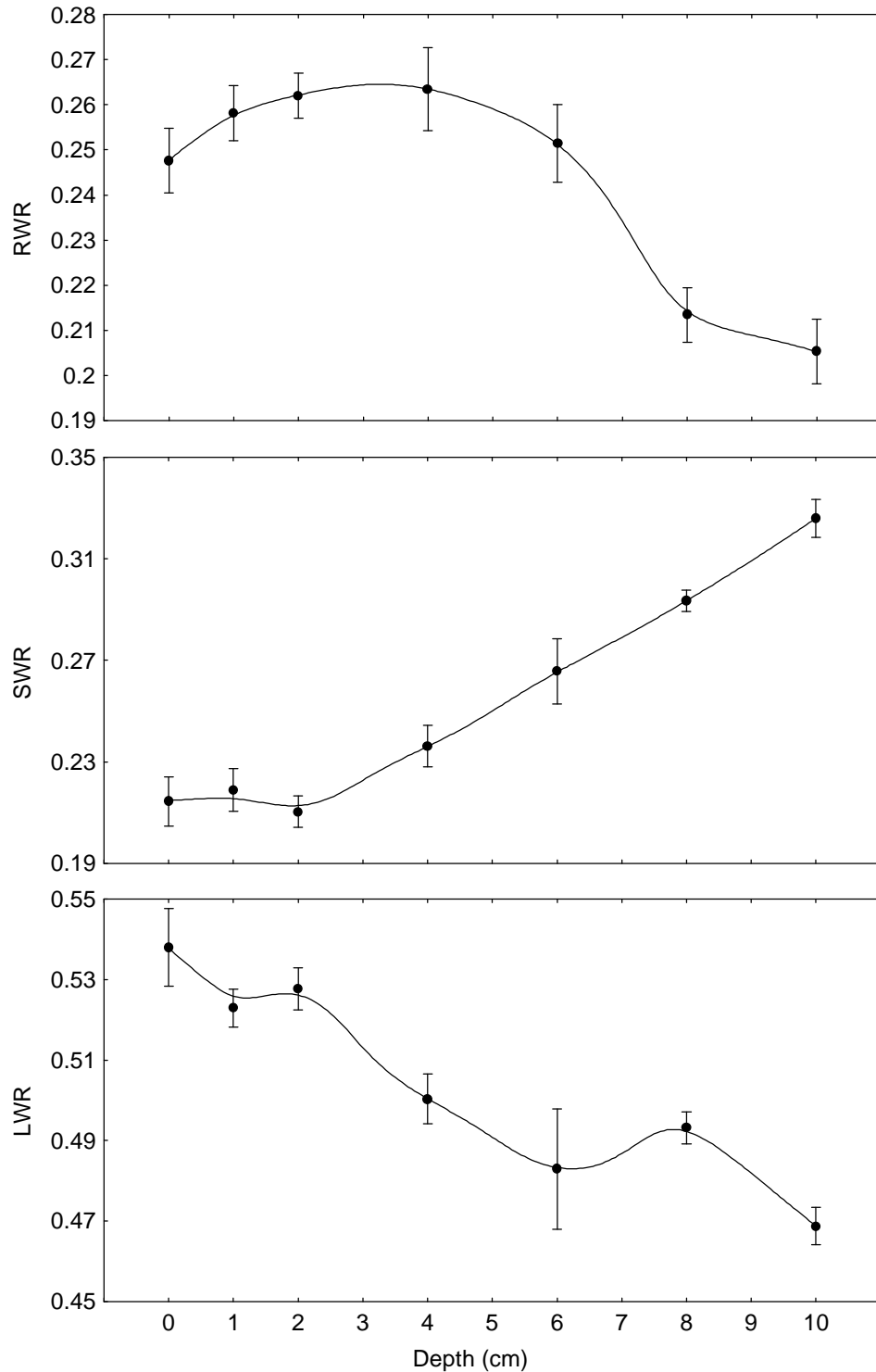


Figure 2.5. Biomass allocation to roots (RWR), stems (SWR) and leaves (LWR) of *Ipomoea* seedlings emerging from various depths. Vertical bars are ± 1 standard error of the mean (n= 5). Curves fitted by distance-weighted least squares.

Experiment 4: Depth of burial on seed longevity

Ipomoea and *Stachytarpheta* showed marked differences in relation to seed longevity in the soil. Relative to the initial viability of *Ipomoea* seed, at the end of the experiment (18 months) a 90, 83 or 80 % loss of viability had been experienced, respectively, by the surface, 5 cm or 10 cm deep seed (Fig. 2.5), while for *Stachytarpheta* the viability loss was only 55, 52 or 24 %, respectively, for the surface, 5 cm or 10 cm deep seed (Fig. 2.5). The shape of the longevity curve observed for *Stachytarpheta* seed (Fig. 2.5) indicates that this species can build up in the soil seed bank (i.e., is capable of dispersing in time), and that soil cultivation may actually enhance its persistence in agricultural environments by promoting seed burial. On the other hand, the decline observed in the viability of seed at the soil surface (Fig. 2.5) suggests that a fallow period would have a limited success as a control technique for *Stachytarpheta*. Conversely, the observed longevity of *Ipomoea* seed suggests that eradication of this species could be feasible in a relatively short term if seed production of established plants could be prevented (by periodic mowing, for example) and emerging seedlings controlled. The lack of a specialized long distance dispersion mode known to exist in *Ipomoea* (Dias Filho, 1990) could further help in the success of an eradication program of this species from agricultural areas. The present data also suggest that, unlike *Stachytarpheta*, a fallow period may be successful as a control technique for *Ipomoea*.

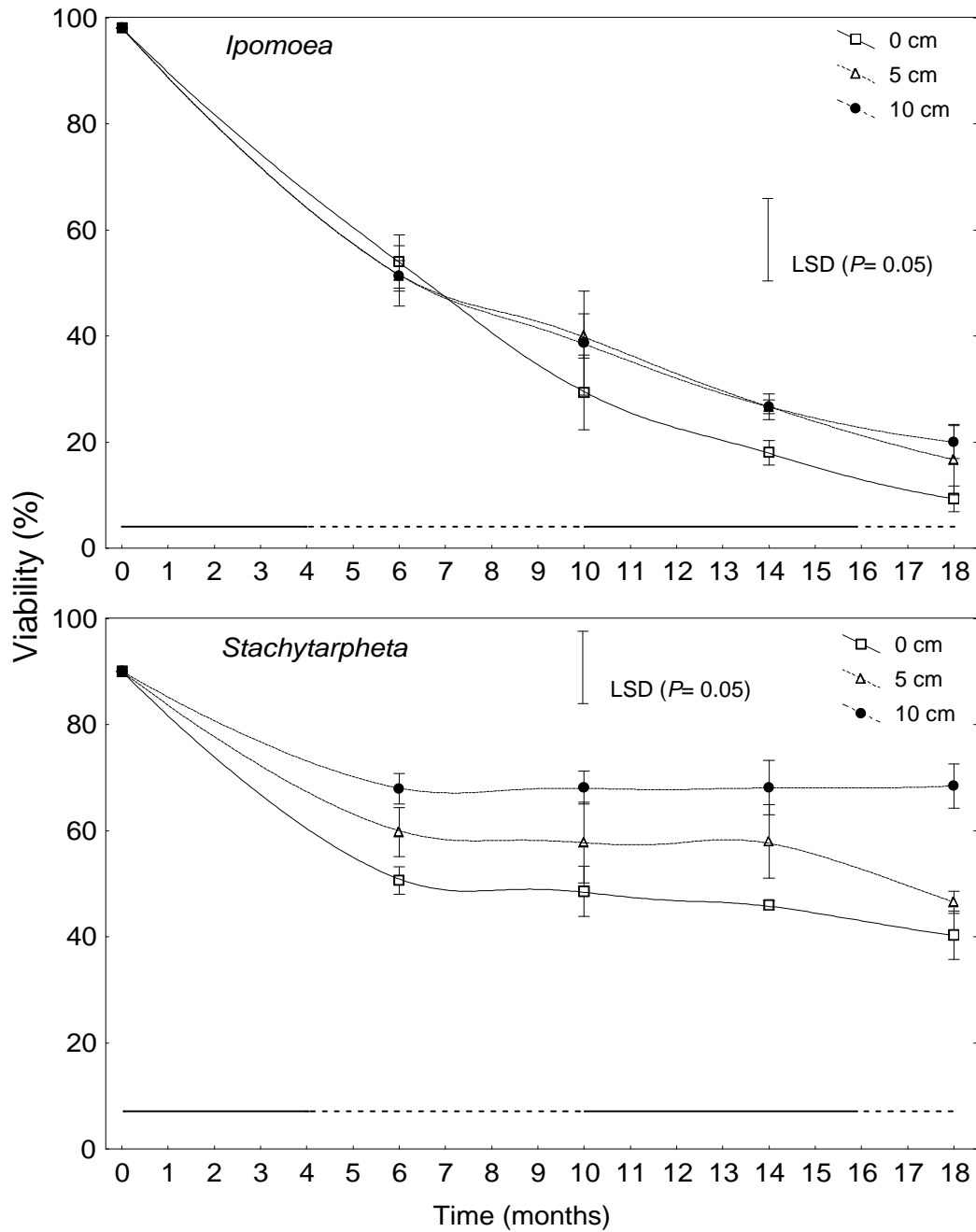


Figure 2.6. Seed viability as a function of time and burial depth in *Ipomoea* and *Stachytarpheta*. Each value is the mean of 50 (*Ipomoea*) or 100 (*Stachytarpheta*) seeds each, with three replications. The horizontal line indicates the length of the dry (solid line) and wet (dashed line) seasons during the experimental period. Error bars are ± 1 standard error of the mean. The LSD bar compares depth means at the same time period. Curves fitted by distance-weighted least squares.

For both species, the shape of the curve fitted to the viability data (Fig. 2.5) suggests that the decline in viability is relatively lower for buried seeds. This is probably caused by the extremely variable conditions (e.g., great diurnal fluctuations in temperature and humidity) that may have been experienced by seed at the soil surface; this environment could help overcome the hard-seededness known to exist in *Ipomoea*, increasing germination and thus decreasing seed survival. In addition, as *Stachytarpheta* seed are known to have a positive photoblastic behavior (see Experiments 2 and 3), seed at the soil surface would also be more prone to germination than buried seed. As a consequence, for both *Ipomoea* and *Stachytarpheta*, a relatively higher proportion of seed was probably lost via germination at the surface than at 5 or 10 cm deep. This result supports the general findings from tropical and temperate studies that the deeper the seed burial, the longer the persistence in the seed bank (Bourdôt & Hurrell 1992, Bridgemohan et al. 1991, Eberlein 1987, Ralphs & Cronin 1987, Schwerzel 1976).

Although the methodology used did not allow for a positive estimation of the exact proportion of seed lost through germination *in situ*, as opposed to the one from seed that died without germinating, traces of seedlings could be observed in the burial packets at all planting depths and throughout all evaluation dates for *Ipomoea* (data not shown). This observation suggests that germination may play an important part in the decline of soil seed bank for this species. Yet, no traces of seedlings could be observed in the burial packets of *Stachytarpheta*. However, the small seedling size of this species probably makes seedling detection very difficult.

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SOME ASPECTS OF THE SEED ECOLOGY OF *SOLANUM CRINITUM* AND *VISMIA GUIANENSIS*

Introduction

During the past 30 years large areas of forest in the Amazonian humid tropics of Brazil have been cleared for agricultural activities. Due to the extreme shifts in the environmental conditions (e.g., increases in irradiance, greater diurnal variability in soil and air temperatures, and marked changes in soil moisture regimes) in these cleared areas, some native plant species that were originally restricted to forest margins and gaps have increased in abundance. As a consequence their ecological and agronomic importance for Brazilian Amazonia has also changed significantly. For example, many of these species have become important weeds in active agricultural areas or have flourished in abandoned ones (see Albuquerque 1980, Dantas 1989, Dias Filho 1990).

Information on life history traits of plant species is critical for helping to explain and predict their occurrence and abundance patterns under specific environmental and management conditions. For invading species, seed germination behavior can be a critical feature in this context. Knowledge of seed germination requirements of weed species can be relevant to both agronomic and ecological perspectives. For example, much of the loss of seeds from the soil (decline in soil seed bank) seems to be attributable to germination (Schafer & Chilcote 1970); therefore, a decline

in the soil seed bank would be greatest under conditions favoring germination of specific species. The significance of seed germination to weed control programs can be stressed by the fact that, unlike dormant seeds that are often unaffected by most methods of weed control, germinating seeds are usually vulnerable. Thus, knowledge of germination patterns and the influence of environmental factors on seed germination is essential for development of preventive weed control programs.

Vismia guianensis (Aubl.) Choisy (Guttiferae) and *Solanum crinitum* Lam. (Solanaceae) are native successional woody species from tropical America found as colonizers of man-made clearings and natural gaps in forests and in abandoned or active agricultural areas in Brazilian Amazonia (Albuquerque 1980, Dantas 1989, Dias Filho 1990). Both species are dispersed mainly by bats (Charles-Dominique 1986, Whalen 1984), although birds are also known to eat their fruits. In pasture areas fruits of *Solanum* are also consumed by cattle, which further helps to disperse seeds of this species (M. B. Dias-Filho, personal observation). Due to their invasive nature, these species are considered as troublesome weeds of perennial agricultural areas like cultivated pastures in Brazilian Amazonia (Dias Filho 1990). Although both species are capable of reproducing vegetatively (Dias Filho 1990), they rely mostly on seed dispersal and germination to invade and colonize active and abandoned agricultural areas and forest gaps (M. B. Dias-Filho, personal observation).

Even though *Vismia* and *Solanum* are ecologically and agriculturally important species for Brazilian Amazonia, there is no published information on their germination ecology and seed longevity in the soil. Such knowledge can add important information to help determine their

potential for occurrence and abundance in certain microhabitats and also could help predict if such species are on the verge of massive range extensions.

Because in tropical pastures and agricultural areas soil water potential and nitrate levels can vary due to temporal changes in soil water availability and microorganism activity, and the light environment can be extremely variable due to vegetation and litter cover, it is critical to know the germination response of weed seeds to these factors. Also, in these environments livestock trampling, soil cultivation and other physical and biotic agents may often change the position of seeds in the soil profile; hence, it is important to know the emergence response of seedlings to different planting depths. Emergence responses to planting depth can also be useful for determining the ability of species, immediately after germination, to elongate their hypocotyl to overcome physical barriers for light capture by the developing seedling. Furthermore, information on the survival of seed buried in the field may provide important information on the patterns of persistence and depletion of seeds in the soil seed bank.

The objectives of this research were to determine the way in which light, nitrate, water stress and planting depth may affect germination and emergence responses of *Vismia* and *Solanum*. In addition, I determined the influence of burial depth and duration on *Solanum* seed longevity in the field. This information could aid in understanding and predicting their occurrence patterns under natural conditions, and also help to provide a basis for the development of management control strategies of these species in agricultural environments.

Materials and methods

Seed of both species were collected from abandoned pasture areas near Paragominas, PA (3° 05' S - 47° 21' W) in Eastern Brazilian Amazonia. After collection, seed were cleaned and stored in low humidity at room temperature until initiation of the experiments 6-10 months later.

Experiment 1: Germination response to light and nitrate

Soil water stress for germinating seeds is imposed by osmotic and matric forces in the soil matrix. As such, the effects of nitrate and light were determined in a growth chamber (Percival, Model PT-80, Boone, IA) with temperature set at 31°C (day) and 24°C (night), and a photoperiod of 12 h. Fluorescent lighting provided a mean photosynthetic photon flux density (PPFD) of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Two sets of 9-cm glass petri dishes lined with two sheet of filter paper (Whatman No. 1. Whatman International Ltd. Maidstone, England) received 7 ml of either 0, 5 or 10 mM of KNO_3 . Deionized water alone was used for the 0 mM standard. One set of petri dishes was wrapped in two layers of aluminum foil to exclude light. Twenty seeds of similar sizes from each species were placed in each petri dish. All petri dishes were sealed with a strip of Parafilm (Laboratory film. American National Can, Greenwich, CT). The experiment was concluded after 21 d for both species and germination was determined. Preliminary trials showed that this period was ideal for maximum germination of these species in the growth chamber.

Experiment 2: Germination response to osmotic stress

The effect of osmotic stress on germination was assessed in water solutions with osmotic potentials of -0.2, -0.4, -0.6, -0.8 and -1.0 MPa, prepared by dissolving appropriate amounts of polyethylene glycol (PEG 8000) in deionized water (Smith et al. 1992). Deionized water alone was used for the 0 MPa standard in the experiment. Seeds were incubated in 9-cm glass petri dishes on two sheets of filter paper in a growth chamber set at 12-h photoperiod and 31/24°C temperature regime. Each petri dish received 20 seeds of each species and 7 ml of the appropriate solution. Solutions and filter papers were renewed every other day to minimize osmotic potential change through time (Emmerich & Hardegee 1990). All petri dishes were sealed with a strip of Parafilm. Prior to incubation, *Solanum* seeds were scarified with concentrated sulfuric acid for 30 min to overcome hard-seededness; a previous trial showed that this treatment could increase germination of this species by approximately 80 %; no hard-seededness characteristics were detected in *Vismia* (M.B. Dias Filho, unpublished observation). Germination counts were made every two days for 36 d for *Vismia* or 32 d for *Solanum*. Preliminary trials indicated that these periods were at least 50 % longer than the ones required for maximum germination of these species in the growth chamber.

Experiment 3: Emergence response to planting depth

Seed from each species were planted in 15-cm-diam plastic pots on the soil surface and at depths of 1, 2, 4, 6, 8, and 10 cm. Pots were filled with 250 g (air dry weight) of a potting soil mixture (peat:vermiculite:perlite, 1:1:1) and placed in a greenhouse with temperatures ranging from $33 \pm 2.1^\circ\text{C}$

during the day to $24 \pm 2.2^{\circ}\text{C}$ at night. In addition to natural light, 400 W lamps extended day length to 12 h and maintained PPFD, measured at the soil surface, at about $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. The soil was initially subirrigated to saturation, then watered daily from the top. Ten seeds of uniform sizes per pot were planted for *Vismia* or *Solanum*. Prior to planting *Solanum* seeds were scarified with sulfuric acid for 30 min. Emergence counts were recorded daily for 60 (*Vismia*) or 50 (*Solanum*) days. Preliminary trials indicated that these periods were at least twice as long as the ones required for maximum germination of these species in the greenhouse. Seedlings were considered to have emerged after they had broken the soil surface.

Experiment 4: Depth of burial on longevity of Solanum seeds

The influence of burial depth on *Solanum* seed longevity was evaluated in an experiment established in August 1992, on a clayey yellow Latosol (Oxisol) at an abandoned pasture area near Paragominas, in Eastern Brazilian Amazonia. The area has an annual rainfall of 1750 mm and experiences distinct wet (December to June) and dry (July to November) seasons (Dias Filho et al. 1992). Freshly collected seed from a local field population were cleaned, dried in the shade at ambient temperature (ca. 27°C) for two days, and stored in paper bags at ambient temperature until the beginning of the experiment, one day later. The initial viability of the seeds, determined in the laboratory by germination test of acid-scarified seed was 85 %. Lots of 100 seed each were enclosed in small (ca. 15 cm^2) nylon mesh packets and placed at the soil surface (slightly covered by soil) or buried at 5 or 10 cm deep.

Packets were retrieved 6, 10, 14 and 18 months after burial. On each occasion seed were removed from the packets and the number of viable seeds determined. Seeds were considered to be viable if they were whole, undamaged and firm when pressed with the tip of a pair of forceps. Viability was further confirmed by testing germination of firm seeds under the same conditions as described in Experiment 1 for seed treated with 5 mM of KNO₃. Seed that still did not germinate were treated with sulfuric acid for 30 min and germinated as previously described. The remaining ungerminated seed were soaked in water for 30 min, seed coats were sliced off on one side parallel to the embryo and put in 1 % tetrazolium solution. The seed were left in the dark at 40 °C for four to five hours. Seed with embryos that stained pink to red after incubation were considered viable. For the 14- and 18-month-seeds, only the tetrazolium test was performed for confirming viability of firm seeds.

Statistical analysis

For the germination experiments (Experiments 1 and 2), each treatment was replicated five times in a completely randomized block design (Experiment 2) or a completely randomized design (Experiment 1). For the depth of emergence experiment (Experiment 3), treatments were replicated four times in a completely randomized block design (each pot represented one replication of a given depth). The *Solanum* seed longevity experiment (Experiment 4) was a split-plot arrangement of a randomized complete block design with burial duration as main plots, burial depth as subplot, and three replications. All controlled-environment experiments were repeated once with similar results, but only one set of data is presented.

Each data set was subjected to Levene's test for homogeneity of variance or to residual plots to check for homoscedasticity. Normal probability plots were constructed to examine the assumption of normality. Arcsine (\sqrt{y}) transformation was required for all experimental data, with the exception of the data from the light and nitrate trial from *Vismia* and the data from Experiment 4. Data from each experiment were subjected to analysis of variance. Transformed data were retransformed for presentation. Within each species and experiment, treatment means were separated by single degree of freedom contrasts or by the Tukey's HSD method of multiple comparison ($P= 0.05$). Means from Experiment 4 were separated by the LSD procedure according to Milliken & Johnson (1992, pg. 300). Statistical analyses were performed by STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994), MINITAB release 9.2 for Windows (MINITAB 1993), or SYSTAT Version 5.03 (Wilkinson 1990).

Results and discussion

Experiment 1: Germination response to light and nitrate

Germination response to light indicated that both *Vismia* and *Solanum* seeds have a positive photoblastic behavior (Fig. 3.1); however, this behavior was stronger in *Vismia*. Although germination in the dark was much reduced in *Vismia*, this species was still capable of germinating in the absence of light (Fig. 3.1).

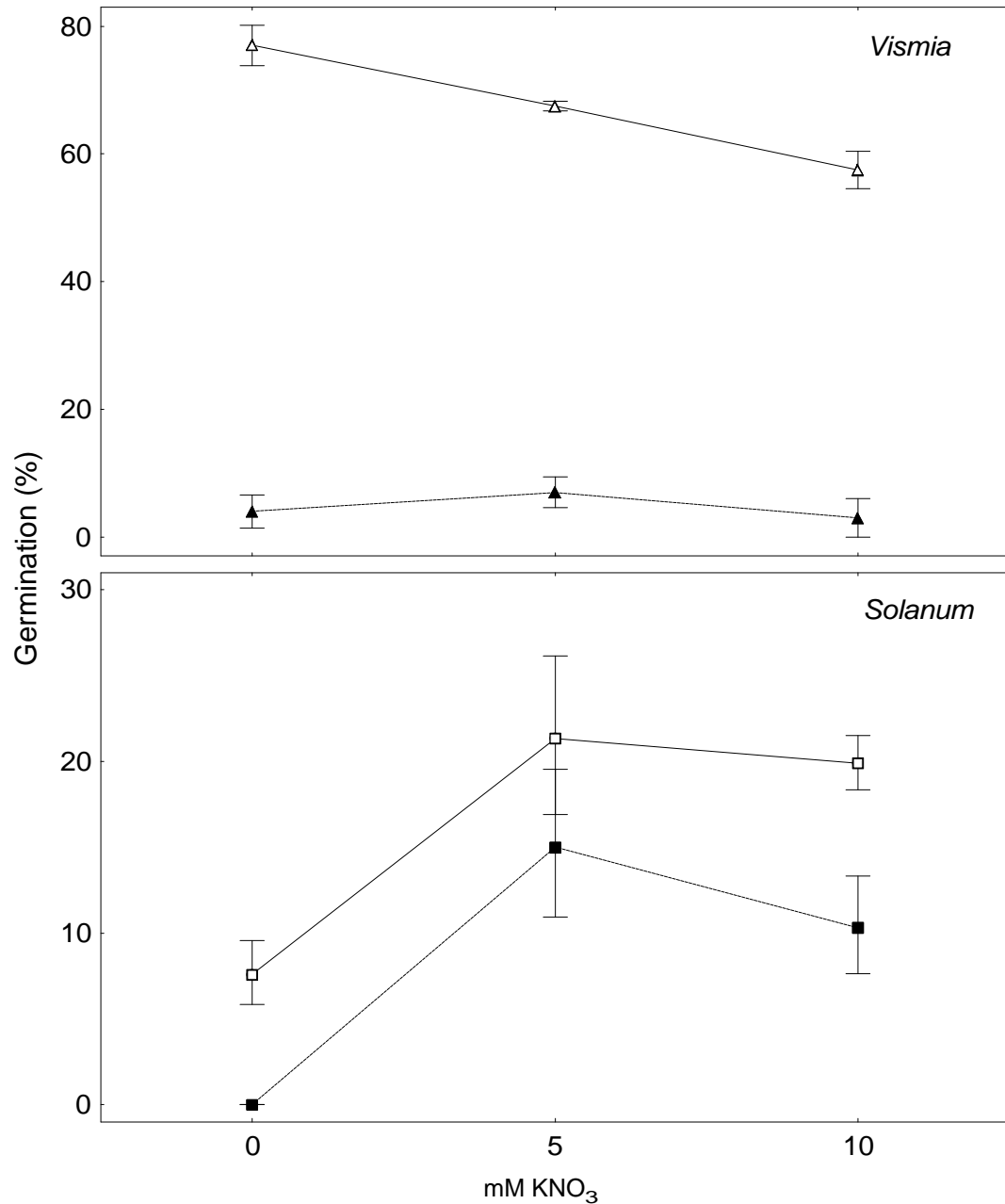


Figure 3.7. Effect of light and nitrate levels on percent germination of *Vismia* and *Solanum*, at 21 days after planting. Each value is the mean of 20 seeds each, with five replications. Vertical bars are ± 1 standard error of the mean. Light = open symbols and solid lines; dark = closed symbols and dashed lines.

No effect of nitrate could be detected on *Vismia* in the dark ($F_{1,24} = 0.1$; $P = 0.76$), however, nitrate had a negative effect ($F_{1,24} = 20.4$; $P <$

0.001) on *Vismia* germination under light, reducing germination by 12 and 25 %, respectively, in the 5 and 10 mM treatments. Unlike *Vismia*, germination of *Solanum* was positively stimulated by nitrate under both light ($F_{1,24} = 13.8$; $P = 0.001$) and dark ($F_{1,24} = 49.1$; $P < 0.0001$) conditions (Fig. 3.1). The inhibitory effect of nitrate on *Vismia* seeds was probably not caused by a sensitivity to high osmotic potentials as, contrary to *Solanum*, this species was able to germinate at relatively high osmotic potentials (see Experiment 2). In a similar study with a group of successional species from Venezuelan Amazonia, including one species from the genus *Solanum* and one from *Vismia*, it was shown that dark germination was not influenced by nitrate (Uhl & Clark 1983). However, it is possible that the very high nitrate concentration used in that study (0.1 M) may have inhibited germination of the studied species.

Light-regulated dormancy is well established as an important mechanism by which seeds can respond to gaps in vegetation or litter. This mechanism, however, can only operate on or very close to the soil surface, as it has been demonstrated that physiologically and ecologically significant amounts of light rarely penetrate more than 4-5 mm through the soil, and that any penetration beyond 10 mm would generally not be significant (Tester & Morris 1987). It has also been proposed that breaking of seed dormancy by nitrate in the absence of light would operate as a gap detection mechanism (Pons 1989). This mechanism would enable buried seeds of certain species to “sense” the presence of nearby plants through the nitrate concentration in the soil solution; a relatively high nitrate concentration would be indicative of no or few neighboring plants (Pons 1989). The present results show that such mechanisms might be

operating in *Solanum* seeds. By decreasing the probability of a premature seedling competing for light or other resources with neighboring plants, this mechanism could be of great adaptive significance for a sun-loving, gap-invader species like *Solanum*. In addition, the finding that germination of *Solanum* is stimulated by nitrate in the absence of light may, to some extent, explain the fact that, in pasture areas, this species is known to emerge from within dung pats well before these pats are completely disintegrated (M. B. Dias-Filho, unpublished observation). As in the present study no germination was observed from seeds incubated in the dark in a nitrate-free media, it seems reasonable to conclude that, under natural conditions, *Solanum* seeds inside a dung pat probably experience nitrate concentrations adequate to stimulate their germination. Since fruits of this species are known to be consumed by grazing ruminants as well as other mammals, it could be speculated that breaking of seed dormancy by nitrate in the absence of light may also have evolved as an adaptive response to this dispersal mode.

Because the concentration of nitrate in the soil solution fluctuates seasonally in the field due to the changing activity of the soil microorganisms, under natural conditions *Solanum* may experience a flush of germination during periods of relatively high nitrate concentration in the soil such as after soil rewetting, following a period of soil drying. It could be also hypothesized that, in the field, fertilizers containing nitrates could also stimulate the germination of dormant seeds of this species. Previous research in Brazilian Amazonia has shown that a pasture area fertilized with nitrogen, at the establishment phase, had a greater percentage of weeds than unfertilized or phosphorus fertilized areas (Dias Filho 1986). It

could be speculated that such response was at least in part caused by the stimulating effect of nitrate on weed seed germination.

Experiment 2: Germination response to osmotic stress

Vismia and *Solanum* showed different responses to increasing osmotic stress. Germination in *Solanum* was very sensitive to osmotic stress, decreasing by 78 % from 0 MPa (no moisture stress) to -0.2 MPa and becoming zero at osmotic potentials lower than -0.2 MPa (Fig. 3.2). Relative to *Solanum*, germination in *Vismia* was much less affected by increasing osmotic stress. For this species germination at -0.2 MPa was reduced by only 33 % compared to germination at 0 MPa (Fig. 3.2). Although decreasing osmotic potentials caused reduced germination in *Vismia*, germination was observed at osmotic potentials of up to -1.0 MPa, where germination was 6 % (Fig. 3.2). The response of *Vismia* to increasing osmotic potentials was similar to the one observed by Smith et al. (1992) for *Sida rhombifolia*, a weed species also known to coexist with *Vismia* in active pasture areas in Brazilian Amazonia (Dias Filho 1990). However, in that study, *S. rhombifolia* was not able to germinate at osmotic stress of -1.0 MPa (Smith et al. 1992).

The germination response of *Vismia* and *Solanum* to increasing osmotic stress is indicative of a greater ability of *Vismia* to colonize sites subjected to higher soil moisture stress and agrees with the results of a comparative physiological study on the response of these species to soil moisture stress (see Chapter 8); in that study, *Vismia* was found to be more drought tolerant and water-use efficient than *Solanum*. Thus, the germination response of *Solanum* to low osmotic potentials may reflect a

strategy to favor seedling survival, allowing germination only when and where conditions for seedling establishment would be adequate.

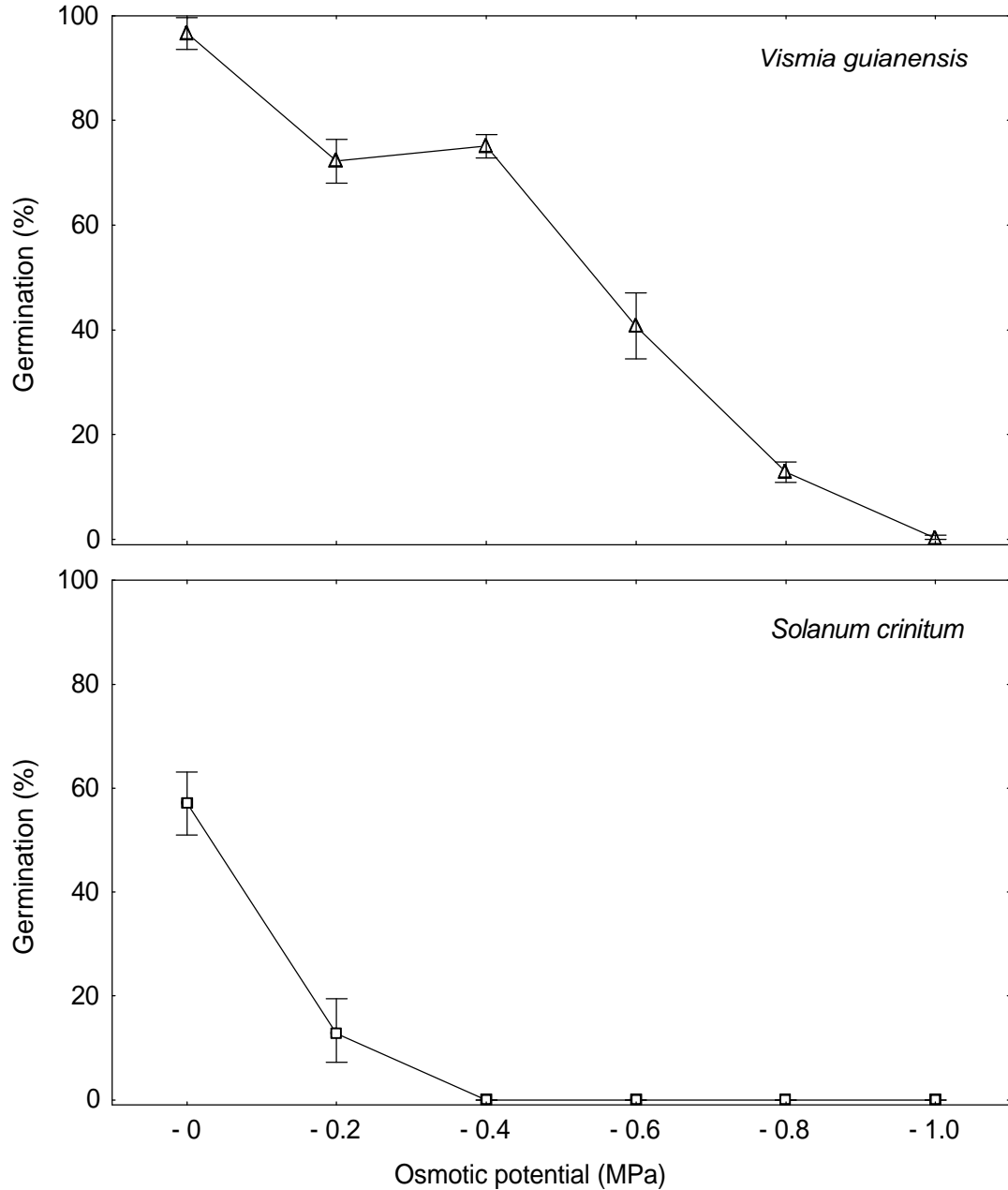


Figure 3.8. Effect of osmotic stress on percent germination of *Vismia* and *Solanum*, at 36 (*Vismia*) or 32 (*Solanum*) days after planting. Each value is the mean of 20 seeds each, with five replications. Vertical bars are ± 1 standard error of the mean.

Experiment 3: Emergence response to planting depth

Emergence in *Vismia* was restricted to seed planted at the soil surface and at depths of up to 2 cm (Fig. 3.3). Considering the very small seed mass of *Vismia* (mean seed weight \pm s.d.; 0.5 ± 0.08 mg, $n= 52$), emergence from depths greater than 2 cm was probably limited by this species' ability to provide enough energy reserves for an adequate hypocotyl elongation and not by the lack of light. In fact, the results from the Experiment 1 showed that *Vismia* is capable of germinating in the dark (Fig. 3.1). Also, by examining the soil after the experiment conclusion, it was observed that some seeds had indeed germinated at planting depths greater than 2 cm, but the extent of hypocotyl elongation (2-3 cm) did not enable the seedlings to reach the soil surface (data not shown).

For a relatively small-seeded species (mean seed weight \pm s.d.; 4.16 ± 0.77 mg, $n= 52$), *Solanum* showed a remarkable capacity to emerge from great planting depths. Seeds were able to emerge from up to 8 cm deep, at which depth emergence was 6 % (Fig. 3.3). However, seedling emergence of this species was greatest from seed planted at lesser depths, yet emergence from seed placed on the soil surface was significantly lower (Tukey's HSD test, $P < 0.0001$) than that of seed planted at 2 and 1 cm deep (Fig. 3.3). As suggested elsewhere (see Fenner 1985), the low emergence from surface-planted seeds was probably due to poor seed-soil contact and desiccation. Similar studies have also found reduced emergence from weed seeds planted at the soil surface (e.g., Baird & Dickens 1991, Kruger & Shanner 1982). The observed germination response of *Solanum* in the osmotic stress trial (Fig. 3.2) supports the

above conclusion, suggesting that germination of this species is indeed very sensitive to moisture stress.

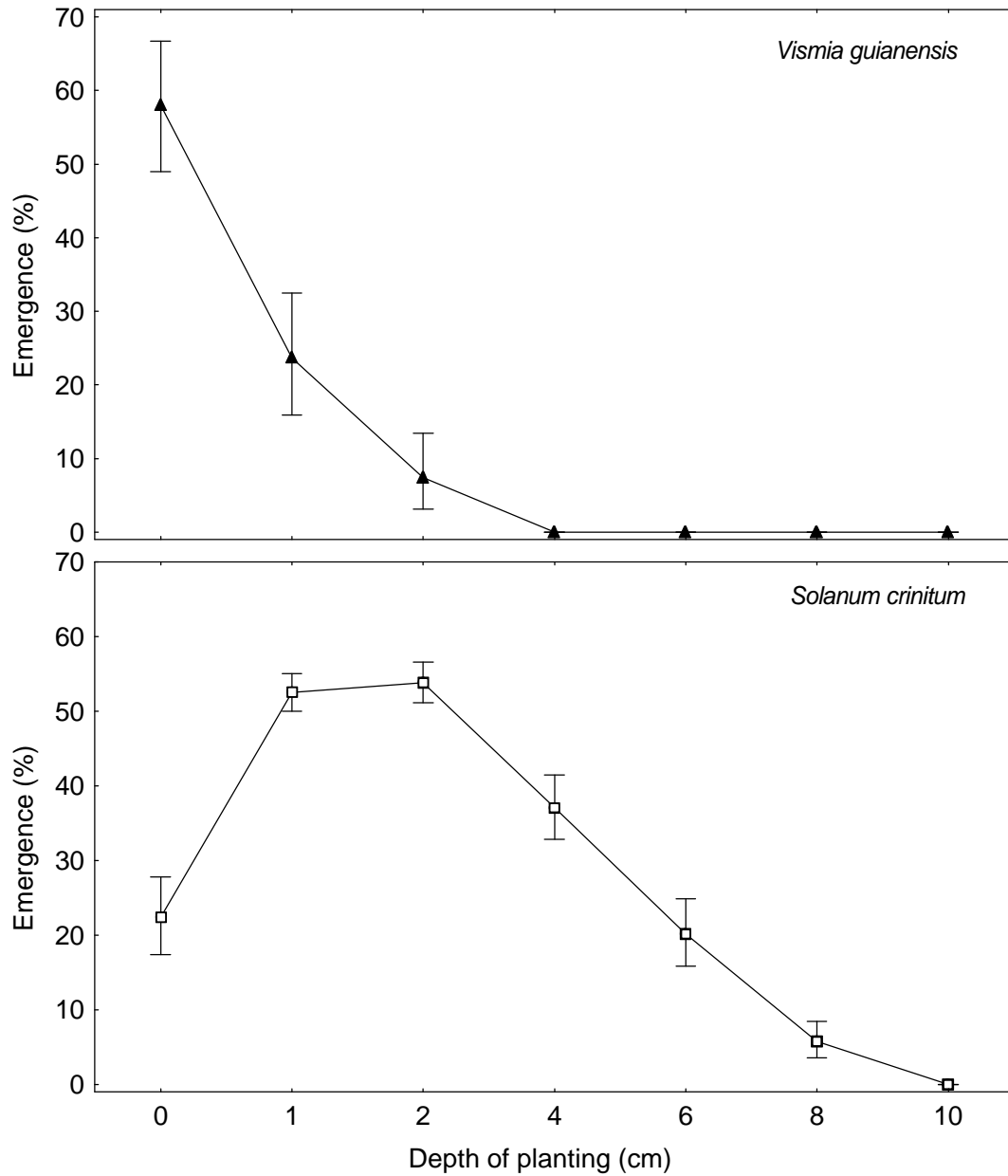


Figure 3.9. Effect of planting depth on percent emergence of *Vismia* and *Solanum*, at 60 (*Vismia*) or 50 (*Solanum*) days after planting. Each value is the mean of 10 seeds each, with four replications. Vertical bars are ± 1 standard error of the mean.

It is interesting to note that *Solanum* had the ability to emerge from deeper in the soil than *Vismia*. As both species germinated in the dark (Experiment 1, Fig. 3.1), it can be speculated that the larger *Solanum* seed (about eight times that of *Vismia*), contains more energy reserves to support seedling emergence from greater planting depths. Lack of adequate seed energy reserves or small seed size has also been suggested in other studies as a possible cause of seedling emergence failure from greater planting depths (MacDonald et al. 1992, Martínez et al. 1992, Mutz & Schifres 1975, Shaw et al. 1991, 1987, Smith et al. 1992).

Because under natural conditions soil physical characteristics (e.g., soil texture, degree of compaction) can vary remarkably among microhabitats and, as a consequence, seeds at the same burial depth but at different horizontal distances in the soil profile might not always experience the same degree of physical impediment for seedling emergence, the present results may not be directly applicable to field conditions. However, these results do indicate that, relative to its seed size, *Solanum* has a remarkable capability for hypocotyl extension (i.e., emergence ability). Under natural conditions, such ability would help improve the potential for seedling establishment when and where there would be need for extra hypocotyl elongation for light capture.

Experiment 4: Depth of burial on longevity of *Solanum* seeds

At all depths, but particularly at the soil surface, there was a significant loss in viability during the period of burial (Fig. 3.4). In contrast to temperate species, most tropical species are usually reported to have much less seed longevity in the soil (for a review see Fenner 1985 and Garwood

1989). Relative to initial viability (85% at time 0) of *Solanum* seeds, at the end of the experiment (18 months) an 84, 60 or 67 % loss of viability had been experienced, respectively, by the surface, 5 cm or 10 cm deep seed.

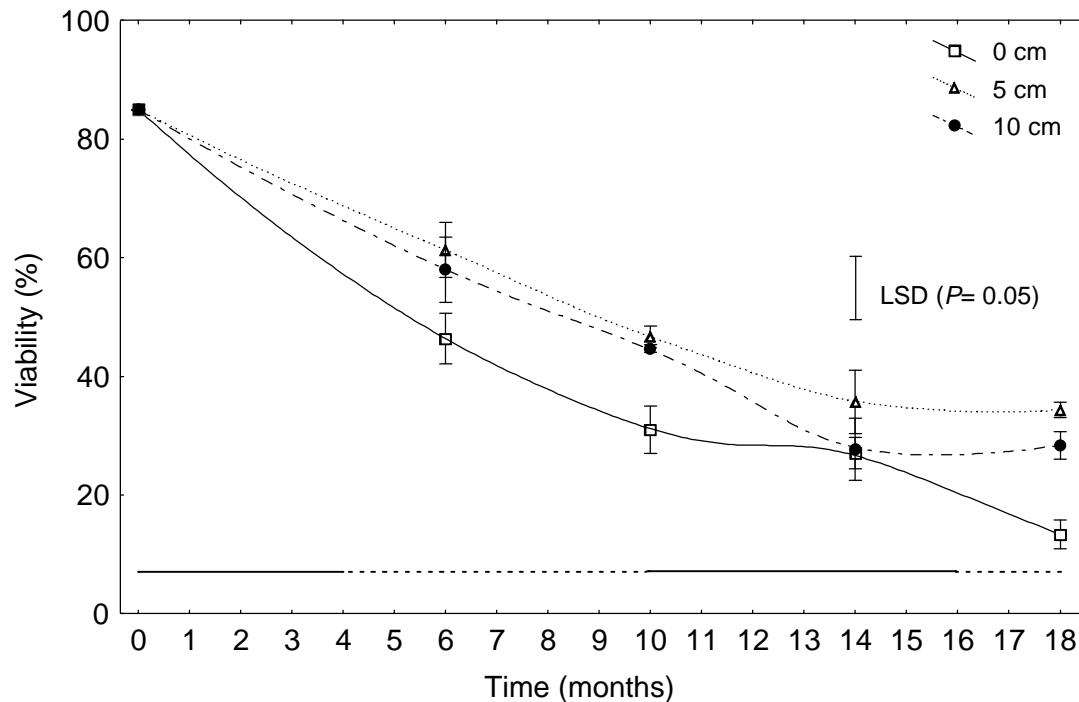


Figure 3.10. Seed viability as a function of time and burial depth in *Solanum*. Each value is the mean of 100 seeds each, with three replications. The horizontal line indicates the length of the dry (solid line) and wet (dashed line) seasons during the experimental period. Error bars are ± 1 standard error of the mean. The LSD bar compares depth means at the same time period. Curves fitted by distance-weighted least squares.

Although the methodology used did not allow for a positive estimation of the exact proportion of seed loss through germination *in situ* versus seed loss from other causes, traces of seedlings could be observed in the burial packets at all planting depths and throughout all evaluation dates (data not shown). This observation suggests that germination may play an important part in the decline of soil seed bank for this species.

The shape of the curve fitted to the viability data from seed placed at the soil surface (Fig. 3.4) suggests that the decline in viability is relatively lower during the dry season and higher during the rainy season. This is probably caused by the extremely variable conditions (e.g., great diurnal fluctuations in temperature and humidity) that may have been experienced by seed at the soil surface during the rainy season; this environment could help overcome the hard-seededness known to exist in *Solanum*, increasing germination and thus decreasing seed survival. Conversely, during the dry season *Solanum* seed at the soil surface probably would seldom experience humidity conditions sufficiently long to trigger germination. The same circumstances may also explain the tendency for a lower persistence of *Solanum* seed at the soil surface observed throughout the evaluation period (Fig. 3.4), since a relatively higher proportion of seed was probably lost via germination at the surface than at 5 or 10 cm deep. This result supports the general findings from tropical and temperate studies that the deeper the seed burial the longer the persistence in the seed bank (Bourdôt & Hurrell 1992, Bridgemohan et al. 1991, Eberlein 1987, Ralphs & Cronin 1987, Schwerzel 1976).

Although other phases of the life cycle, such as seedling establishment and early growth, should also be considered, information on seed germination, and emergence characteristics and seed survival patterns of these species in the field must be taken into account as an important initial step to evaluate the invasive potential of these plants. In conclusion, the seed persistence characteristics of *Solanum*, the germination and emergence characteristics of *Vismia* and *Solanum* as well as their known dispersal mode suggest adaptations that actually help these species to take

advantage of the environmental conditions known to occur in disturbed (e.g., agricultural) habitats in Brazilian Amazonia. This observation indicates that *Vismia* and *Solanum* are likely to maintain or even increase their present status as important invasive species in eastern Brazilian Amazonia.

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**PHYSIOLOGICAL RESPONSE OF *IPOMOEA*
ASARIFOLIA AND *STACHYTARPHETA*
CAYENNENSIS TO CONTRASTING LIGHT
ENVIRONMENTS**

Introduction

All plants have the ability to modify their developmental patterns in response to the light environment (Hart 1988). However, the nature of photomorphogenetic responses can vary considerably among species according to their acclimation capacity (i.e., morphological plasticity) and depending upon the quantity and quality of light (e.g., Clough, Teeri & Alberte 1979; Clough, Alberte & Teeri 1980; Givnish 1988; Seemann 1989; Walters & Field 1987). The ability of an individual species to successfully grow in a low or high light environment (holding quality constant) can be assessed by determining how efficiently and how rapidly allocation patterns and physiological behavior are adjusted in response to a particular light environment.

In agricultural ecosystems the light environment can be extremely variable and in many instances, may determine the composition of the weedy flora of the area. This is particularly true for tropical pastures, where grazing preference behavior may create zones with relatively dense or sparse plant cover and as a consequence, with contrasting light

environments over relatively small areas. Information on the morphological and physiological responses of weedy species to distinct light conditions can be critical in determining their occurrence potential and in helping to understand the competitive ability of these plants under different management situations so as to devise more effective control strategies. Managing tropical pasture weeds through an improved understanding of their ecophysiology is particularly important for areas like Brazilian Amazonia, where ecologically sound weed management strategies could decrease further deforestation by helping to increase the agricultural sustainability of already deforested areas.

The present research involved work with two species: *Ipomoea asarifolia* (Desr.) Roem. & Schultz, a fast-growing Convolvulaceae vine, and *Stachytarpheta cayennensis* (Rich) Vahl., a relatively slow-growing Verbenaceae shrub. Both are recognized as important perennial C₃ weedy species from pastures and crop areas in Brazilian Amazonia (Albuquerque 1980, Dias Filho 1990). Although native from tropical America, *S. cayennensis* also occurs as a weed in Australia (Klenschmidt & Johnson 1987), Hawaii (Haselwood & Motter 1983) and India (Nair, Mohanan & Sreekumar 1982). Also, many *Ipomoea* species are considered as important weeds from warm temperate zones (for a review see Elmore, Hurst & Austin 1990). In active pasture areas, the occurrence of *Stachytarpheta* has been related to overgrazing, being more common in areas with little or no vegetation cover, while *Ipomoea*, although capable of starting growth in relatively shaded areas along fences and near fallen tree trunks, usually occupies available sunny areas (Dias Filho 1990). Also, in abandoned pasture and crop areas in Amazonia, both species tend to

disappear as these areas become increasingly invaded by shrubs and small tree species (M.B. Dias Filho, unpublished observation). The above observations may suggest that light, among other resources, might be an important determinant of these species' presence, and may also play an important role in their ability to establish and successfully compete with crop and pasture species.

The purpose of the present study was to examine the rate of growth, biomass allocation patterns, gas exchange and leaf nitrogen content of *Ipomoea* and *Stachytarpheta* developed at high and low photon flux densities. I hypothesized that the spatial patterns in the distribution of these species observed in the field may, to some extent, be reflected in their physiological and growth responses to the light environment. My ultimate objective was to be able to use this information as a possible management strategy for the control of these weeds. To date, no study is known which has tried to use a knowledge of the physiological ecology of Amazonian weeds for their control.

Materials and methods

Plant material and growing conditions

Ipomoea asarifolia (Convolvulaceae) and *Stachytarpheta cayennensis* (Verbenaceae) seeds were collected from plants growing in pasture areas in eastern Brazilian Amazonia (2° 58' S). Seeds were germinated on filter paper in petri dishes and then planted individually in 1750 ml plastic pots in a mixture of peat:vermiculite:perlite (1:1:1). Plants were initially grown in a greenhouse at temperatures of $24 \pm 2.2^{\circ}\text{C}$ (minimum) to $33 \pm 2.1^{\circ}\text{C}$

(maximum) and a maximum photosynthetic photon flux density (PPFD) of approximately $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. Following expansion of the first two true leaves (about 21 days after germination), plants were transferred from the greenhouse to two Conviron growth chambers (Model PGW36. Controlled Environments, Inc. Pembina, ND) set at 28/24°C day/night air temperatures, 70 % relative humidity, and 12-h photoperiod. Before transference to the growth chambers, seedlings from each species were divided into five size classes, and each class was randomly assigned to a replication (block).

Within each growth chamber, a high- and a low-light environment were simulated by placing multiple layers of neutral density shade cloth beneath the light source of half of each growth chamber. Irradiance, monitored throughout the experiment with a light meter (Model LI-1905 light meter, Li-Cor, Inc. Lincoln, NE) at canopy height, ranged between 800 and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ for high-light and between 200 and $350 \mu\text{mol m}^{-2} \text{s}^{-1}$ for low-light treatments.

All pots were watered daily to full capacity with deionized water and fertilized every five days with 50 ml per pot of a water soluble fertilizer solution (15 % N, 30 % P_2O_5 , 15 % K_2O , 0.02 % B, 0.07 % Cu, 0.15 % Fe, 0.05 % Mn, 0.0005 % Mo and 0.06 % Zn; 3.5 g L^{-1}).

Growth analysis

For both species five harvests were made. The first harvest was on the day plants were transferred to the growth chambers (Day 0), and the others 10, 20, 30 and 40 days later (n= 5 per harvest and light treatment). At each harvest plant material was divided into leaf, support tissue (stem and

petiole), reproductive tissue (for *Stachytarpheta* only) and root. Leaves were removed and leaf area measured using a leaf area meter (Model LI-3000. Li-Cor, Inc. Lincoln, NE) and conveyor belt assembly (Model LI-3050. Li-Cor, Inc. Lincoln, NE). Leaf area was measured three times for each individual leaf and the final area was the mean of these three measurements. Plant dry weight was obtained by drying the plant material in an oven at 70°C for 48 hours. Attributes measured for each plant at each harvest were used to estimate relative growth rate (change in dry weight per total dry weight of plant per day, RGR) and biomass allocation patterns: leaf area ratio (leaf area per unit weight of whole plant, LAR), specific leaf area (leaf area per unit of leaf dry weight, SLA) and leaf, stem and root weight ratios (respectively, leaf, stem or root weight per unit of weight of whole plant, LWR, SWR and RWR). All of the above growth and biomass allocation parameters were calculated according to Hunt (1990).

Gas exchange

Gas exchange parameters were measured on plants just before the fifth harvest, i.e., when the plants had been in the growth chamber for 40 days. A photosynthesis (A) versus irradiance (PPFD) response curve (starting at ca. $1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 (Model LI-6200, LI-COR, Inc., Lincoln, NE). Gas exchange parameters were calculated on a leaf area basis. The amount of leaf area in the chamber (cuvette) was approximately 22 cm^2 for *Ipomoea* and 15 cm^2 for *Stachytarpheta*. The irradiance 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 20 min to each new light level. To absorb long-wave radiation and maintain constant leaf temperatures in the cuvette, a 10 cm deep Plexiglas circulating bath of cool water was suspended between the light source and the leaf cuvette. For *Stachytarpheta*, leaf temperature during gas exchange measurements was maintained at $25.2 \pm 0.9^{\circ}\text{C}$ (low-light plants, mean \pm s.d.) and $25.5 \pm 0.8^{\circ}\text{C}$ (high-light plants), except when it was necessary to measure gas exchange in the dark, which resulted in mean leaf temperature of $23.3 \pm 0.8^{\circ}\text{C}$ (low-light) or $23.3 \pm 0.7^{\circ}\text{C}$ (high-light). For *Ipomoea*, leaf temperatures were $26.7 \pm 0.7^{\circ}\text{C}$ (low-light) or $26.7 \pm 0.8^{\circ}\text{C}$ (high-light); leaf temperatures in the dark were $23.3 \pm 0.2^{\circ}\text{C}$ (low-light) and $23.3 \pm 0.1^{\circ}\text{C}$ (high-light). After exposure to the lowest PPFD, the plants were left for 30 min in the dark and measurements were made to obtain dark respiration (R_d) values. Five replicate plants of each species per experiment and one leaf per plant were sampled. The leaf-to-air vapor pressure gradient inside the cuvette during all measurements was 9-12 mmol mol⁻¹.

Photosynthesis versus irradiance response data provided direct estimates of highest measured value of photosynthetic rate (A_{max}). Apparent quantum yield of CO₂ to incident irradiance (α) was the slope of a regression of five R_d measurements and five low light (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) measurements of CO₂ exchange, for each species and light regime combination. The light compensation point was calculated as the ratio, R_d/α .

Leaf nitrogen analysis

Leaf nitrogen was measured on each individual leaf used for the gas exchange measurements, and also on all leaves of each individual plant at each harvest date and light treatment combination. In all cases, leaf nitrogen content was measured with a nitrogen analyzer (Model NA 1500, series 2. Carlo Erba Strumentazione, Milan, Italy). The instrument was calibrated with both an NBS “citrus leaf” and organic standard. Precision was $\pm 0.17\%$ of N.

Experimental design and statistical analysis

The experiment was arranged in a randomized complete block design with five replications. All pots were rotated within replications (blocks) every day to minimize variation in growth due to possible temperature and light differences within the growth chamber.

Analysis of covariance (ANCOVA), with plant age (days since germination) fitted as covariate, was used to estimate the overall effects of light regime and harvest date and their interaction on biomass allocation parameters. By removing the effect of plant age with the use of ANCOVA, inherent ontogenetic drift effects were avoided. Residual plots and normal probability plots were used to check for homoscedastic residuals and normality; when necessary data were logarithmically transformed. The assumption of homogeneity of slopes (parallelism) was also tested for each ANCOVA. Differences in RGR were tested as a Light regime \times Time interaction in an analysis of variance with logarithmically-transformed dry weight as dependent variable (Poorter & Lewis 1986). A trend analysis over time was performed to detect differences in RGR throughout the

experiment. The statistical packages MINITAB, Release 9.2 for Windows (MINITAB 1993) and SYSTAT Version 5.03 (Wilkinson 1990) were used for the computations of the growth and biomass allocation data.

Differences in net photosynthesis and stomatal conductance response curves for species and light regime treatments were analyzed by analysis of variance with repeated measures (von Ende 1993). The between-subject main effects were species and light regimes, and the within-subjects or repeated measures effect was irradiance level. Homoscedastic residuals were obtained with logarithmically transformed values for photosynthesis and stomatal conductance. No severe departures from the normality assumption were detected by examining half-normal probability plots of z-transformed within-cell correlations for both data sets. Compound symmetry of the covariance matrix of each analysis was tested by the Mauchly's sphericity test. The Huynh-Feldt (see von Ende 1993) correction was considered for both analyses. *Post hoc* contrasts comparing species and light regime differences in photosynthesis and stomatal conductance, within each irradiance level, were calculated. The statistical package STATISTICA for Windows, Release 4.5 (STATISTICA for Windows 1994) was used for the analysis of the gas exchange data.

Results

Biomass allocation

The ANCOVA showed that, for both species, light regime effects were significant for both leaf area variables, SLA and LAR and for leaf and root

weight values (LWR and RWR respectively; $F_{1,35} \geq 13.38$, $P \leq 0.001$).

Mean values (Table 4.1) for the entire experiment showed that plants

Table 4.1. Specific leaf area (SLA, $\text{m}^2 \text{g}^{-1}$), leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$), leaf weight ratio (LWR, g g^{-1}), stem weight ratio (SWR, g g^{-1}) and root weight ratio (RWR, g g^{-1}), as means for the entire experiment (40 d), of *Stachytarpheta cayennensis* and *Ipomoea asarifolia* under high- and low-light regimes. Values are means (\pm s.d.), $n= 25$.

	High-light	Low-light
<i>Stachytarpheta cayennensis</i>		
SLA	0.031 (0.027)	0.049 (0.023)
LAR	180.1 (146.2)	307.4 (141.2)
LWR	0.576 (0.112)	0.623 (0.093)
SWR	0.139 (0.061)	0.152 (0.065)
RWR	0.252 (0.053)	0.197 (0.038)
<i>Ipomoea asarifolia</i>		
SLA	0.027 (0.008)	0.032 (0.007)
LAR	89.0 (67.2)	136.9 (63.2)
LWR	0.350 (0.141)	0.406 (0.129)
SWR	0.440 (0.169)	0.427 (0.177)
RWR	0.207 (0.052)	0.166 (0.063)

grown under low light had greater LAR, LWR and SLA and smaller RWR than plants that grew in high light. This tendency in the mean values was maintained throughout the experimental period. The highest SLA and LAR

occurred early in plant growth and declined throughout the experimental period (data not shown). No significant effect ($F_{1,35} \geq 2.15$, $P \geq 0.104$) of light regimes on SWR could be detected on either species.

In *Ipomoea*, the proportion of biomass allocated to leaf and root tissue, in both high- and low-light plants, was highest in the beginning of plant development and declined throughout plant growth (Fig. 4.1). This decline may be in part due to mobilization of resources to the stems. In low-light *Ipomoea*, the decline with time in RWR was more pronounced than in high-light plants; conversely, high-light plants had a greater decline in LWR (Fig. 4.1).

For *Stachytarpheta*, LWR, under both light regimes, initially increased up to 10 d and then declined during the experiment (Fig. 4.2). Root weight ratio changed little with time in low-light *Stachytarpheta* relative to high-light plants in which RWR had a tendency to increase throughout plant growth (Fig. 4.2). Allocation to reproductive biomass was observed only in *Stachytarpheta* (Fig. 4.2). High-light plants allocated significantly ($F_{1,35} = 8.64$, $P < 0.006$) more biomass to reproductive structures (i.e., flower bearing spikes) than low-light plants. This increased allocation to developing flower bearing spikes together with the larger allocation to roots apparently contributed to the greater decline with time observed in LWR in high-light *Stachytarpheta* relative to low-light plants (Fig. 4.2).

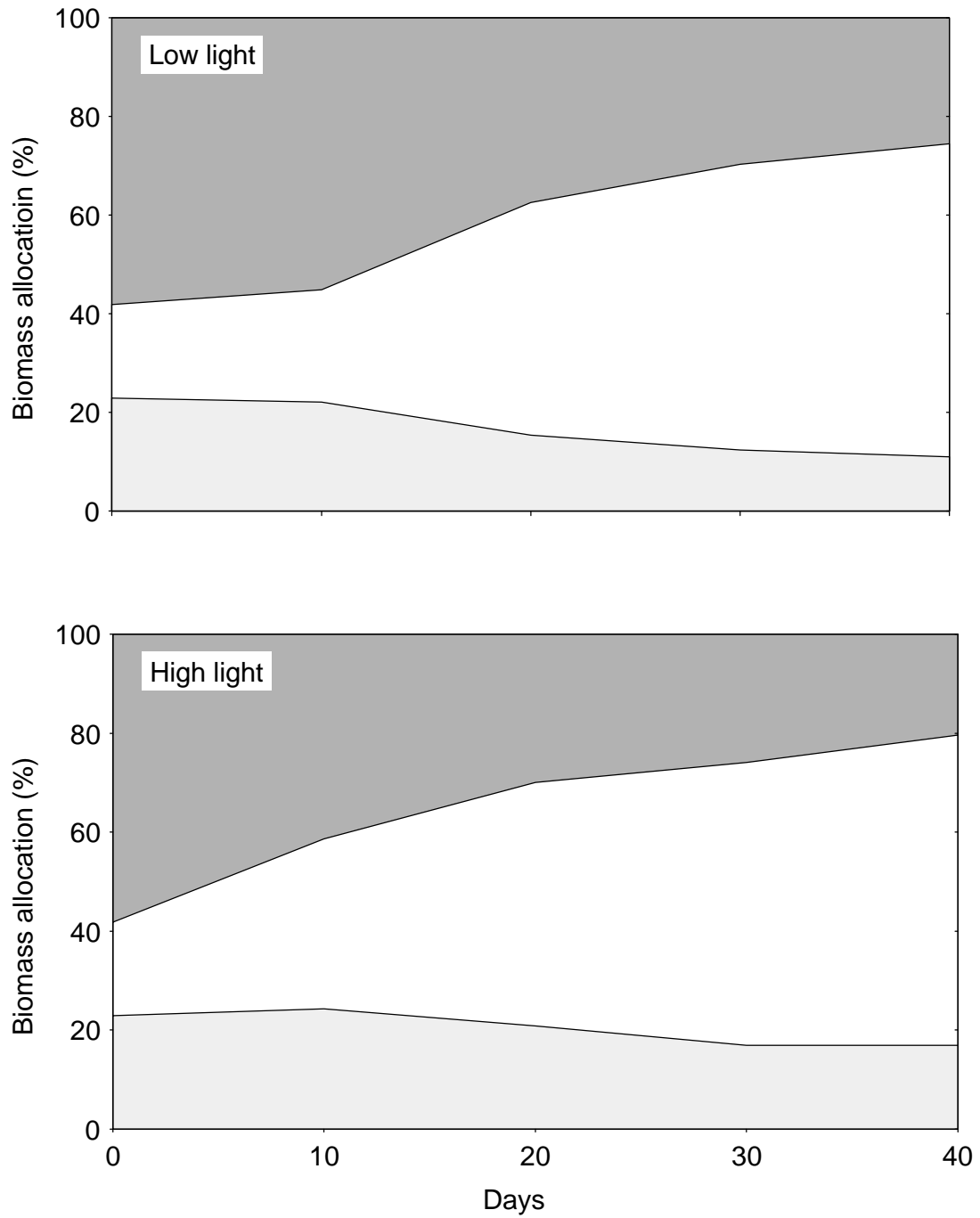


Figure 4.11. Mean proportion of biomass allocated to roots (dotted area), stems (blank area) and leaves (hatched area) as a function of time and light environment in *Ipomoea*.

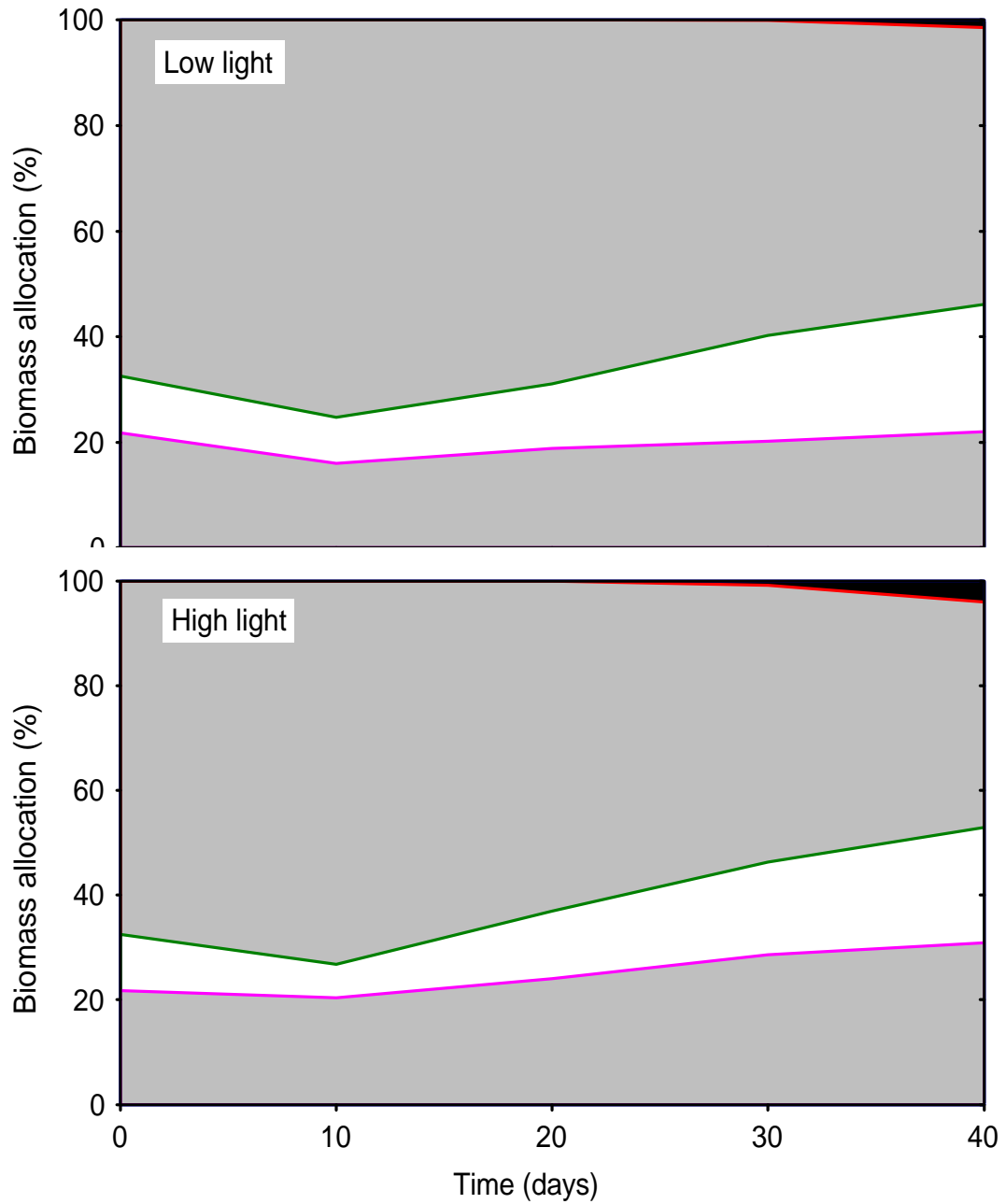


Figure 4.2. Mean proportion of biomass allocated to roots (dotted area), stems (blank area), leaves (hatched area) and flower bearing spikes (solid area) as a function of time and light environment in *Stachytarpheta*.

Growth

The ANOVA for RGR of *Ipomoea* shows a significant Light regime \times Time interaction (Table 4.2), indicating that for this species, RGR was influenced by the light regimes experienced by the plants. The trend analysis over time (i.e., orthogonal polynomials) suggested that the differences in RGR between the two light regimes was not maintained throughout the entire experimental period, since the quadratic component accounts for the greatest proportion of this interactive effect (Table 4.2). An identical response in RGR was also observed for *Stachytarpheta*, as the interactive effect of Light regime \times Time was also significant and most of the sum of squares interaction was due to the quadratic component (Table 4.2).

For *Ipomoea*, high-light grown plants displayed a higher growth rate, relative to low-light plants from the very early stages of seedling development (Fig. 4.3). This difference in growth between light environments became less pronounced by day 30, and was not apparent by the last evaluation date (Fig. 4.3). Differences in growth rates between light environments in *Stachytarpheta* revealed a similar trend to that observed for *Ipomoea*, but, unlike in that species, growth in *Stachytarpheta* was exponential for both light regimes (Fig. 4.3).

Table 4.2. Analysis of variance of growth in *Ipomoea* and *Stachytarpheta* . Dependent variable: total (shoot and root combined) plant dry weight (after log transformation). Independent variables: Treatments, the two light regimes (high and low light); Time, the five harvests, Blocks, the five replicates (blocks). For the interaction a trend analysis over time was performed.

Ipomoea

Sources	df	MS	F	P
Block	4	0.192	12.87	0.0001
Treatments	1	3.236	216.50	0.0001
Time	4	32.781	2193.25	0.0001
Time × Treatments	4	0.364	24.33	0.0001
Linear	1	0.006	0.4	0.531
Quadratic	1	0.844	56.23	0.0001
Cubic	1	0.517	34.47	0.0001
Residual	1	0.087	5.80	0.021
Within cells	36	0.015		

Stachytarpheta

Sources	df	MS	F	P
Block	4	0.749	8.35	0.0001
Treatments	1	6.594	73.47	0.0001
Time	4	92.127	1026.48	0.0001
Time × Treatments	4	0.710	7.92	0.0001
Linear	1	0.081	0.90	0.349
Quadratic	1	2.371	26.34	0.0001
Cubic	1	0.315	3.50	0.069
Residual	1	0.074	0.82	0.371
Within cells	36	0.090		

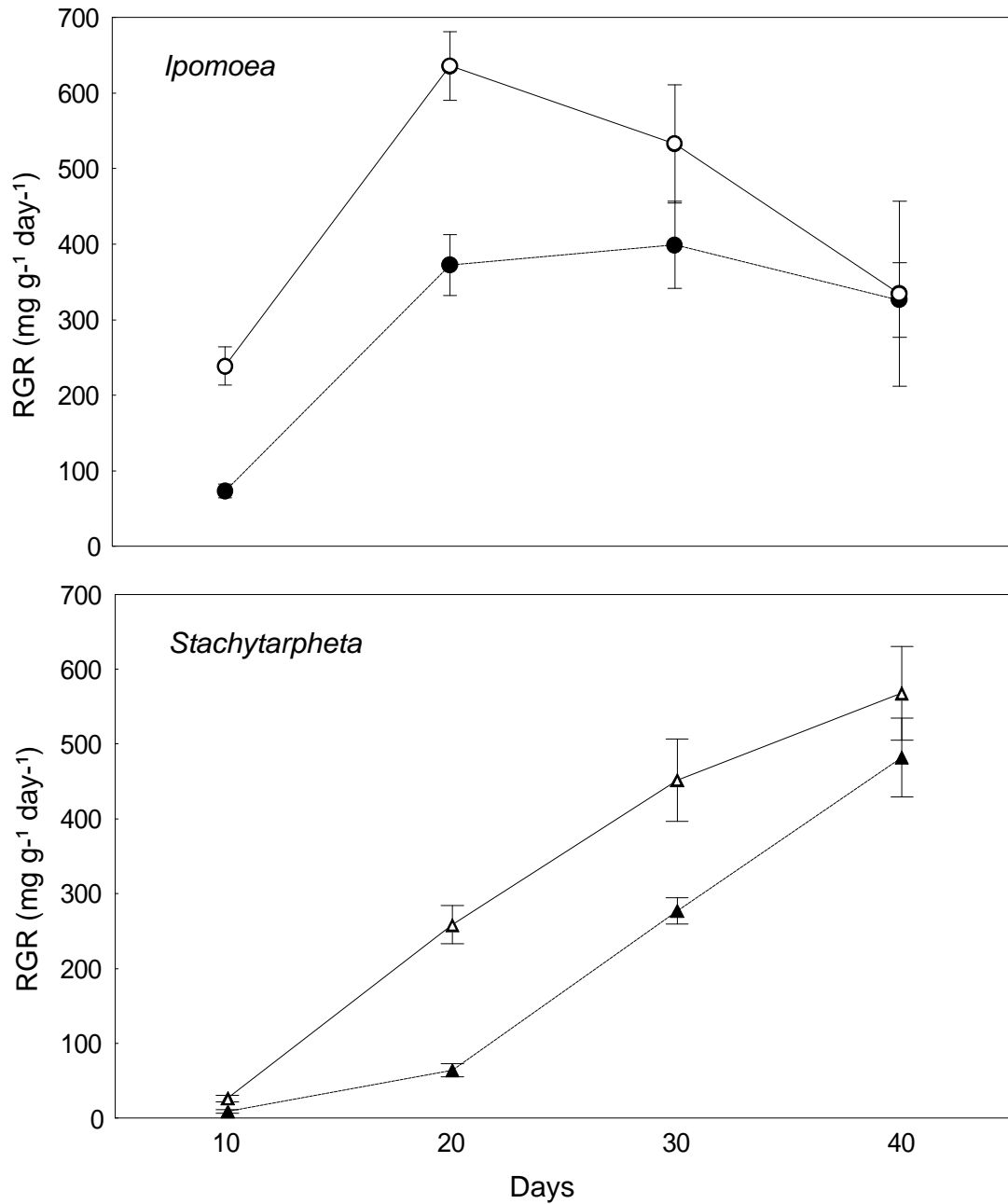


Figure 4.3. Change over time in relative growth rates (RGR) (mean \pm SE, $n=5$) of *Ipomoea* and *Stachytarpheta* under low- (closed symbols and dashed lines) and high-light (open symbols and solid lines) conditions.

CO₂ assimilation

There were significant Species and Species \times Light regime main effect differences in CO₂ assimilation rates; no significant difference could be detected for the Light regime main effect (Table 4.3, Fig. 4.4). Among the within-subjects main effects only irradiance level and its interactive effect with the light regimes were statistically significant (Table 4.3). For both

Table 4.3. Analysis of variance of net photosynthesis with repeated measurement on irradiance levels. Species (*I. asarifolia* and *S. cayennensis*) and treatments (high light and low light) are the fixed main effects.

Sources	df	MS	F	<i>P</i>	H-F
<i>Between subjects</i>					
Species (Sp)	1	16.83	28.28	< 0.0001	----
Treatments (Tr)	1	0.455	0.765 0	.39	----
Sp \times Tr	1	2.78	4.67	0.046	----
Error	16	0.595			
<i>Within subjects</i>					
Irradiance level (I)	5	27.86	94.28	----	<0.0001
I \times Sp	5	0.323	1.095	----	0.38
I \times Tr	5	3.636	12.3	----	<0.0001
I \times Sp \times Tr	5	0.211	0.715	----	0.61
Error	80	0.295			

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

species, low-light-grown plants had a tendency to display higher assimilation values under the lowest irradiance levels (Fig. 4.4). *Post hoc*

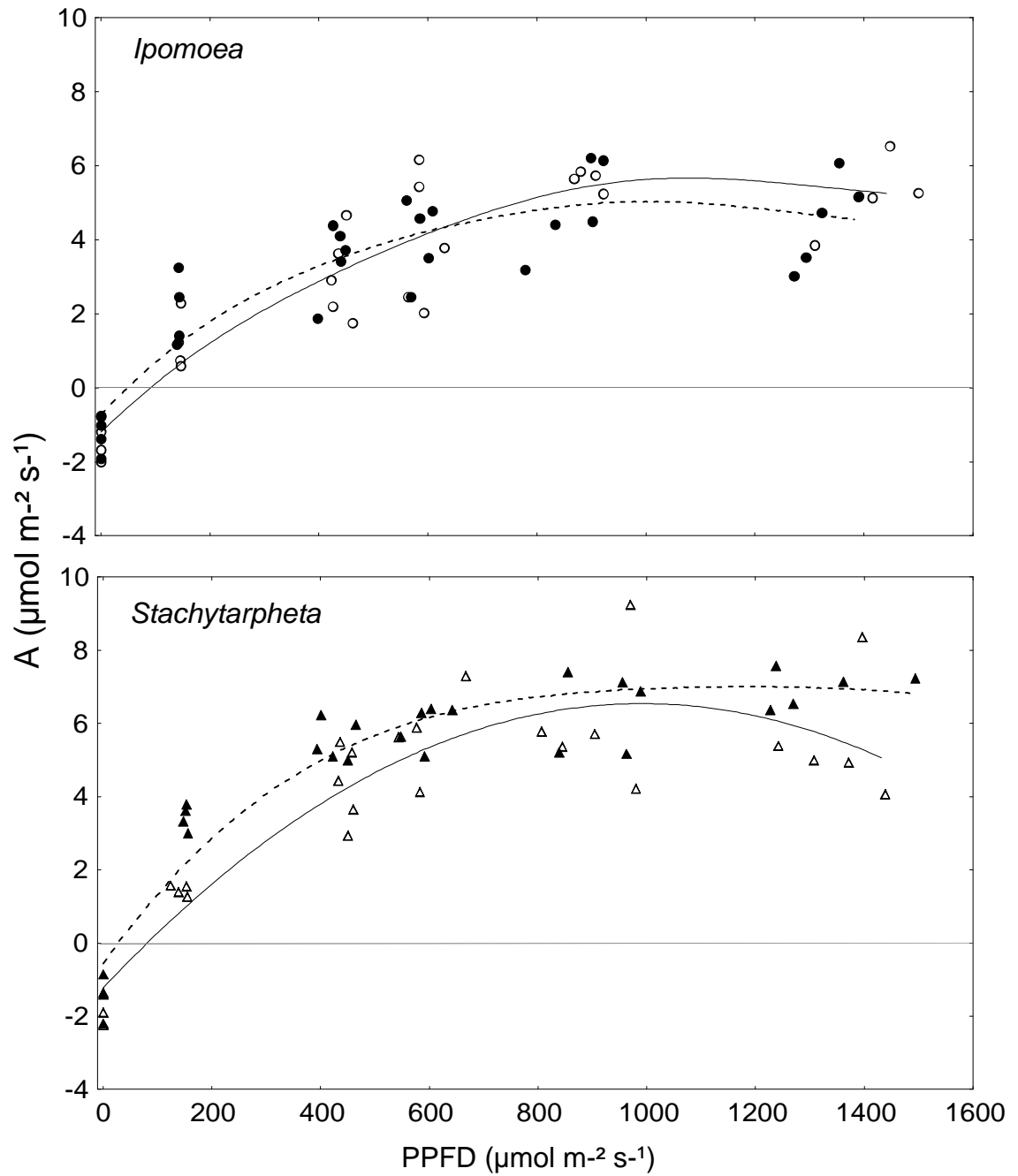


Figure 4.4. Light response curves of photosynthesis of *Ipomoea* and *Stachytarpheta* grown under low- (closed symbols and dashed lines) and high-light (open symbols and solid lines) conditions. Curves fitted by distance-weighted least squares.

contrasts indicated that in *Ipomoea* significant differences in the irradiance response curve between light environments were observed at the first (ca. 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 5.4$, $P = 0.03$), second (ca. 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 5.4$, $P = 0.03$) and fifth (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 19.5$, $P < 0.001$) irradiance levels. High-light grown *Ipomoea* leaves had higher CO_2 assimilation rates at the two highest irradiance levels (i.e., ca. 1400 and 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$), but lower assimilation at the lowest irradiance level (i.e., ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$). For *Stachytarpheta*, significant differences in CO_2 assimilation rates between light regimes could be detected only at the fifth (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 23.03$, $P < 0.0001$) irradiance level with higher CO_2 assimilation for low-light grown plants. *Post hoc* contrasts on differences between species, within each light regime, showed that under the high light regime the two species differed in CO_2 assimilation only at the fourth (ca. 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 4.5$, $P = 0.048$) and the fifth (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 7.6$, $P = 0.013$) irradiance levels, with higher rates for *Stachytarpheta*. Comparison of low-light grown plants revealed higher assimilation rates for *Stachytarpheta* at all irradiance levels ($F_{1,16} \geq 7.09$, $P \leq 0.017$; Fig. 4.4).

Stomatal conductance

Leaf stomatal conductance, g , in *Stachytarpheta* behaved differently from that in *Ipomoea*; it was sensitive to growing conditions and was significantly reduced by growth at high photon flux density (Fig. 4.5). Comparisons between light regimes assessed by *post hoc* contrasts showed significant differences in g for *Stachytarpheta* at the first (ca. 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 7.9$, $P = 0.01$) and fifth (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,16} = 11.1$, $P = 0.004$) irradiance levels, and in the dark ($F_{1,16} = 4.6$, $P = 0.04$); low-light

Stachytarpheta leaves had higher g in these irradiance levels, but lower g in the dark (Fig. 4.5). No significant differences in g between light regimes could be detected for *Ipomoea*.

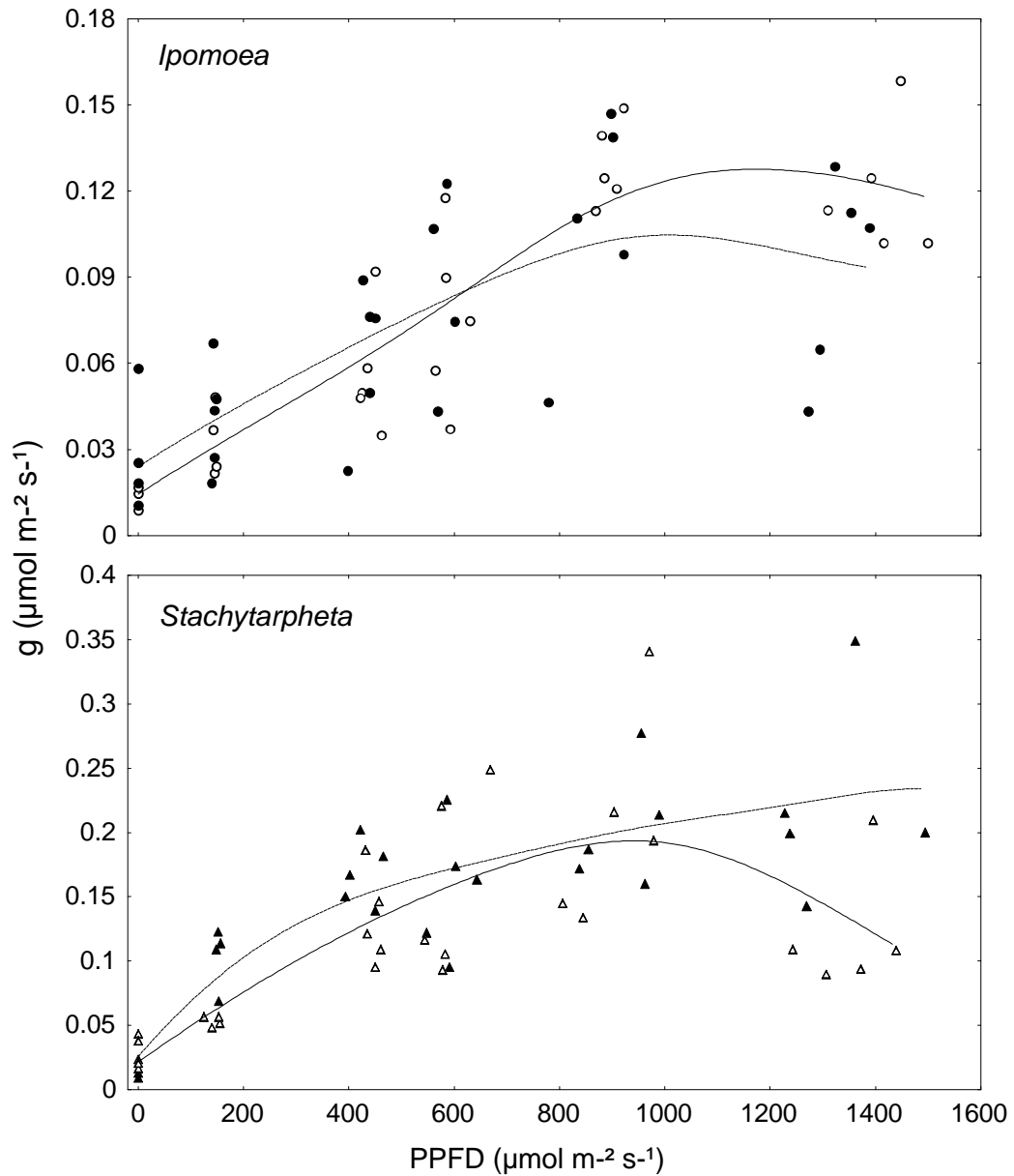


Figure 4.5. Light response curves of stomatal conductance of *Ipomoea* and *Stachytarpheta* grown under low- (closed symbols and dashed lines) and high-light (open symbols and solid lines) conditions. Curves fitted by distance-weighted least squares.

Photosynthesis parameters

Light-saturated photosynthesis (A_{max} , Table 4.4, Fig. 4.4) within each species was higher for plants subjected to the high-light treatment.

Between species, A_{max} was higher for *Stachytarpheta*, under both light regimes. Within species differences in R_d , assessed by *post hoc* contrasts of the light response curves, revealed that high-light grown *Ipomoea* leaves

Table 4.4. Photosynthetic parameters of *Stachytarpheta cayennensis* and *Ipomoea asarifolia* under high- and low-light regimes. Symbols and units; A_{max} is light saturated photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); α is apparent quantum efficiency ($\text{mol CO}_2 \text{ photon}^{-1}$); R_d is dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and R_d/α is light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Values are means (\pm s.d.), n=5.

	High-light	Low-light
<i>Stachytarpheta cayennensis</i>		
A_{max}	9.25	7.56
α	0.022 (0.001)	0.032 (0.002)
R_d	1.72 (0.41)	1.37 (0.55)
R_d/α	76.50 (16.7)	42.21 (15.1)
<i>Ipomoea asarifolia</i>		
A_{max}	6.54	6.22
α	0.019 (0.005)	0.023 (0.004)
R_d	1.52 (0.53)	1.24 (0.44)
R_d/α	80.87 (26.6)	54.63 (23.0)

displayed higher (more negative) R_d than low-light leaves ($F_{1,16} = 8.9$, $P = 0.008$). No other statistically significant difference in R_d within and between species and treatments could be detected. However, a tendency for higher R_d values for high-light grown plants from both species and for *Stachytarpheta* compared to *Ipomoea*, can be observed in Table 4.4.

The apparent quantum efficiency, α , was sensitive to the light regime during growth (Table 4.4). Growth at the low-light environment caused an average increase in α of 19% and 50%, respectively in *Ipomoea* and *Stachytarpheta* relative to high-light plants; this difference, however, was statistically significant only for *Stachytarpheta* ($t=7.67$, $P < 0.0001$). If we consider the reciprocal of α , the quantum requirement (quanta CO_2^{-1}), as a measure of efficiency of photosynthesis, high-light *Stachytarpheta* was significantly ($t= 32.9$, $P < 0.0001$) more efficient than low-light plants (mean \pm s.d., 44.62 ± 2.5 vs. 31.27 ± 2.6), while no significant difference in photosynthetic efficiency could be detected between high- (54.92 ± 11.6) and low-light (43.58 ± 7.3) *Ipomoea*. Light compensation point, R_d/α , was also influenced by the light regimes, being at least 45% higher in high-light grown *Ipomoea* and *Stachytarpheta*. As observed in Table 4.4, most of the difference in R_d/α between species can be attributed to differences in α . As a result of the higher α observed in *Stachytarpheta*, R_d/α in this species was lower than that in *Ipomoea* (Table 4.4).

Nitrogen content

In both species, nitrogen content per unit leaf weight was higher for low-light plants (Fig. 4.6). However, when expressed on a leaf area basis, nitrogen content in high-light *Stachytarpheta* was higher than in low-light

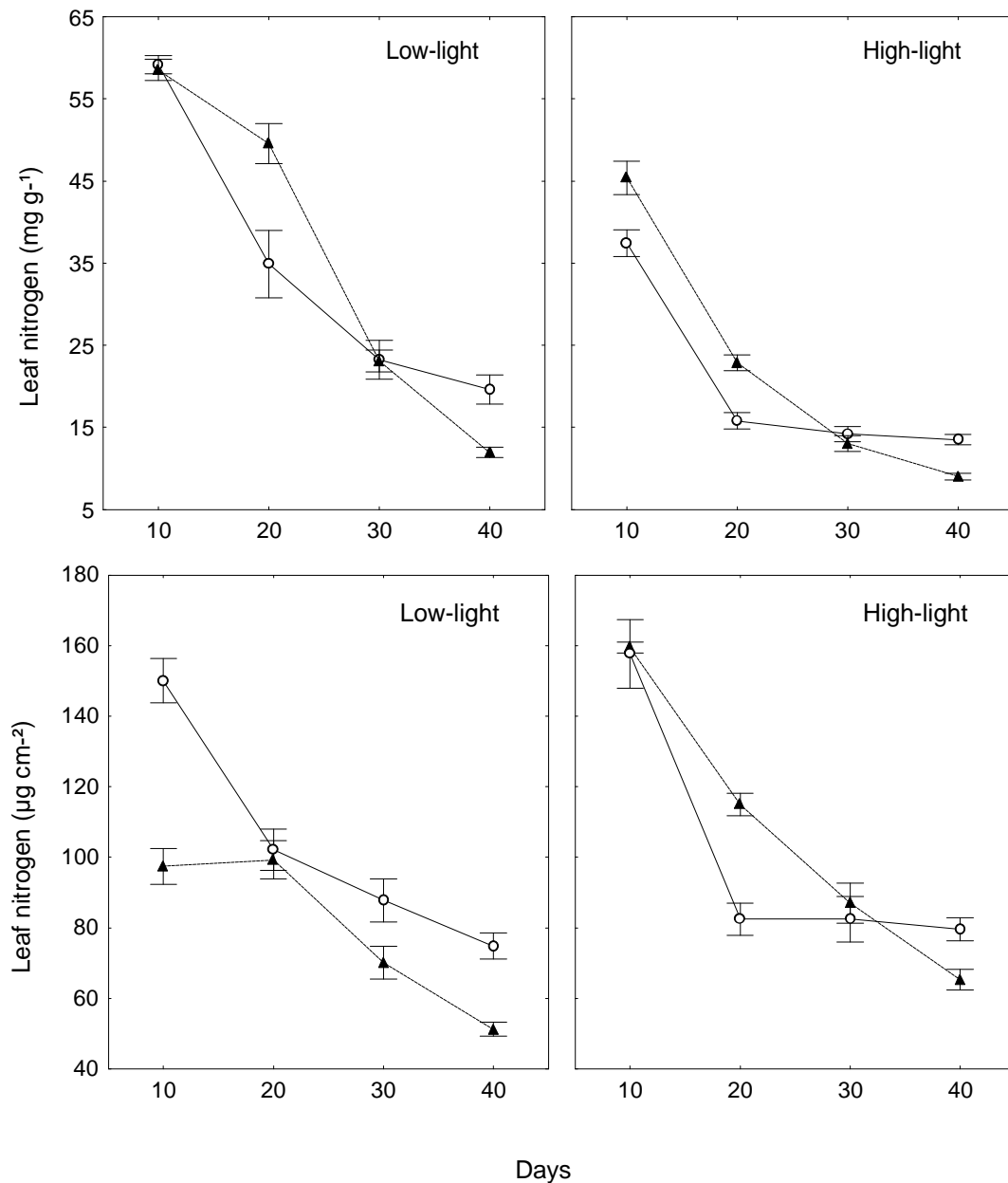


Figure 4.6. Leaf nitrogen content (mean \pm SE, n= 4) on a mass (mg g^{-1}) and area ($\mu\text{g cm}^{-2}$) basis for *Ipomoea* (open symbols, solid lines) and *Stachytarpheta* (closed symbols, dashed lines) under low- and high-light conditions.

plants. For *Ipomoea*, no systematic tendency was evident, as nitrogen content, on a leaf area basis, varied throughout time in an inconsistent pattern between light regimes (Fig. 4.6). A positive correlation between

nitrogen content on a weight basis and CO₂ assimilation under the highest irradiance level (ca. 1400 μmol m⁻² s⁻¹) was observed in high-light *Stachytarpheta* and *Ipomoea*; in low-light plants, a weaker correlation was found for *Stachytarpheta*, but not for *Ipomoea*, which displayed a stronger correlation between CO₂ assimilation and leaf nitrogen at low light (Table 4.5). Stomatal conductance, *g*, in *Stachytarpheta* was positively and significantly correlated with leaf nitrogen content (Table 4.5), the slope of this relationship being steeper for low-light plants. Thus, there was a stronger response of *g* to leaf nitrogen on a mass basis in low-light plants. *Ipomoea* behaved differently from *Stachytarpheta*, no relationship could be detected between *g* and leaf nitrogen in high-light plants, yet, a weak, but nonsignificant correlation between these attributes was also discernible in low-light *Ipomoea* (Table 4.5).

Table 4.5. Slope (*s*), correlation coefficient (*r*) and significance level (*= <0.05 , **= <0.01) of the correlations between CO₂ assimilation (*A*), stomatal conductance (*g*), and the amount of biomass allocated to reproductive tissue (*R*) vs. leaf nitrogen content (mg g⁻¹). *n*= 4.

	<i>Stachytarpheta</i>				<i>Ipomoea</i>			
	High-light		Low-light		High-light		Low-light	
	s	r	s	r	s	r	s	r
<i>A</i>	0.748	0.93*	0.323	0.57	0.083	0.42	0.384	0.78
<i>g</i>	0.022	0.95*	0.042	0.99**	0.001	0.07	0.006	0.47
<i>R</i>	-0.079	-0.51	-0.027	-0.31	---	---	---	---

In *Stachytarpheta*, the amount of biomass allocated to reproductive tissue (i.e., flowering bearing spikes) was negatively correlated to CO₂ assimilation ($r = -0.53$ for high-light and $r = -0.33$, for low-light plants), stomatal conductance ($r = -0.74$ for high-light and $r = -0.33$, for low-light plants) and also to the nitrogen content (on a mass basis) from the leaf used for the gas exchange measurements (the youngest fully expanded leaf) (Table 4.5). Yet, none of these relationships were statistically significant ($P > 0.05$). However, when mean nitrogen content from all leaves of each individual plant was considered, as opposed to the leaf used for the gas exchange measurements, a strong and highly significant negative correlation was found between leaf nitrogen (on a mass basis) at the 30- and 40-day evaluation periods (when most plants have started reproduction) versus the corresponding biomass allocated to flower bearing spikes during those periods by low- ($r = -0.98$, $P < 0.0001$, $n = 8$) and high-light ($r = -0.79$, $P = 0.02$, $n = 8$) *Stachytarpheta* plants. When leaf nitrogen on an area basis was considered, a similar relationship was observed for low- ($r = -0.86$, $P = 0.007$) and high-light ($r = -0.67$, $P = 0.07$) plants. Due to the nonlinear relation between mean leaf nitrogen from all leaves of each plant and the corresponding reproductive biomass of high- and low-light plants, these correlations were measured by Spearman rank order correlation (Potvin & Roff 1993).

Discussion

Growth and biomass allocation

Growth in *Stachytarpheta* was exponential while in *Ipomoea* RGR started to decrease after day 20 or 30, respectively, in high- and low-light plants

(Fig. 4.3). This distinct response between species was probably associated with self-shading and a much larger investment in supporting structures in *Ipomoea* (Table 4.1, Fig. 4.1) which may have inflated the respiration load of this species by decreasing the amount of photosynthetically active area per unit of plant weight. In *Stachytarpheta*, due to its growth form, preferential allocation to leaf area (i.e., higher LAR) and leaf arrangement architecture, overall photosynthetic gain was relatively unaffected over time.

Interspecific differences in RGR at the early stages of seedling development (i.e., up to day 20) (Fig. 4.3) were well related to initial seedling size and seed weight differences between *Ipomoea* and *Stachytarpheta*. *Ipomoea* has a mean seed mass 53 times greater than that of *Stachytarpheta*, and the mean seedling mass at the beginning of the experiment (day 0) was 30 times greater for *Ipomoea*. These differences may help maximize the potential of establishment and persistence of *Ipomoea* under conditions of low resource such as in a shaded environment, as observed in the present experiment for low-light plants (Fig. 4.3).

Light regime during growth had significant effects upon the allocation of carbon and the structure of *Ipomoea* and *Stachytarpheta* plants (Table 4.1, Figs. 4.1 and 4.2). The patterns of biomass allocation reported here for both species are consistent with previous studies which have shown that development under low quantum flux density promotes allocation to leaves and increases SLA (for a review see Lambers & Poorter 1992). Consistent with their growth form, however, *Ipomoea* and *Stachytarpheta* differed in the relative fraction of total plant biomass

allocated to leaves, stems and roots. Relative to *Stachytarpheta*, *Ipomoea*, under both light regimes, partitioned larger portion of biomass into stems and a smaller portion into leaves (Figs 1 and 2). Being a relatively fast growing vine would require *Ipomoea* to constantly allocate biomass to stems in order to grow, and as stems are not normally shed during plant growth, their biomass increases steadily over time relative to leaves and roots, which are continually renewed. This characteristic may have contributed to the much higher SWR observed in *Ipomoea* relative to *Stachytarpheta* on both light regimes (Table 4.1).

A common response for low-light plants from both species was a reduced (ca. 20 %) overall investment into roots relative to high-light plants (Fig. 4.1 and 4.2, Table 4.1). This is a characteristic feature in many plant species grown under shade, and have been reported in a number of studies (Mahall & Schlesinger 1982; Dall'Armellina & Zindahl 1988; Zollinger & Kells 1991; Thompson, Kriedemann & Craig 1992a; Walters, Kruger & Reich 1993). This decreased allocation to roots under low light conditions has been observed to be maximized mainly in sun-loving plants (Thompson et al. 1992a, Walters et al. 1993) and is very likely to be related to traits that improve the rates of carbon gain in low light such as an increased LAR and LWR, or that reflect a light seeking strategy such as vertical growth. In the present study, mean LAR and LWR were, respectively, 71 % and 8 % higher in low-light *Stachytarpheta* and 54 % and 16 % higher in low-light *Ipomoea*, relative to high-light plants (Table 4.1). Also, at the last harvest date (40 d), mean plant height (or main stem length in *Ipomoea*) was 16 % higher ($t= 1.9$, $P= 0.09$) in low-light

Stachytarpheta, but only 7 % longer ($t= 0.68$, $P= 0.51$) in low-light *Ipomoea* (data not shown).

An important feature observed in *Stachytarpheta* was a significantly higher allocation to developing reproductive structures in high-light plants (Fig. 4.2). Also, low-light grown plants had the onset of flowering delayed in comparison to high-light plants (Fig. 4.2). These results are in accord with the knowledge that in wild plants, reproductive partitioning generally decreases with resource limitation (for a review see Chiariello & Gulmon 1992), and suggest that in *Stachytarpheta* the light environment may provide an important external signal for induction and enhancement of flowering and, as a consequence for the success of this species as a weed. Similar responses have been described for the perennial weeds *Sonchus arvensis* (Zollinger & Kells 1991), *Convolvulus arvensis* and *Centaurea repens* (Dall'Armellina & Zindahl 1988) grown under contrasting light environments.

Gas Exchange Response

The shape of the light response curve observed for *Ipomoea* and, to some extent, for *Stachytarpheta*, grown under the contrasting light environments (Fig. 4.4), was similar to those observed by Ramos & Grace (1990) and Riddoch, Lehto & Grace (1991a) for a group of tropical trees and by Regnier, Salvicci & Stoller (1988) for the weed *Abutilon theophrasti*, grown under high and low light. Low-light grown plants had higher assimilation rates under lower irradiances and lower assimilation under higher irradiance levels. However, in the present study, high-light *Stachytarpheta* leaves had a tendency to exhibit lower CO₂ assimilations under the highest irradiance level, when compared to low-light plants. This

unexpected behavior of high light *Stachytarpheta* leaves may be related to the amount of biomass allocated to reproductive tissue by these plants, as a negative relationship between the amount of biomass allocated to flower bearing spikes and CO₂ assimilation was suggested by the data. This, in turn, was probably associated with the developing reproductive structures acting as a “competitive sink” with leaves for nitrogen (and probably other resources), leading to the lower leaf nitrogen content in plants with a higher proportion of biomass allocated to reproduction, as also suggested by the data. It is possible that the low leaf nitrogen content of high-light plants may have rendered these plants more susceptible to photoinhibition as observed for other tropical species (e.g., Seemann et al. 1987).

Developing reproductive structures acting as a sink for nitrogen has also been suggested for tropical legumes (Humphreys 1991, pg. 64) and for crop species (Sadras, Hall & Connor 1993; Sklensky & Davies 1993).

The positive relationship between leaf CO₂ assimilation or stomatal conductance and leaf nitrogen content per unit area observed for *Stachytarpheta* and, to some extent in *Ipomoea* (Table 4.5), was expected and has also been reported in other studies involving tropical trees (Tuohy, Prior & Stewart 1991; Riddoch et al. 1991a; Ramos & Grace 1990) and crops (for a review see Sinclair & Horie 1989). Interestingly, no relationship between leaf nitrogen and stomatal conductance could be detected in low-light *Ipomoea* (Table 4.5).

Analysis of the parameters calculated from the light response curves data (Table 4.4) shows that within species, statistically significant differences between light treatments in the initial slope of the photosynthetic light response curves can be observed only for

Stachytarpheta. Low-light treated plants of this species displayed a 50 % higher quantum efficiency. Yet a tendency for higher quantum efficiency in low-light *Ipomoea* is also apparent (Table 4.4). Other studies have shown that light regime during growth does not normally alter apparent quantum efficiency in temperate (Björkman 1981; Mahall & Schlesinger 1982) or tropical (Sims & Pearcy 1989; Ramos & Grace 1990; Riddoch et al. 1991a) species. However, a tendency for higher α values in low-light plants is usually observed in these studies. The larger α value in low-light *Stachytarpheta* relative to high-light plants can explain the rapid raise in assimilation rate with increasing irradiance observed in this species at the low-light treatment (Fig. 4.4). When compared to low-light *Ipomoea*, low-light *Stachytarpheta* was particularly more efficient at the lower irradiance levels (i.e., ca. 200 and 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$), displaying significantly higher CO_2 assimilation rates at these irradiances than high-light plants (Fig. 4.4).

The observed tendency for lower R_d values in low-light plants (Table 4.4) is a common response also reported for other tropical species under similar conditions (Ramos & Grace 1990; Riddoch et al. 1991a; Thompson, Kriedemann, & Craig 1992b), and may, in part, have contributed to the net photosynthetic advantage exhibited by shade grown plants at the lower irradiances levels (Fig. 4.4). Light compensation point, R_d/α (Table 4.4), of both species followed the same trend observed in other studies involving tropical species, in which higher irradiance during growth leads to higher values of R_d/α (Ramos & Grace 1990, Thompson et al. 1992b). The values of R_d/α calculated for *Ipomoea* and *Stachytarpheta* agree with values reported by Riddoch et al. (1991b) for two “weeds of gaps” from Nigeria, and do not suggest differences

between these species in relation to their shade tolerance. However, it has been suggested from work with tropical tree seedlings that shade tolerance may not necessarily depend on leaf characteristics such as light compensation point (Thompson et al. 1992b).

The present research has shown that both *Stachytarpheta* and *Ipomoea* quickly develop morphological and foliar adjustments as buffering mechanisms against light limitation. Although such adjustments help these species to partially offset loss of photoassimilate under low light conditions, and as a result enable growth maintenance, it could be speculated that, as a result of a much higher carbon investment in above ground tissues relative to roots, they might also render them more vulnerable to additional stresses that are common in a tropical pasture management system (Dias Filho 1987) such as mowing, fire or herbivory. This response may in turn decrease their ability to cope with edaphic constraints like reduced water and nutrient availability. Moreover, both species showed responses to the low-light environment that might suggest a reduced competitive ability, due to a negative effect on their sexual (*Stachytarpheta*) or vegetative (*Ipomoea*) reproductive capacity.

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PHYSIOLOGICAL RESPONSE OF *VISMIA* *GUIANENSIS* TO CONTRASTING LIGHT ENVIRONMENTS

Introduction

Depending to their acclimation capacity, plants can have distinct photomorphogenetic responses to the light environment (quantity and quality of light) (e.g., Clough et al. 1979, Givnish 1988, Seemann 1989, Walters & Field 1987). The ability of a particular species to efficiently and rapidly adjust its allocation patterns and physiological behavior in response to a low or high light environment (holding quality constant) is key in determining its growth potential to that particular environment.

Knowledge of the morphological and physiological responses of invading species to contrasting light conditions can be critical in helping to explain and predict their occurrence and abundance patterns under specific environmental conditions. Moreover this information can be useful to explain the invasive potential and the competitive ability of these plants under different management situations in agricultural areas so as to devise more effective control strategies.

Vismia guianensis (Aubl.) Choisy (Guttiferae) is a native successional woody species from tropical America found as a colonizer of man-made clearings and natural gaps in forests and in abandoned or active

agricultural areas in Brazilian Amazonia (Albuquerque 1980, Dantas 1989, Dias Filho 1990). In this chapter I investigate the sun-shade acclimation characteristics of *Vismia* by measuring its rate of growth, biomass allocation patterns, and photosynthetic features under development at high and low photon flux densities. The results are discussed in relation to their ecological and practical implications to Brazilian Amazonia.

Materials and methods

Plant material and growing conditions

Vismia guianensis seeds were collected from plants growing in pasture areas near Paragominas PA (3° 05' S - 47° 21' W) in Eastern Brazilian Amazonia. Seeds were germinated on filter paper in petri dishes and then planted individually in 15 cm plastic pots with a mixture of peat:vermiculite:perlite (1:1:1). Plants were initially grown in a greenhouse at temperatures of $24 \pm 2.2^{\circ}\text{C}$ (minimum) to $33 \pm 2.1^{\circ}\text{C}$ (maximum) and a maximum photosynthetic photon flux density (PPFD) of approximately $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. When plants were about 25 days old they were transferred from the greenhouse to a Conviron growth chamber (Model PGW36, Controlled Environments, Inc. Pembina, ND) set at 28/25°C day/night air temperatures, 80 % relative humidity, and 12-h photoperiod. Before transference to the growth chambers, seedlings from each species were divided into five size classes, and each class was randomly assigned to a replication (block).

A high- and a low-light environment were simulated by placing multiple layers of neutral density shade cloth beneath the light source of half of the growth chamber. Irradiance, monitored throughout the

experiment with a light meter (Model LI-1905 light meter, Li-Cor, Inc. Lincoln, NE) at canopy height, ranged between 800 and 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for high-light and between 120 and 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for low-light treatment. During one hour after the lights went on and one hour before the lights went off, the irradiance level was set to a lower level to provide the plants with a more natural transition period between the light and the dark periods. This transitional light level measured with a light meter at canopy height, ranged between 300 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for high-light and between 50 and 80 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the low-light treatment.

All pots were watered daily to full capacity with deionized water and fertilized every other day with 50 ml per pot of a water soluble fertilizer solution (15 % N, 30 % P_2O_5 , 15 % K_2O , 0.02 % B, 0.07 % Cu, 0.15 % Fe, 0.05 % Mn, 0.0005 % Mo and 0.06 % Zn; 3.5 g L^{-1}).

Growth analysis

Five harvests were made; the first harvest was on the day plants were transferred to the growth chambers (Day 0), and the others 15, 30, 45 and 60 days later (n= 5 per harvest and light treatment). At each harvest plant material was divided into leaf, support tissue (stem and petiole) and root. Leaves were removed and leaf area measured using a leaf area meter (Model LI-3000. Li-Cor, Inc. Lincoln, NE) and conveyor belt assembly (Model LI-3050. Li-Cor, Inc. Lincoln, NE). Plant dry mass was obtained by drying the plant material in an oven at 70°C for 48 hours. Attributes measured for each plant at each harvest were used to estimate relative growth rate (change in dry weight per total dry weight of plant per day, RGR) and biomass allocation patterns: leaf area ratio (leaf area per unit mass of whole plant, LAR), specific leaf area (leaf area per unit of leaf dry

mass, SLA) and leaf, stem and root weight ratios (respectively, leaf, stem or root mass per unit of weight of whole plant, LWR, SWR and RWR). All of the above growth and biomass allocation parameters were calculated according to Hunt (1990).

Gas exchange

Gas exchange parameters were measured on plants just before the fifth harvest, i.e., when the plants had been in the growth chamber for 60 days. A photosynthesis (A) versus irradiance (PPFD) response curve (starting at ca. $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 (Model LI-6200, LI-COR, Inc., Lincoln, NE). Gas exchange parameters were calculated on a leaf area basis. The amount of leaf area in the chamber (cuvette) was approximately 20 cm^2 . The irradiance 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 20 min to each new light level. To absorb long-wave radiation and maintain constant leaf temperatures in the cuvette, a 10 cm deep Plexiglas circulating bath of cool water was suspended between the light source and the leaf cuvette. After exposure to the lowest PPFD, the plants were left for 30 min in the dark and measurements were made to obtain dark respiration (R_d) values. Five replicate plants of each species per experiment and one leaf per plant were sampled. The leaf-to-air vapor pressure gradient inside the cuvette during all measurements was 9-12 mmol mol⁻¹.

Photosynthesis versus irradiance response data provided direct estimates of highest measured value of photosynthetic rate (A_{max}). Apparent quantum yield of CO₂ to incident irradiance (α) was the slope of a regression of five R_d measurements and five low light (ca. 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) measurements of CO₂ exchange, for each species and light regime combination. The light compensation point was calculated as the ratio, R_d/α .

Experimental design and statistical analysis

The experiment was arranged in a randomized complete block design with five replications. All pots were rotated within replications (blocks) every day to minimize variation in growth due to possible temperature and light differences within the growth chamber.

Analysis of variance (ANOVA) was used to estimate the overall effects of light regime and harvest date and their interaction on biomass allocation parameters. The assumption of homogeneity of variances and normality was tested for each ANOVA and when necessary data was logarithmically transformed. Transformed values were retransformed for presentation. Differences in RGR were tested as a Light regime \times Time interaction in an ANOVA with logarithmically-transformed dry weight as dependent variable (Poorter & Lewis 1986). A trend analysis over time was performed to detect differences in RGR throughout the experiment. The statistical packages MINITAB, Release 9.2 for Windows (MINITAB 1993) and SYSTAT Version 5.03 (Wilkinson 1990) were used for the computations of the growth and biomass allocation data.

Differences in the net photosynthesis response curve for light regime treatments were analyzed by analysis of variance with repeated measures (von Ende 1993). The between-subject main effects was light regime, and the within-subjects or repeated measures effect was irradiance level. Homoscedastic residuals were obtained with untransformed values. No severe departures from the normality assumption were detected by examining half-normal probability plots of z-transformed within-cell correlations. The compound symmetry for the repeated measures ANOVA was not rejected by the Mauchly's sphericity test ($p = 0.11$), however, the Huynh-Feldt adjusted significance level (see von Ende 1993) is presented because the epsilon for this test was equal to one, which gives identical adjusted and unadjusted significance levels. *Post hoc* contrasts comparing light regime differences within each irradiance level, were calculated. The statistical package STATISTICA for Windows, Release 4.5 (STATISTICA for Windows 1994) was used for the analysis of the gas exchange data.

Results

Biomass allocation

Light regime effect, assessed by ANOVA, was significant for specific leaf area and leaf area ratio (SLA and LAR; $F_{1,36} \geq 302.1$, $P < 0.001$) and for stem and root mass values (SWR and RWR, respectively; $F_{1,36} \geq 6.32$, $P \leq 0.02$). Mean values (Table 5.1) for the entire experiment showed that low-light grown *Vismia* had greater, SLA, LAR and SWR and smaller RWR than plants that grew in high light. No significant effect ($F_{1,36} = 0.07$, $P = 0.8$) of light treatments could be detected for LWR (Table 5.1).

Table 5.1. Specific leaf area (SLA, $\text{m}^2 \text{g}^{-1}$), leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$), leaf weight ratio (LWR, g g^{-1}), stem weight ratio (SWR, g g^{-1}) and root weight ratio (RWR, g g^{-1}), as means for the entire experiment (60 d), of *Vismia guianensis* under high- and low-light regimes. Values are means (\pm s.d.), n= 25.

	High-light	Low-light
SLA	0.029 (0.016)	0.049 (0.013)
LAR	194.5 (1.6)	332.7 (1.26)
LWR	0.665 (0.057)	0.668 (0.052)
SWR	0.138 (0.033)	0.158 (0.039)
RWR	0.189 (0.013)	0.165 (0.014)

The higher values of the leaf area variables (SLA and LAR) for low light grown plants was maintained throughout the experimental period (data not shown). For both regimes the highest SLA and LAR values occurred at the early stages of plant development, declining throughout the experimental period (data not shown).

The proportion of biomass allocated to leaves (LWR) under both light treatments, initially increased up to 15 d and then showed a tendency to decline during the remaining evaluations (Fig. 5.1). For both light regimes root weight ratio (RWR) was highest at the beginning of plant development and declined throughout plant growth (Fig. 5.1). Yet, this decline was more pronounced for low-light plants that experienced a 48 % decrease in RWR between the first and the last evaluation periods, while for high-light plants this decline was only 29 % (Fig. 5.1). Relative to high-light plants, plants subjected to the low-light treatment allocated a

higher proportion of biomass to support tissue (i.e., stem and petiole) throughout all the evaluation dates (Fig. 5.1).

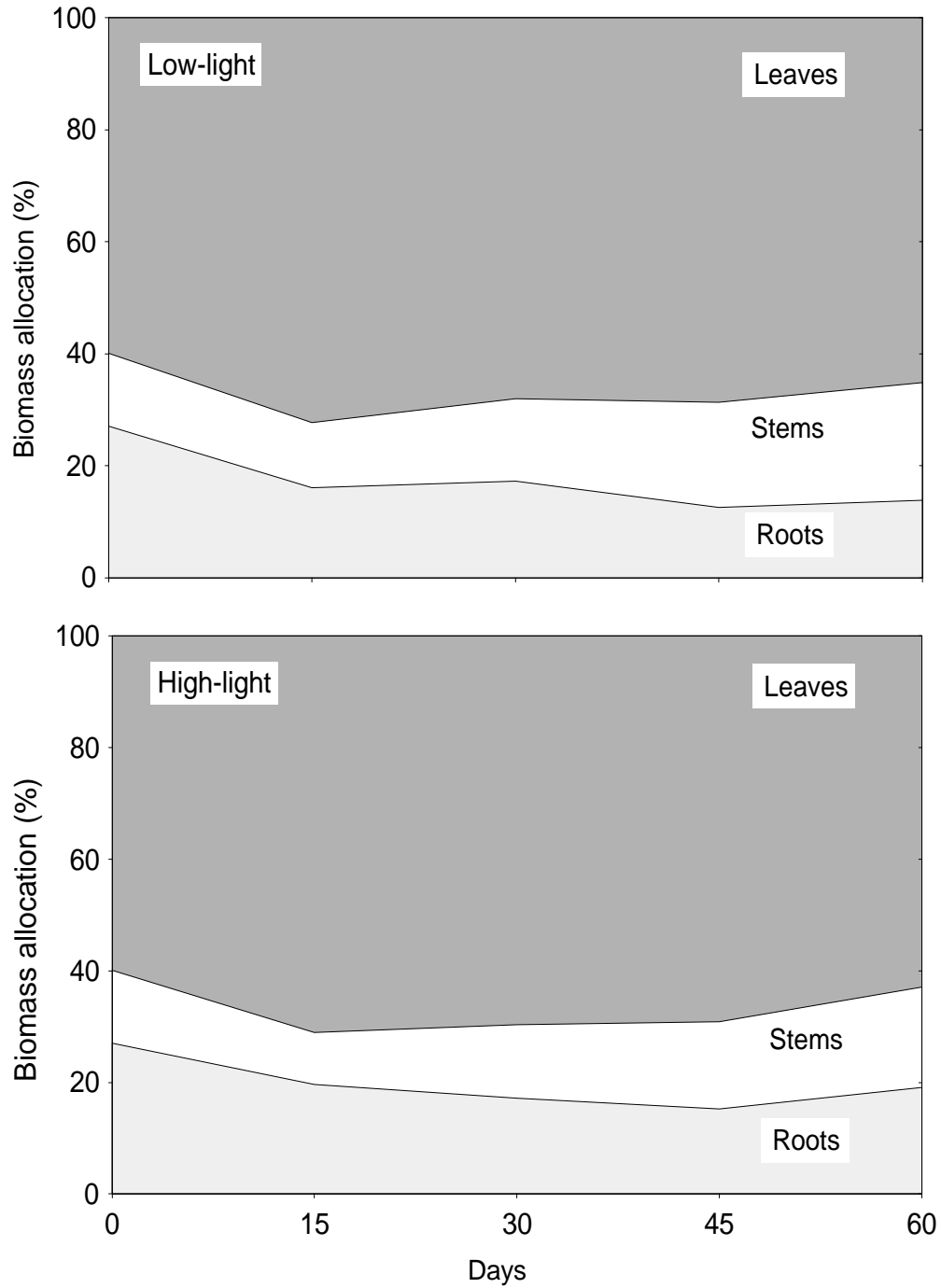


Figure 5.12. Mean proportion of biomass allocated to roots, stems and leaves as a function of time and light environment in *Vismia*.

Growth

The ANOVA for RGR shows a significant Light regime \times Time interaction (Table 5.2), indicating that RGR was influenced by the light regime treatments. The trend analysis over time (i.e., orthogonal polynomials) suggested that the differences in RGR between the two light treatments was not maintained throughout the entire experimental period, since the quadratic component accounts for the greatest proportion of the interactive effect (Table 5.2).

Table 5.2. Analysis of variance of growth in *Vismia*. Dependent variable: total (shoot and root combined) plant dry weight (after log transformation). Independent variables: Treatments, the two light regimes (high and low light); Time, the five harvests, Blocks, the five replicates (blocks). For the interaction a trend analysis over time was performed.

Sources	df	MS	F	<i>P</i>
Block	4	1.104	12.72	< 0.001
Light regime (Re)	1	15.202	175.44	< 0.001
Time	3	54.21	624.58	< 0.001
Time \times (Re)	3	0.302	3.48	0.029
Linear	1	0.00	0.00	1.0
Quadratic	1	0.768	8.83	0.006
Cubic	1	0.138	1.59	0.218
Within cells	28	0.087		

At the very early stage of seedling development (i.e., day 15) no difference in RGR could be detected between treatments (Fig. 5.2).

However, throughout the remaining evaluation period high-light grown

plants displayed a higher growth rate than low-light grown plants. This difference in RGR increased with time (Fig. 5.2).

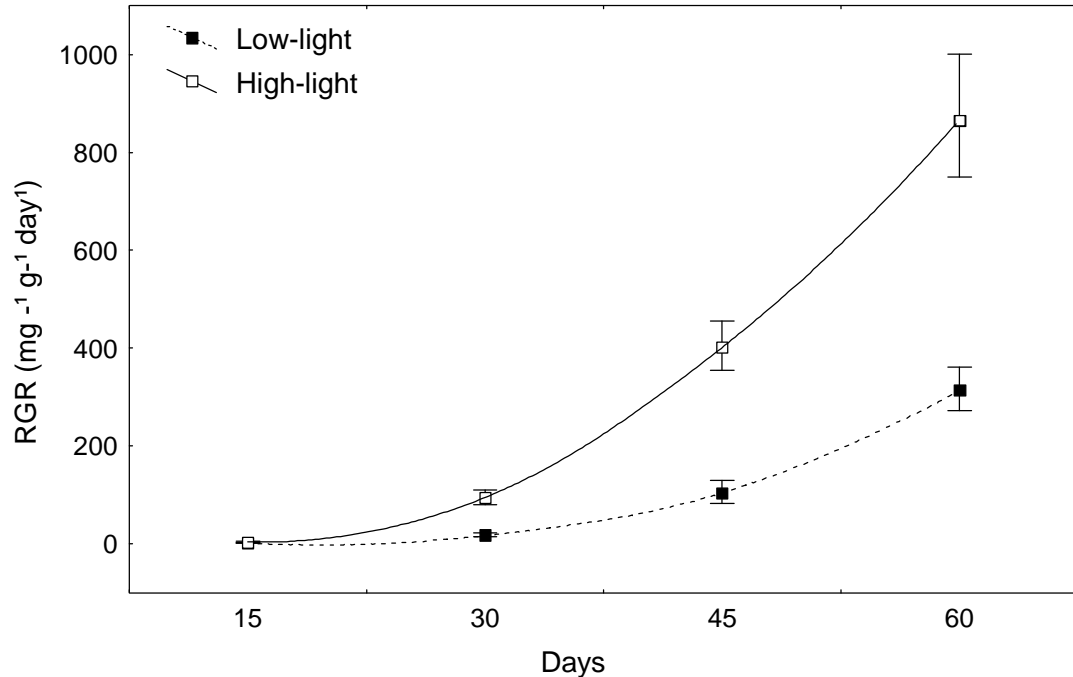


Figure 5.2. Change over time in relative growth rate (RGR) (mean \pm SE, $n = 5$) of *Vismia* under low- and high-light conditions. Curves fitted by distance-weighted least squares.

CO₂ assimilation

There was a significant Irradiance level \times treatment for the within-subjects main effects (Table 5.3). No statistically significant differences between light environments in the irradiance response curve could be detected by *post hoc* contrasts. However, at the lowest irradiance level (i.e., $150 \mu\text{mol m}^{-2} \text{s}^{-1}$) low-light grown plants had a tendency to display a higher mean assimilation rate (Fig. 5.3) relative to high-light plants; however, this difference was only marginally significant ($F_{1,8} = 4.95$, $P = 0.057$).

Table 5.3. Analysis of variance of net photosynthesis with repeated measurement on irradiance levels. Treatment (high light and low light regimes) is the fixed main effect.

Sources	df	MS	F	<i>P</i>	H-F
<i>Between-subjects</i>					
Treatment (Tr.)	1	0.258	0.089	0.77	----
Error	8	2.87			
<i>Within subjects</i>					
Irradiance level (I)	5	61.79	90.6	----	<0.001
I × Tr.	5	1.72	2.52	----	0.04
Error	40	0.68			

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

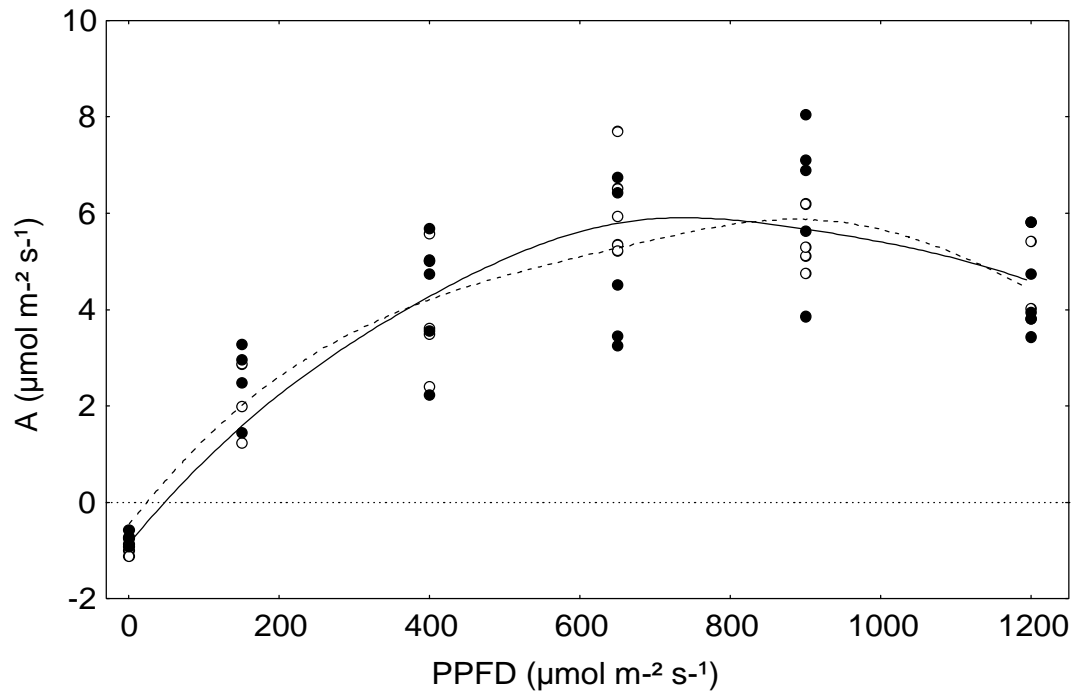


Figure 5.3. Light response curve of photosynthesis of *Vismia* grown under low- (closed symbols and dashed lines) and high-light (open symbols and solid lines) conditions. Curves fitted by distance-weighted least squares.

Photosynthesis parameters

Light-saturated photosynthesis (A_{max} , Table 5.4, Fig. 5.3) was similar between light treatments. Differences between treatments in dark respiration, R_d , assessed by post hoc contrasts showed that high-light grown leaves displayed higher (more negative) R_d than low-light leaves ($F_{1,8} = 7.25$, $P = 0.027$).

The apparent quantum efficiency, α , was sensitive to light regime during growth (Table 5.4). Low-light *Vismia* had a 24 % higher ($t = 2.29$, $P = 0.019$) α than high-light plants. Light compensation point, R_d/α , was also influenced by the light treatments, being 40 % higher ($t = 3.31$, $P = 0.01$) for high-light *Vismia* (Table 5.4).

Table 5.4. Photosynthetic parameters of *Vismia guianensis* under high- and low-light regimes. Symbols and units; A_{max} is light saturated photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); α is apparent quantum efficiency ($\text{mol CO}_2 \text{ photon}^{-1}$); R_d is dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and R_d/α is light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Values are means (\pm sample s.d.), $n=5$.

	High-light	Low-light
A_{max}	7.70	8.04
α	0.0179 (0.001)	0.0236 (0.003)
R_d	0.956 (0.157)	0.711 (0.129)
R_d/α	52.52 (12.9)	31.35 (6.1)

Discussion

Growth and biomass allocation

The effect of light regime on growth of *Vismia* (Table 5.2, Fig. 5.2) suggests that this species is sensitive to the light environment during growth and that plants grown under shade may have their development considerably suppressed. However, although relative to high-light plants growth in low-light *Vismia* was negatively affected, this species was still able to maintain a positive growth throughout all the experimental period (Fig. 5.2).

The growth, carbon allocation and structure patterns in response to contrasting quantum flux density observed in this study were consistent with the results reported from most studies (reviewed by Lambers & Poorters 1992). Growing under low light promoted an increased SLA and LAR in *Vismia*. Yet, allocation to leaves (LWR) was not significantly influenced by development under low quantum flux density (Table 5.1, Fig. 5.1).

Consistent with a number of studies (e.g., Mahall & Schlesinger 1982, Dall'Armellina & Zindahl 1988, Zollinger & Kells, Thompson et al. 1992a, Walters et al. 1993) the low-light treatment promoted a reduced biomass allocation to roots relative to high-light plants (Table 5.1, Fig. 5.1). As suggested elsewhere (see Thompson et al. 1992a, Walters et al. 1993), this negative effect of low-light regime on biomass allocation to roots is observed to be greatest on sun-loving plants and is probably a response to traits that improve carbon gain in low light such as an increased LAR or LWR, or that reflect a light seeking strategy such as stem growth. Although in the present study LWR was identical between treatments, mean LAR of low-light *Vismia* was 41 % higher than in high-

light plants (Table 5.1). In addition, low-light plants displayed an overall 13 % higher allocation to support tissue (SWR) relative to high-light plants (Table 5.1).

Gas exchange response

The shape of the light response curves in Figure 5.3 suggests a very similar response of low- and high-light grown *Vismia* to increasing irradiance levels. However, consistent with what has been observed with other tropical tree species (e.g., Ramos & Grace 1990, Riddoch et al. 1991a), low-light plants had a tendency to display a higher photosynthetic rate at the lowest irradiance level ($150 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 5.3). The photosynthetic features of leaves of low-light *Vismia* (Fig. 5.3) suggests that, despite growth in shade, this species is capable of retaining its ‘full’ photosynthetic capacity.

The significantly lower quantum efficiency observed for low-light plants (Table 5.4) contrasts with the results reported from other similar studies with tropical species (Sims & Percy 1989, Ramos & Grace 1990, Riddoch et al. 1991a). In these studies it is shown that light regime during growth does not normally alter α (but see Fahl et al. 1994). The higher α observed in low-light *Vismia* can in part explain the tendency for a higher efficiency in CO_2 assimilation observed in low-light plants at the lowest irradiance level (Fig. 5.3). Also, the lower dark respiration measured in low-light plants (Table 5.4) may have contributed for the tendency of a higher net photosynthesis observed in low-light plants. The negative effect of a low quantum efficiency on R_d is a common response that has been

observed in other tropical species (Ramos & Grace 1990, Riddoch et al. 1991a, Thompson et al. 1992b).

The effect of the light treatment on the light compensation point, R_d/α , reported in the present study (Table 5.4) followed the same trend observed in other investigations involving tropical species. In these studies low light during growth decreases R_d/α values (Ramos & Grace 1990, Thompson et al. 1992b). Here, the lower R_d/α of low-light plants was derived equally from a low respiration rate and a lower light compensation point observed in low-light plants (Table 5.4).

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PHYSIOLOGICAL RESPONSE OF *SOLANUM CRINITUM* TO CONTRASTING LIGHT ENVIRONMENTS

Introduction

Depending to their acclimation capacity, plants can have distinct photomorphogenetic responses to the light environment (quantity and quality of light) (e.g., Clough et al. 1979, Givnish 1988, Seemann 1989, Walters & Field 1987). The ability of a particular species to both efficiently and rapidly adjust its allocation patterns and physiological behavior in response to a particular light intensity (holding quality constant) is critical in determining its growth potential to that particular environment.

Knowledge of the morphological and physiological responses of invading species to contrasting light conditions can be critical in helping to explain and predict their occurrence and abundance patterns under specific environmental conditions. Moreover this information can be useful to explain their invasive potential and competitive ability under different management situations in agricultural areas. Ultimately this information can help in the development of more effective control strategies.

Solanum crinitum Lam. (Solanaceae) is a native successional woody species from tropical America found as colonizer of man-made clearings and natural gaps in forests and in abandoned or active agricultural areas in

Brazilian Amazonia (Albuquerque 1980, Dantas 1989, Dias Filho 1990).

In this chapter I investigate the sun-shade acclimation characteristics of this species by examining the rate of growth, biomass allocation patterns, gas exchange and leaf nitrogen content of plants developed at high and low photon flux densities. The results are discussed in relation to their ecological and practical implications.

Materials and methods

Plant material and growing conditions

Solanum crinitum seeds were collected from plants growing in pasture areas near Paragominas PA (3° 05' S - 47° 21' W) in Eastern Brazilian Amazonia. Seeds were germinated on filter paper in petri dishes and then planted individually in 1750 ml plastic pots in a mixture of peat:vermiculite:perlite (1:1:1). Plants were initially grown in a greenhouse at temperatures of $24 \pm 2.2^{\circ}\text{C}$ (minimum) to $33 \pm 2.1^{\circ}\text{C}$ (maximum) and a maximum photosynthetic photon flux density (PPFD) of approximately $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. When plants were about 25 days old they were transferred from the greenhouse to two Conviron growth chambers (Model PGW36, Controlled Environments, Inc. Pembina, ND) set at 28/24°C day/night air temperatures, 70 % relative humidity, and 12-h photoperiod. Before transference to the growth chambers, seedlings were divided into five size classes, and each class was randomly assigned to a replication (block).

Within each growth chamber, a high- and a low-light environment were simulated by placing multiple layers of neutral density shade cloth beneath the light source of half of each growth chamber. Irradiance,

monitored throughout the experiment with a light meter (Model LI-1905 light meter, Li-Cor, Inc. Lincoln, NE) at canopy height, ranged between 800 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for high-light and between 200 and 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for low-light treatments.

All pots were watered daily to full capacity with deionized water and fertilized every 11 days with 50 ml per pot of a water soluble fertilizer solution (15 % N, 30 % P_2O_5 , 15 % K_2O , 0.02 % B, 0.07 % Cu, 0.15 % Fe, 0.05 % Mn, 0.0005 % Mo and 0.06 % Zn; 3.5 g L^{-1}).

Growth analysis

Four harvests were made; the first harvest was on the day plants were transferred to the growth chambers (Day 0), and the others 22, 44 and 66 days later (n= 5 per harvest and light treatment). At each harvest plant material was divided into leaf, support tissue (stem and petiole) and root. Leaves were removed and leaf area measured using a leaf area meter (Model LI-3000. Li-Cor, Inc. Lincoln, NE) and conveyor belt assembly (Model LI-3050. Li-Cor, Inc. Lincoln, NE). Plant dry weight was obtained by drying the plant material in an oven at 73°C for 48 hours. Attributes measured for each plant at each harvest were used to estimate relative growth rate (change in dry weight per total dry weight of plant per day, RGR) and biomass allocation patterns: leaf area ratio (leaf area per unit weight of whole plant, LAR), specific leaf area (leaf area per unit of leaf dry weight, SLA) and leaf, stem and root weight ratios (respectively, leaf, stem or root weight per unit of weight of whole plant, LWR, SWR and RWR). All of the above growth and biomass allocation parameters were calculated according to Hunt (1990).

Gas exchange

Gas exchange parameters were measured on plants just before the fourth harvest, i.e., when the plants had been in the growth chamber for 66 days. A photosynthesis (A) versus irradiance (PPFD) response curve (starting at ca. $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ 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 (Model LI-6200, LI-COR, Inc., Lincoln, NE). Gas exchange parameters were calculated on a leaf area basis. The amount of leaf area in the chamber (cuvette) was approximately 20 cm^2 . The irradiance 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 15 min to each new light level. To absorb long-wave radiation and maintain constant leaf temperatures in the cuvette, a 10 cm deep Plexiglas circulating bath of cool water was suspended between the light source and the leaf cuvette. After exposure to the lowest PPFD, the plants were left for 20 min in the dark and measurements were made to obtain dark respiration (R_d) values. Five replicate plants per treatment and one leaf per plant were sampled. The leaf-to-air vapor pressure gradient inside the cuvette during all measurements was 9-12 mmol mol^{-1} .

Photosynthesis versus irradiance response data provided direct estimates of the highest measured value of photosynthetic rate (A_{max}). Apparent quantum yield of CO_2 to incident irradiance (α) was the slope of a regression of five R_d measurements and five low light (ca. $150 \mu\text{mol m}^{-2}$

s⁻¹) measurements of CO₂ exchange, for each light regime combination. The light compensation point was calculated as the ratio, R_d/α .

Leaf nitrogen analysis

Leaf nitrogen was measured on all leaves of each individual plant at each harvest date and light treatment combination. Leaf nitrogen content was measured with a nitrogen analyzer (Model NA 1500, series 2. Carlo Erba Strumentazione, Milan, Italy). The instrument was calibrated with both an NBS ‘‘citrus leaf’’ and organic standard. Precision was $\pm 0.17\%$ of N.

Experimental design and statistical analysis

The experiment was arranged in a randomized complete block design with five replications. All pots were rotated within replications (blocks) every day to minimize variation in growth due to possible environmental differences within the growth chamber.

Analysis of variance (ANOVA) was used to estimate the overall effects of light regime and harvest date and their interaction on biomass allocation parameters. The assumption of homogeneity of variances and normality was tested for each ANOVA and when necessary data was logarithmically transformed. Transformed values were retransformed for presentation. Differences in RGR were tested as a Light regime \times Time interaction in an ANOVA with logarithmically-transformed dry weight as dependent variable (Poorter & Lewis 1986). A trend analysis over time was performed to detect differences in RGR throughout the experiment. The statistical packages MINITAB, Release 9.2 for Windows (MINITAB

1993) and SYSTAT Version 5.03 (Wilkinson 1990) were used for the computations of the growth and biomass allocation data.

Differences in net photosynthesis and stomatal conductance response curves for species and watering treatments were analyzed by multivariate analysis of variance with repeated measures. The multivariate approach was preferred over its univariate counterpart because, in the latter, the compound symmetry of the covariance matrix was rejected for the data, and there was never total agreement between the Huynh-Feldt and the Greenhouse-Geisser corrected significance levels (see von Ende 1993). The between-subject main effects were species and watering regimes, and the within-subject or repeated measures effect was light level. No severe departures from the normality assumption were identified by examining half-normal probability plots of z-transformed within-cell correlations for both data sets. *Post hoc* contrasts were calculated comparing species and watering regimes differences in photosynthesis and stomatal conductance, within each irradiance level, and pooling all irradiance levels. The statistical package STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994) was used for all computations of the data.

Results

Biomass allocation

Both specific leaf area and leaf weight ratio were significantly increased ($P= 0.001$) by shade (Table 6.1). Means values for the entire experimental period showed that low-light plants allocated significantly less biomass in root tissue and more biomass in support tissues (stem and petiole).

However, no significant difference between light treatments could be detected in the mean proportion of biomass allocated to leaves (Table 6.1).

Patterns of biomass allocation throughout the experimental period were distinct between treatments (Fig. 6.1). In low-light plants the proportion of biomass allocated to leaves (LWR) declined steadily through time while in high-light plants a quadratic pattern was observed, with LWR declining between day 22 and 44 and increasing at day 66 (Fig. 6.1).

Table 6.1. Specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$), leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$), leaf weight ratio (LWR, g g^{-1}), stem weight ratio (SWR, g g^{-1}) and root weight ratio (RWR, g g^{-1}), as means for the entire experiment (60 d), of *Solanum crinitum* under high- and low-light regimes. Values are means (\pm s.e.), $n=20$. For each variable, means within rows are significantly different at the $P = 0.05$ level (*), at the $P = 0.01$ level (**), or at the $P = 0.001$ level (***), in the ANOVA; ns= not significant.

	High-light	Low-light
SLA	215.5 (1.18)***	312.3 (1.13)***
LAR	109.9 (1.15)***	162.9 (1.11)***
LWR	0.569 (0.01) ns	0.579 (0.01) ns
SWR	0.135 (0.01)*	0.162 (0.01)*
RWR	0.283 (0.08)**	0.241 (0.08)**

The proportion of biomass allocated to support tissue (SWR) was relatively constant through time in high light plants, however, in low-light plants, SWR showed a tendency to increase between days 44 and 66 (Fig. 6.1). In both treatments, allocation of biomass to roots started to decline after day 44, yet, this decline was relatively more pronounced in low-light

plants. Comparatively, however, high-light plants always allocated a higher proportion of biomass to roots (Fig. 6.1).

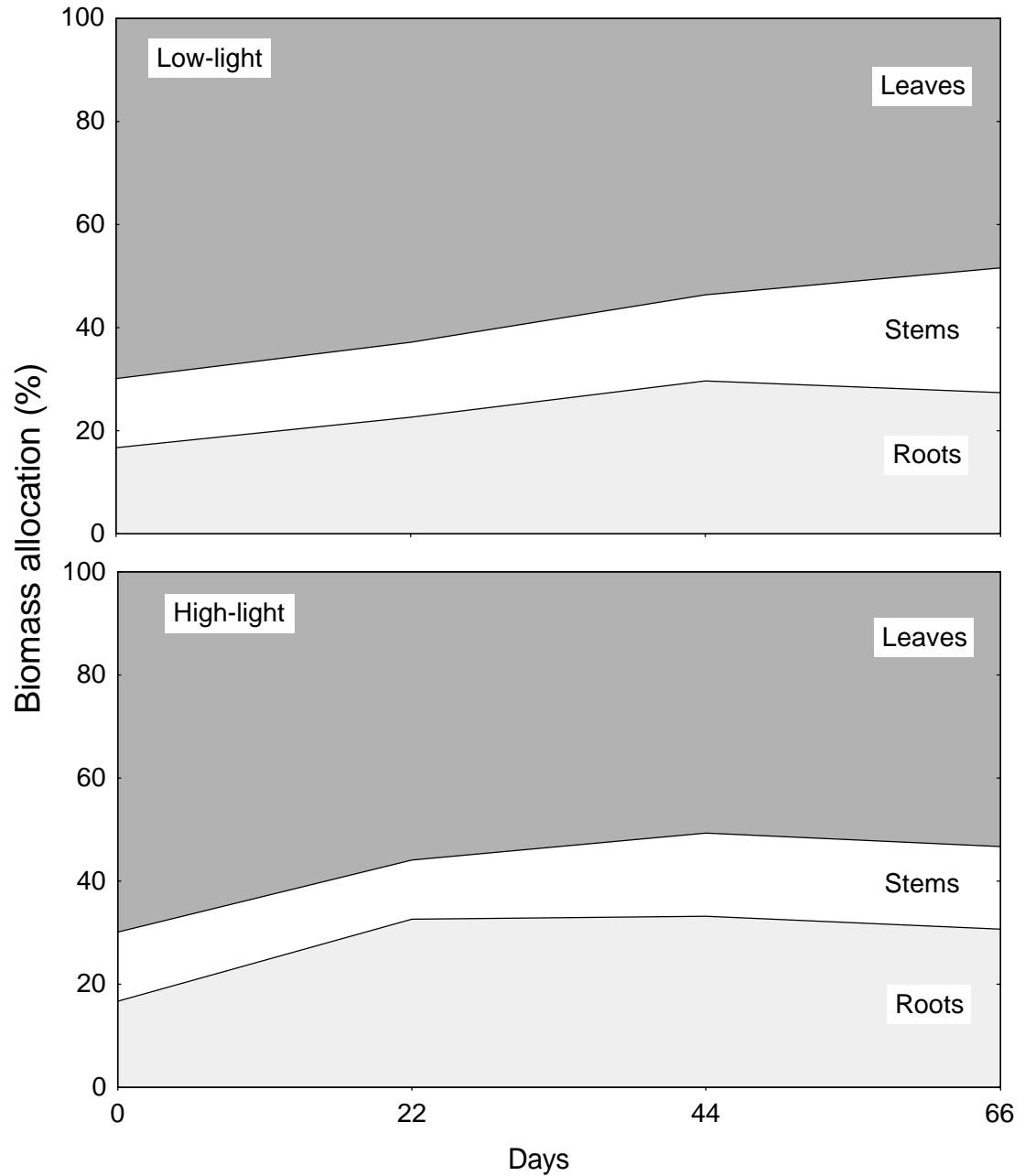


Figure 6.13. Mean proportion of biomass allocated to roots, stems and leaves as a function of time and light environment in *Solanum*.

Growth

The results of the ANOVA (Table 6.2) showed that no statistical difference could be detected for the interaction between Time and Treatments (light regimes). This suggests that mean RGR in *Solanum* was not significantly influenced by the light regimes. However, high-light plants showed a tendency for a higher growth rate throughout most of the experimental period, losing this superiority at the last evaluation period (Fig. 6.2).

Table 6.2. Analysis of variance of growth in *Solanum*. Dependent variable: total (shoot and root combined) plant dry weight (after log transformation). Independent variables: Treatments, the two light regimes (high and low light); Time, the five harvests, Block, the five replicates (blocks). For the interaction a trend analysis over time was performed.

Sources	df	MS	F	<i>P</i>
Block	4	0.1168	4.02	0.02
Light regime (Re)	1	0.0702	2.42	0.14
Time	2	0.8423	29.04	<0.001
Time × (Re)	2	0.069	2.38	0.14
Linear	1	0.113	3.89	0.06
Quadratic	1	0.024	0.82	0.37
Within cells	20	0.029		

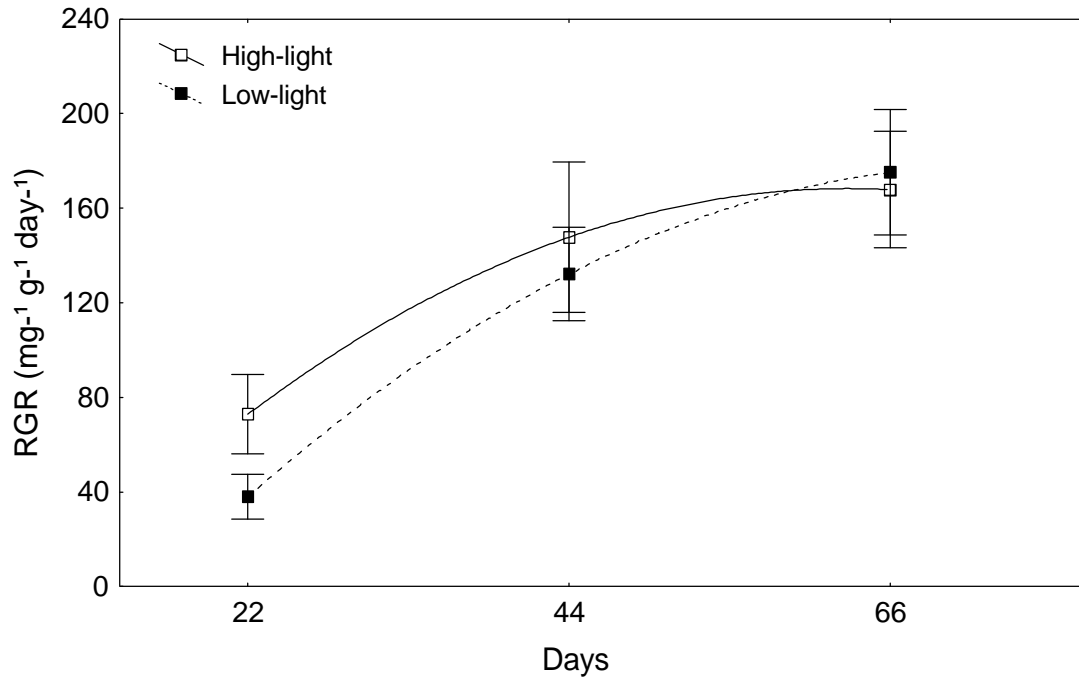


Figure 6.2. Change over time in relative growth rate (RGR) (mean \pm s.e., $n = 5$) of *Solanum* under low- and high-light conditions. Curves fitted by distance-weighted least squares.

CO₂ assimilation

Results from the repeated measures MANOVA (Table 6.3) showed significant Irradiance levels \times Treatments differences in CO₂ assimilation. Also, there was a significant Treatment main effect difference in CO₂ assimilation (Table 6.3).

In general, leaves from high-light plants had higher photosynthetic capacity than low-light leaves. *Post hoc* contrasts revealed significant differences between treatments in the irradiance response curve at the first (ca. 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 39.7$, $P < 0.001$), second (ca. 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 64.8$, $P < 0.001$), third (ca. 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 6.0$, $P = 0.04$) and fourth (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 9.8$, $P = 0.01$) irradiance levels.

High-light grown plants had higher CO₂ assimilation rates at these irradiance levels (Fig. 6.3).

No significant difference between treatments in CO₂ assimilation could be detected at the lowest irradiance level (ca. 150 μmol m⁻² s⁻¹, Fig. 6.3).

Table 6.3. Multivariate analysis of variance of CO₂ assimilation with repeated measures on irradiance levels. Treatments (high and low light is the fixed main effect).

Source	df	MS	F	<i>P</i>
<i>Between subjects</i>				
Treatments (Tr)	1	29.3	37.03	< 0.001
Error	8			
<i>Within subjects</i>				
Source	df	Pillai's trace	F	<i>P</i>
Irradiance (I)	5	0.998	481.6	< 0.001
I×Tr	5	0.89	6.49	0.047
Error	4			

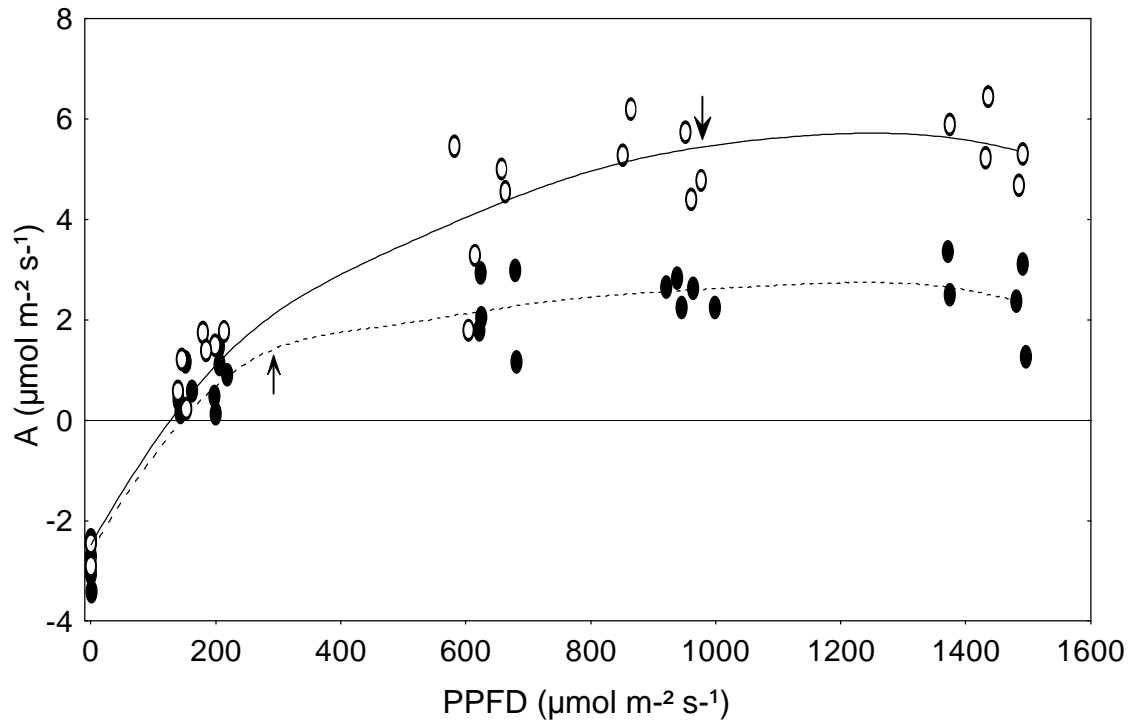


Figure 6.3. Light response curve of photosynthesis of *Solanum* grown under low- (closed symbols and dashed lines) and high-light (open symbols and solid lines) conditions. Curves fitted by distance-weighted least squares. Arrows indicate light regime during growth.

Photosynthesis parameters

Light-saturated photosynthesis (A_{max} , Table 6.4, Fig. 6.3) was higher for high light plants. For all other photosynthetic parameters shown in Table 6.4 no statistically significant difference could be detected between treatments. However, low-light plants had a tendency to display higher values of dark respiration and light compensation point.

Table 6.4. Photosynthetic parameters of *Solanum crinitum* under high- and low-light regimes. Symbols and units; A_{max} is light saturated photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); α is apparent quantum efficiency ($\text{mol CO}_2 \text{ photon}^{-1}$); R_d is dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and R_d/α is light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Values are means (\pm sample s.d.), $n=5$.

	High-light	Low-light
A_{max}	6.45	3.35
α	0.023 (0.004)	0.022 (0.004)
R_d	2.76 (0.21)	2.81 (0.43)
R_d/α	123.1 (17.8)	128.1 (15.0)

Nitrogen content

Nitrogen content per unit of leaf weight was significantly higher ($F_{1,22}= 8.5$, $P= 0.008$) in low-light grown plants (Fig 6.4). When expressed on a area basis, however, leaf nitrogen was significantly lower ($F_{1,22}= 14.6$, $P= 0.001$) in low-light plants (Fig. 6.4).

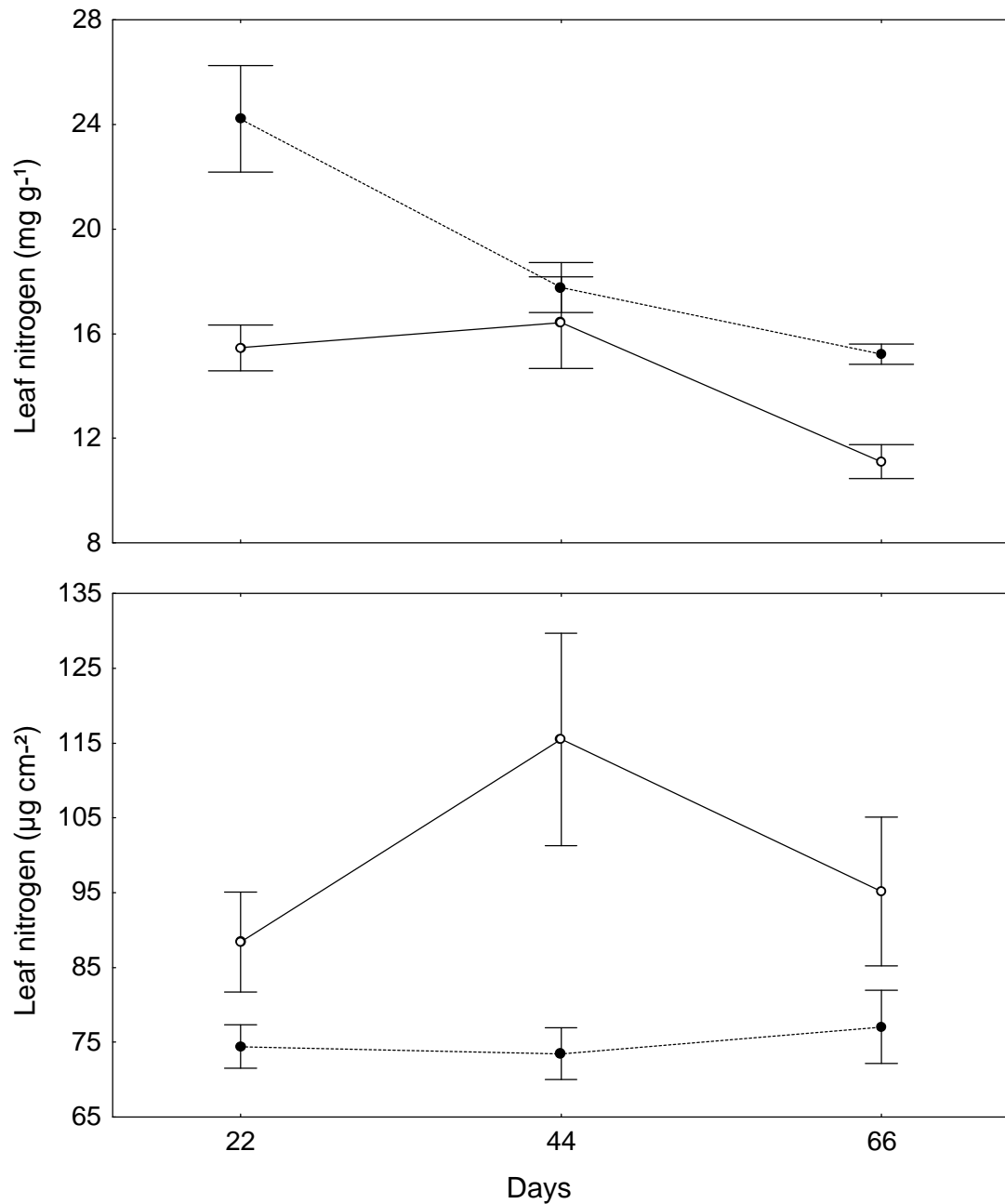


Figure 6.4. Leaf nitrogen content (mean \pm s.e., $n=4$) on a mass (mg g^{-1}) and area ($\mu\text{g cm}^{-2}$) basis for *Solanum* under low- (closed symbols and dashed lines) and high- (open symbols and solid lines) light conditions.

Discussion

Growth and biomass allocation

A common response to shade reported in many studies is a reduced allocation to roots (e.g., Dale & Causton 1992, Dall'Armellina & Zindahl 1988, Mahall & Schlesinger 1982, Messier 1992, Thompson et al. 1992, Walters et al. 1993, Zollinger & Kells 1991). In the present study, allocation to roots in low-light *Solanum* (averaged over the entire experimental period) was reduced by 15 % relative to high-light plants (Table 6.1). As suggested elsewhere (e.g., Thompson et al. 1992, Walters et al. 1993), this lower allocation to roots under low light conditions is known to be maximized in sun-loving plants, and probably reflect a response to attributes that improve carbon gain under reduced irradiance such as an increase in LAR and LWR, or that reflect a light seeking strategy such as an increase in height. Although no significant difference between treatments could be detected in LWR, low-light plants had indeed a 33 % higher mean LAR than high-light plants (Table 6.1), and also, at the last evaluation date, were 26 % higher than high-light plants ($t= 2.7$, $P= 0.03$) (data not shown).

The significantly lower specific leaf area (SLA, Table 6.1) in high-light *Solanum* suggests leaf anatomical differences brought about by low quantum flux density (see Lambers & Poorter 1992), and reflects a strategy to increase this species' competitive ability under low light through an increase in leaf area. An increase in SLA is a common response observed in plants under low light conditions (e.g., Buisson & Lee 1993, Ducrey 1992, Fahl et al. 1994, George & Nair 1990, Stoneman & Dell 1993) and

is usually associated with extra layers of mesophyll cells (see Riddoch et al. 1991a, Thompson et al. 1992a).

The growth patterns observed in Fig. 6.2 suggest that *Solanum* seedlings were able to maintain relative growth rate (RGR) under low-light conditions to levels comparable to that of high-light plants. As suggested for herbaceous plants (Björkman 1981), it could be speculated that in low-light *Solanum*, the significant adjustment in LAR may have in part contributed to partially offset light-limited photosynthesis so that the whole-plant RGR was less affected.

Gas exchange response

The shape of the light response curve of photosynthesis (Fig. 6.3) indicates that the light saturation points of both treatments were very close to the actual maximum PPFD received during growth.

No significant difference between treatments could be detected in dark respiration (Table 6.4). Dark respiration values in *Solanum* were much higher than the ones reported for other tropical species (e.g., Riddoch et al. 1991b, Ramos & Grace 1990, Thompson et al. 1992b). However, these values were similar to the ones obtained in a similar study with this species (see Chapter 8). As suggested elsewhere (see Thompson et al. 1992b), a high respiration is characteristic of leaves with high rates of expansion and short life spans. Although there is no information on *Solanum* leaf life span, this species does have a high leaf expansion rate.

As a consequence of the higher dark respiration measured in *Solanum*, the light compensation point calculated for this species on both treatments was also very high (Table 6.4). No significant difference

between treatments could be detected for this parameter. It could be speculated that the high light compensation point of *Solanum* would make this species more prone for recruitment in wide disturbance gaps, such as the ones characteristic of most anthropogenic disturbances in Brazilian Amazonia.

Consistent with the responses observed from other similar studies with tropical species (e.g., Ramos & Grace 1990, Riddoch et al. 1991a, Sims & Pearcy 1989, Wiebel et al. 1993) quantum efficiency did not differ significantly between treatments. The α derived for *Solanum* was similar to the ones reported by Riddoch et al. (1991b) for some tropical pioneer trees and by Wiebel et al. (1993) to the tropical tree *Gracinia mangostana*.

Nitrogen content

Leaf nitrogen followed the same pattern reported for other studies with tropical species (e.g., Thompson et al. 1992a, Fahl et al. 1994,) in that when expressed on an area basis it was higher for high-light leaves, but when expressed on a mass basis, it was higher for low-light leaves.

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**PHYSIOLOGICAL RESPONSES TO SOIL
MOISTURE STRESS IN *IPOMOEA ASARIFOLIA*
AND *STACHYTARPHETA CAYENNENSIS***

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 plants they co-occur with. This is particularly important for Brazilian Amazonia, where ecologically sound weed management strategies could decrease further deforestation by helping increase the agricultural sustainability of pastures.

Tropical pastures within Brazilian Amazonia are subjected to marked variation in light and water stress levels. It is unknown how these stresses may limit growth or distribution; however, improving our understanding of how tropical pasture weeds respond to variation in light, water, and other resource limitations, I believe, 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 Brazilian Amazonia (Albuquerque 1980, Dias Filho 1990). 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 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 (M. Dias Filho, unpublished observation). 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 (e.g., Gealy 1989, Gealy et al. 1991, Geber & Dawson 1990, Regnier et al. 1988, Zimdahl et al. 1991), few similar studies can be found for tropical weeds (e.g., Rajendrudu et al. 1987). No previous work on the gas exchange behavior exists for Amazonian weeds and inferences about their

physiology are based on related species from regions other than tropical America (Dias Filho 1990).

The purpose 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. I relate this information to its possible ecological significance and to its management implications.

Materials and methods

Plant material

Seeds of *Ipomoea asarifolia* (Desr.) Roem. & Schultz (Convolvulaceae, herbaceous vine) and *Stachytarpheta cayennensis* (L.C. Rich) Vahl. (Verbenaceae, woody shrub) were collected from pasture areas near Paragominas (3° 05' S) in 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 $21 \pm 2.2^{\circ}\text{C}$ (night) to $33 \pm 2.1^{\circ}\text{C}$ (day) and a maximum photosynthetic photon flux density (PPFD) of approximately $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$.

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 (15 % N, 30 % P_2O_5 , 15 % K_2O ,

0.02 % B, 0.07 % Cu, 0.15 % Fe, 0.05 % Mn, 0.0005 % Mo and 0.06 % Zn; 3.5 g L⁻¹).

Response of gas exchange to irradiance

The photosynthesis (A) vs. light (PPFD) response curves for the youngest fully-expanded intact leaf of four to five-week-old plants were determined in the laboratory with a portable photosynthesis system (LI-6200, LI-COR, Lincoln, NE). Leaves were exposed sequentially to five decreasing levels of light intensity (varying from 1700 to 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$). 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 minutes 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. After exposure to the lowest PPFD, the plants were left for 30 minutes 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 (ANOVAR). 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 logarithmically transformed values for stomatal conductance. Compound symmetry of the covariance matrix of each ANOVAR was tested by the Mauchly's sphericity test. The Huynh-Feldt (Huynh & Feldt 1970) correction were considered for both analysis. *Post hoc* contrasts comparing species and watering regimes differences in photosynthesis and stomatal conductance were calculated. The statistical package STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994) was used for all computations of the data.

Results

Interspecific differences

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

each species achieved light saturation at approximately $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 7.1). Upon rejection of the compound symmetry of the ANOVAR for

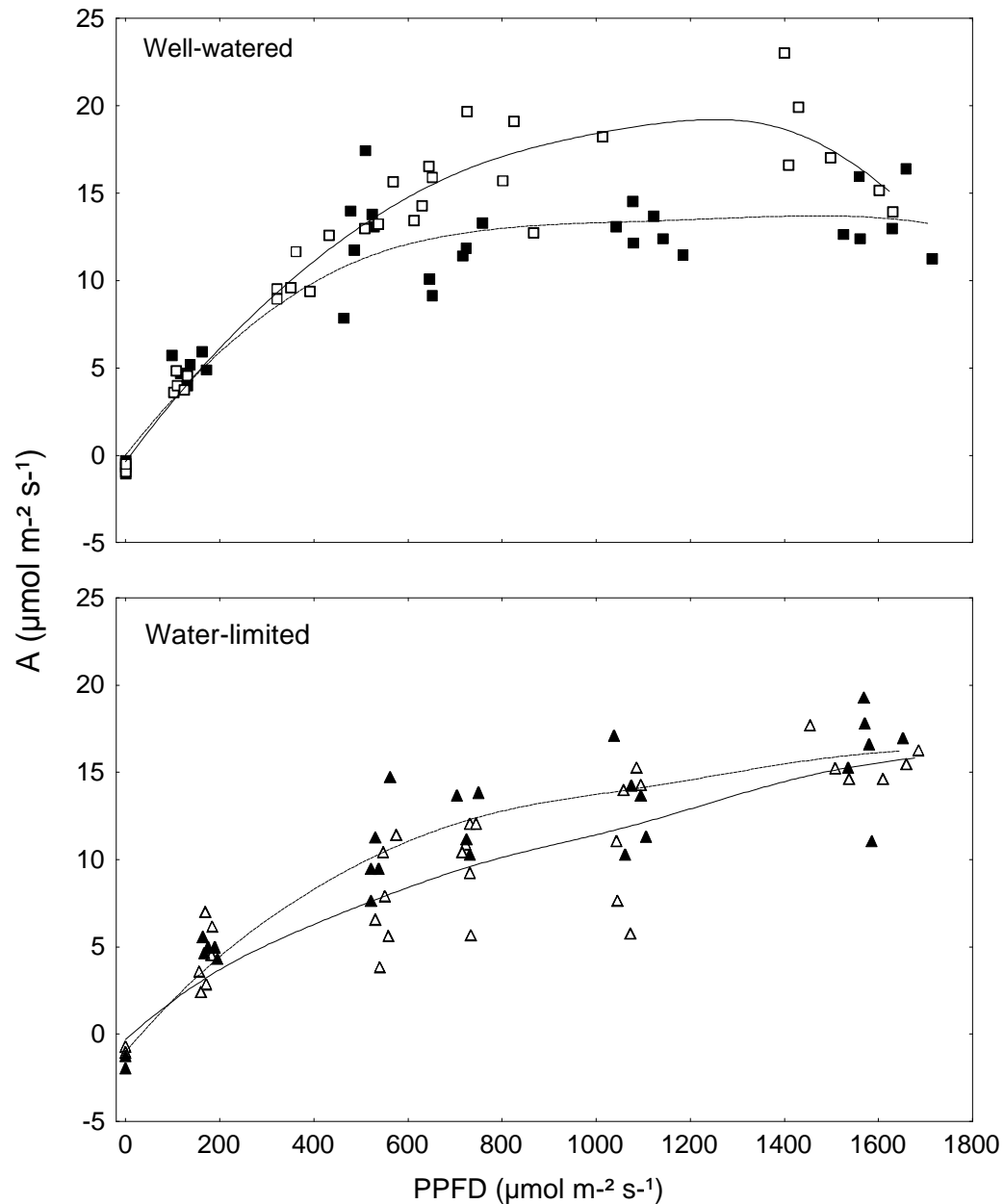


Figure 7.14. Light-response curves of the youngest-fully-expanded leaves of *I. asarifolia* (open symbol, solid line) and *S. cayennensis* (closed symbol, dashed line) under well watered and water limited conditions. A = rate of net photosynthesis, $PPFD$ = Photon flux density.

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 7.1). Similarly, the

Table 7.1. 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	<i>P</i>	H-F
<i>Between-subjects</i>					
Species (Sp)	1	0.054	0.01	0.917	----
Regime (Re)	1	47.18	9.72	0.005	----
Sp × Re	1	55.47	11.43	0.002	----
Error	20	4.85			
<i>Within subjects</i>					
Light	5	937.36	239.87	----	0.001
Light × Sp	5	15.66	4.01	----	0.002
Light × Re	5	9.7	2.48	----	0.04
Light × Sp × Re	5	14.88	3.81	----	0.003
Error	100	3.91			

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

effect of light and its interaction with all other effects were also significant (Table 7.1). *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 water limited conditions (Fig. 7.1). 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. 7.1), 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 7.2 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 7.2). The analysis of the within-subject effects revealed that just light and the interaction light by species by regime were significant (Table 7.2). Well watered *I. asarifolia* had an average 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. 7.3). 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. 7.2); for plants under water limited conditions this could further increase water stress effects.

Table 7.2. 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
<i>Between-subjects</i>					
Species (Sp)	1	0.057	0.44	0.51	----
Regime (Re)	1	6.24	47.8	0.001	----
Sp × Re	1	10.38	79.48	0.001	----
Error	20	2.61			
<i>Within subjects</i>					
Light	5	22.25	129.89	----	0.001
Light × Sp	5	0.28	1.68	----	0.146
Light × Re.	5	0.34	1.99	----	0.08
Light × Sp × Re	5	0.46	2.69	----	0.02
Error	100	0.171			

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

Dark respiration and light compensation point of well watered plants showed no differences between species (Table 7.3). Under drought stress,

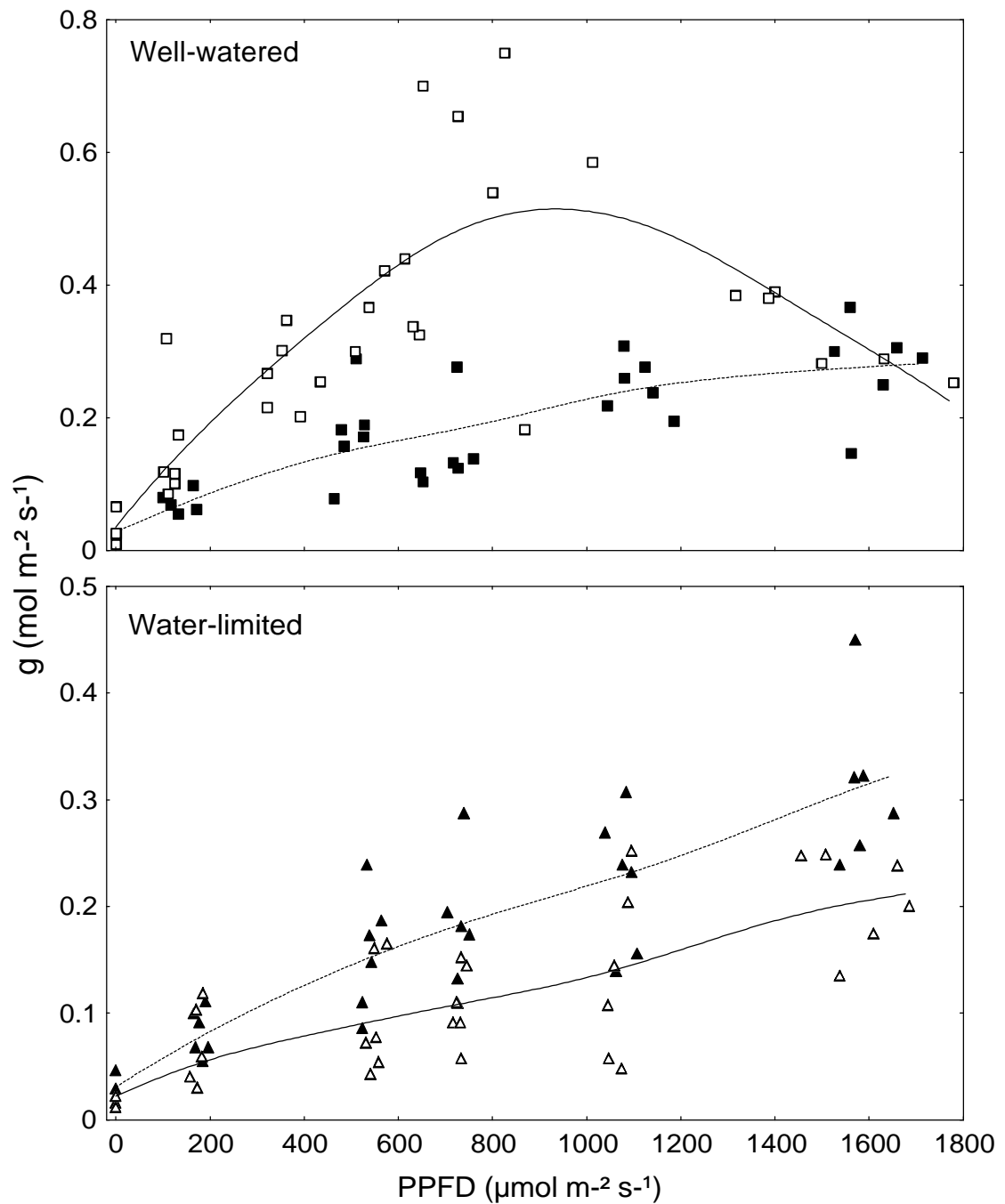


Figure 7.15. Light-response of stomatal conductance of *I. asarifolia* (open symbol, solid line) and *S. cayennensis* (closed symbol, dashed line) under well watered and water limited conditions. g = stomatal conductance, $PPFD$ = Photon flux density.

however, *I. asarifolia* had dark respiration and light compensation point, respectively, 60 and 35% lower than *S. cayennensis* (Table 7.3).

Table 7.3. Effect of water regime on photosynthetic parameters of *Ipomoea asarifolia* and *Stachytarpheta cayennensis*. Means and (standard errors)¹.

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 ($P < 0.05$).

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 7.1, Fig. 7.1). Stomatal conductance also showed differences between species in relation to their sensitivity to water stress (Table 7.2, Fig. 7.3). *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. 7.3). 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.

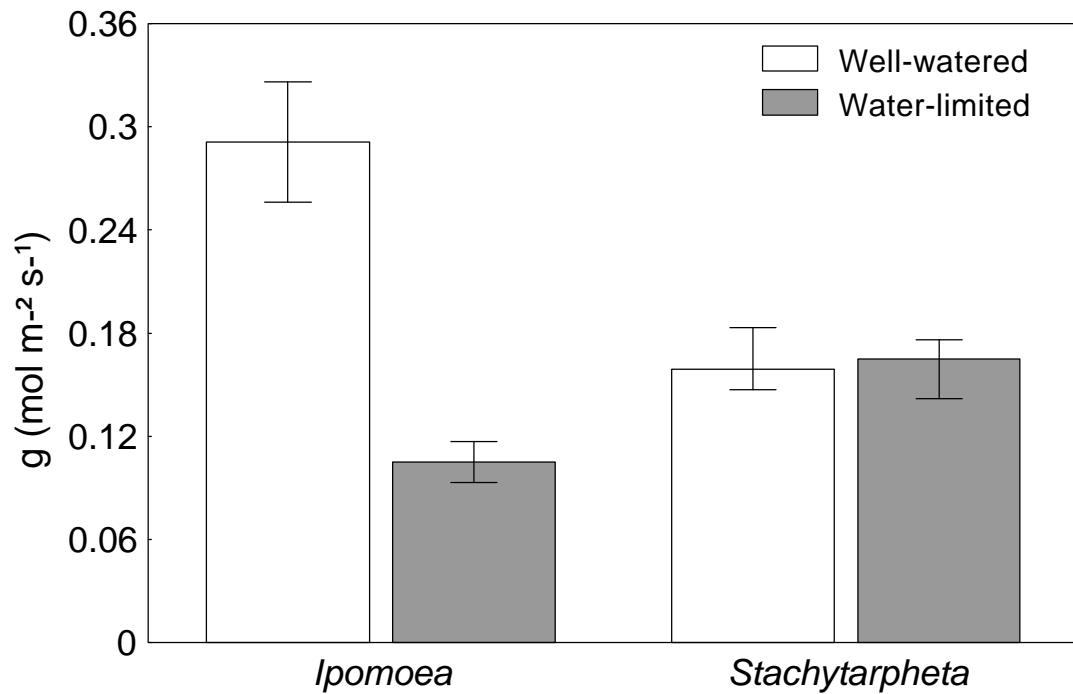


Figure 7.16. Mean (\pm s.e.) stomatal conductance of *I. asarifolia* and *S. cayennensis* under two watering regimes. $n = 36$.

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 7.3). 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 7.3).

Discussion

Availability of water and light is known to limit plant productivity and distribution throughout the world (e.g., 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.

The present results show that *I. asarifolia* has a limited ability compared with *S. cayennensis* to tolerate water limited conditions. These findings are in accord 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).

Riddoch 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. 7.3). *I. asarifolia* appears to have greater transpirational water loss than *S. cayennensis*. The plot of the stomatal conductance against PPFD (Fig. 7.2) 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 Riddoch 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* (Riddoch 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 7.3). 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*.

This research contributes to the basic understanding of the ecophysiology of *I. asarifolia* and *S. cayennensis*. 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.

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**PHYSIOLOGICAL RESPONSES TO SOIL
MOISTURE STRESS IN *SOLANUM CRINITUM*
AND *VISMIA GUIANENSIS***

Introduction

Water availability is a major environmental factor influencing the distribution and abundance of plant species in natural communities. This is true because as soil moisture becomes more limiting, different species demonstrate marked variation in their ability to tolerate such conditions and thus respond physiologically in a variety of ways (Jones et al. 1981, Dawson 1990). Many critical physiological processes in plants such as transpiration and carbon assimilation are acutely influenced by moisture limitation (Turner & Jones 1980, Bradford & Hsiao 1982, Schulze 1986) which in turn can affect cell expansion and growth. When moisture is limiting, plants possessing mechanisms that aid in decreasing tissue water loss *and* that promote the maintenance of positive turgor pressures, as tissue water content decreases, may be more successful in colonizing drought prone environments or dominating xeric habitats than species lacking these mechanisms (Turner & Jones 1980, Bradford & Hsiao 1982, Robichaux et al. 1986).

As colonizers of forest gaps and invaders of active pastures and abandoned agricultural areas, *Solanum crinitum* Lam. and *Vismia*

guianensis (Aubl.) Choisy are perennial treelets of major ecological and agronomic importance in eastern Brazilian Amazonia (Albuquerque 1980, Dantas 1989, Dias Filho 1990). In these environments, water stress, in the form of soil water deficit or high evaporative demand, can often be significant, restricting the ability of some taxa to establish successfully (Nepstad 1989, Dias Filho, Simao Neto & Serrao 1991). For example, in a seedling transplant experiment Nepstad (1989) demonstrated that *Vismia* was more drought tolerant than *Solanum*, yet my personal observations indicate that both species are remarkably successful in withstanding the relatively severe dry season conditions characteristic of eastern Brazilian Amazonia.

Both *Vismia* and *Solanum* have a suite of discrete morphological characteristics that suggest the presence of different mechanisms that favor water conservation and thus aid in their survival in drought-prone environments. For example, although *Solanum* has relatively large leaves (ca. 150 cm²), they are covered by dense, short hairs, a feature particularly noticeable in younger leaves. Leaf hairs have been shown to be important to plants inhabiting xeric habitats because they reduced heat load and improve leaf energy balance (Ehleringer 1981, 1982). *Vismia*'s leaves are smaller (ca. 50 cm²), have a relatively thick cuticular layer, and start development as clasped pairs, until almost fully expanded, when they are gradually released from each other, from the base to the tip of the leaves (M. B. Dias Filho, unpublished observation). While these above ground morphological characteristics may, in part, contribute to the species' ability to avoid tissue dehydration or damage and may permit their success in drought-prone habitats, physiological mechanisms that enable prolonged

maintenance of higher tissue turgor pressures, under low moisture availability, might play a far more important role in their ability to tolerate drought-prone environments. The physiological characteristics that may enable *Vismia* and *Solanum* to succeed in colonizing seasonally dry environments in Brazilian Amazonia are, however, unknown.

Here, I present the results of a greenhouse study which compared the bulk tissue water relations of *Solanum* and *Vismia* to determine whether the drought resistance characteristics observed in the field are reflected in their tissue properties. Furthermore, I report the effects of soil moisture deficits on the gas exchange response of these two species. I hypothesized that *Solanum* and *Vismia* have distinct responses to drought, and that variation in these responses would be a useful indicator of the mechanisms that enable these species to tolerate water stress in order to survive in drought prone habitats in Brazilian Amazonia.

Materials and methods

Plant material and growing conditions

Vismia guianensis (Aubl.) Choisy (Guttiferae) and *Solanum crinitum* Lam. (Solanaceae) seeds, collected from plants growing in abandoned pasture areas in Brazilian Amazonia, were germinated on filter paper in petri dishes and then planted individually in pots with a mixture of peat:vermiculite:perlite (1:1:1). Plants were grown in a greenhouse at temperatures of $24 \pm 2.2^\circ \text{C}$ (night) to $33 \pm 2.1^\circ \text{C}$ (day) and a maximum photosynthetic photon flux density (PPFD) of approximately $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. PPFD was supplemented and photoperiod extended to 12 hours by 400 W high-pressure sodium vapor lamps. Plants received ample water and

were fertilized twice a month with 50 ml of a water soluble fertilizer solution (15:30:15; N:P₂O₅:K₂O; 3.5 g L⁻¹).

Pressure-volume analysis

Pressure-volume (PV) analysis (Tyree & Jarvis 1982), employing the bench drying method (Kikuta et al. 1985; Koide *et al.* 1989), was performed on four replicate mature leaves (*Solanum*) or four replicate terminal branches (ca. 15 cm long) with 2-4 mature leaves (*Vismia*), collected from individual eight to nine-month-old plants. On the evening before PV analysis, the basal 1-2 cm of the leaf petioles and branch stems were recut under deionized water. The leaves or branches were enclosed in a plastic bag and allowed to rehydrate for 12-14 h in a humid, dark environment, with their cut surfaces submerged in test tubes of deionized water. After obtaining the fully hydrated leaf and shoot weights (saturated weight), tissue water potentials (Ψ) were measured using a pressure bomb (PMS Instruments, model 1000, Corvallis, Oregon, USA). Between measurements of Ψ , leaves (*Solanum*) and branches (*Vismia*) were allowed to transpire at room temperature on a laboratory bench. Periodically (5-40 min), the fresh weight of each leaf or shoot was determined before and after each pressure chamber measurement and the mean weight used to calculate relative water content [RWC = (fresh weight - dry weight) ÷ (saturated weight - dry weight)]. About 10 min were needed to complete one measurement set of pre- and post-pressure weights and Ψ . A total of 16 to 25 measurements were obtained per leaf or branch, with more than six measurements before turgor loss. Upon completion of PV analysis, leaves and branches were dried in an oven at 70° C for 24 h to get dry weight.

Response of gas exchange to irradiance

A photosynthesis (A) versus irradiance (PPFD) response curve (starting at ca. $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ and decreasing in four 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 amount of leaf area in the chamber was approximately 20 cm^2 . 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 (R_d) values. Six replicate plants of each species per experiment and one leaf per plant were sampled.

Photosynthesis vs. irradiance response data provided direct estimates of mean maximum photosynthesis (A_{max}) under saturating irradiance (ca. $800 \mu\text{mol m}^{-2} \text{s}^{-1}$). Apparent quantum yield of CO_2 to incident irradiance (α) was the slope of a regression of six R_d measurements and six low light (ca. $130 \mu\text{mol m}^{-2} \text{s}^{-1}$) measurements of CO_2 exchange, for each species and watering regime combination. The light compensation point was calculated as the ratio, R_d/α . Intrinsic water-use efficiency (Osmond et al. 1980) was calculated as the ratio, A/g .

Response of gas exchange to water deficit

Six replicate plants of each species grown in the greenhouse as described above had irrigation withheld until soil water content reached approximately 50 % of well-watered plants on a weight basis (approximately 6 d). The soil water content of water limited *Solanum* and *Vismia* plants, before gas exchange measurements, averaged 49.2 (± 3.9) and 47.6 (± 3.9) % of well-watered plants, respectively. Water potential of water limited plants, measured with the pressure chamber, averaged -0.2 to -0.5 MPa, more negative than well-watered plants (average was -0.25 (± 0.03) MPa).

Data analysis

A pressure-volume (PV) plot of the reciprocal balance pressure ($1/\Psi$) versus relative water content (RWC) was constructed (Tyree & Richter 1981; 1982). Osmotic potential near full hydration ($\Psi\pi_{\text{hyd}}$) and at turgor loss point ($\Psi\pi_{\text{tlp}}$), the RWC at turgor loss (RWC_{tlp}) were calculated following Robichaux *et al.* (1986) employing a modified version of a microcomputer-aided analysis designed by Schulte & Hinckley (1985) (see Dawson & Bliss 1989). Bulk modulus of elasticity (ϵ) was calculated as the slope of the turgor pressure versus the RWC relationship, for five consecutive values near saturation multiplied by the average RWC of these five points minus the estimated apoplastic water content (Koide *et al.* 1989).

Differences in the A/g ratio means for species and watering regimes were assessed by *post-hoc* multiple comparison using Tukey's HSD procedure (Milliken & Johnson 1992). Homogeneity of variances and

normality for the A/g data were confirmed respectively by the Hartley's F-Max test ($P= 0.126$) and by inspection of a normal probability plot.

Differences in net photosynthesis and stomatal conductance response curves for species and watering treatments were analyzed by multivariate analysis of variance with repeated measures. The multivariate approach was preferred over its univariate counterpart because, in the latter, the compound symmetry of the covariance matrix was rejected for our data, and there was never total agreement between the Huynh-Feldt and the Greenhouse-Geisser corrected significance levels (Milliken & Johnson 1992). The between-subject main effects were species and watering regimes, and the within-subject or repeated measures effect was light level. Homoscedasticity of the residuals, assessed by the Box M test, was confirmed both for the net photosynthesis ($P= 0.104$) and the stomatal conductance ($P= 0.523$) data. No severe departures from the normality assumption were identified by examining half-normal probability plots of z-transformed within-cell correlations for both data sets. *Post hoc* contrasts were calculated comparing species and watering regimes differences in photosynthesis and stomatal conductance, within each irradiance level, and pooling all irradiance levels. The statistical package STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994) was used for all computations of the data.

Results

Pressure-volume curves

The PV analysis indicated that *Vismia* and *Solanum* differed significantly in their osmotic and elastic tissue properties (Table 8.1, Fig. 8.1). No

significant variation in RWC_{tlp} between the two species was observed, however, $\Psi\pi_{tlp}$ was significantly different, with *Vismia* eventually losing turgor at a lower (more negative) water potential than *Solanum*. Tissue osmotic potential at full saturation ($\Psi\pi_{hyd}$) was also different between species, being substantially lower for *Vismia*. The bulk modulus of elasticity (ϵ) also revealed differences between species. *Vismia* displayed significantly higher ϵ than *Solanum* (Table 8.1); possessing more inelastic tissues.

Table 8.1. Pressure-volume curve parameters for *Vismia guianensis* and *Solanum crinitum*. Values are means (s.d.), n= 4. Symbols and units; $\Psi\pi_{hyd}$ and $\Psi\pi_{tlp}$ are osmotic potential at full hydration and at the turgor loss point, respectively (MPa). ϵ is the bulk tissue elastic modulus near full hydration (MPa), and RWC_{tlp} is the relative water content at the turgor loss point (%).

	<i>V. guianensis</i>	<i>S. crinitum</i>	<i>t</i> values
$\Psi\pi_{hyd}$	-1.34 (0.174)	-0.89 (0.052)	4.89**
$\Psi\pi_{tlp}$	-1.55 (0.106)	-1.05 (0.076)	7.65**
ϵ	13.67 (2.86)	8.56 (0.65)	3.47*
RWC_{tlp}	89.1 (0.025)	87.9 (0.012)	0.81

Differences between species were analyzed using Student's *t*-test for independent samples. Significant differences are indicated by * ($P = 0.04$) and ** ($P < 0.01$).

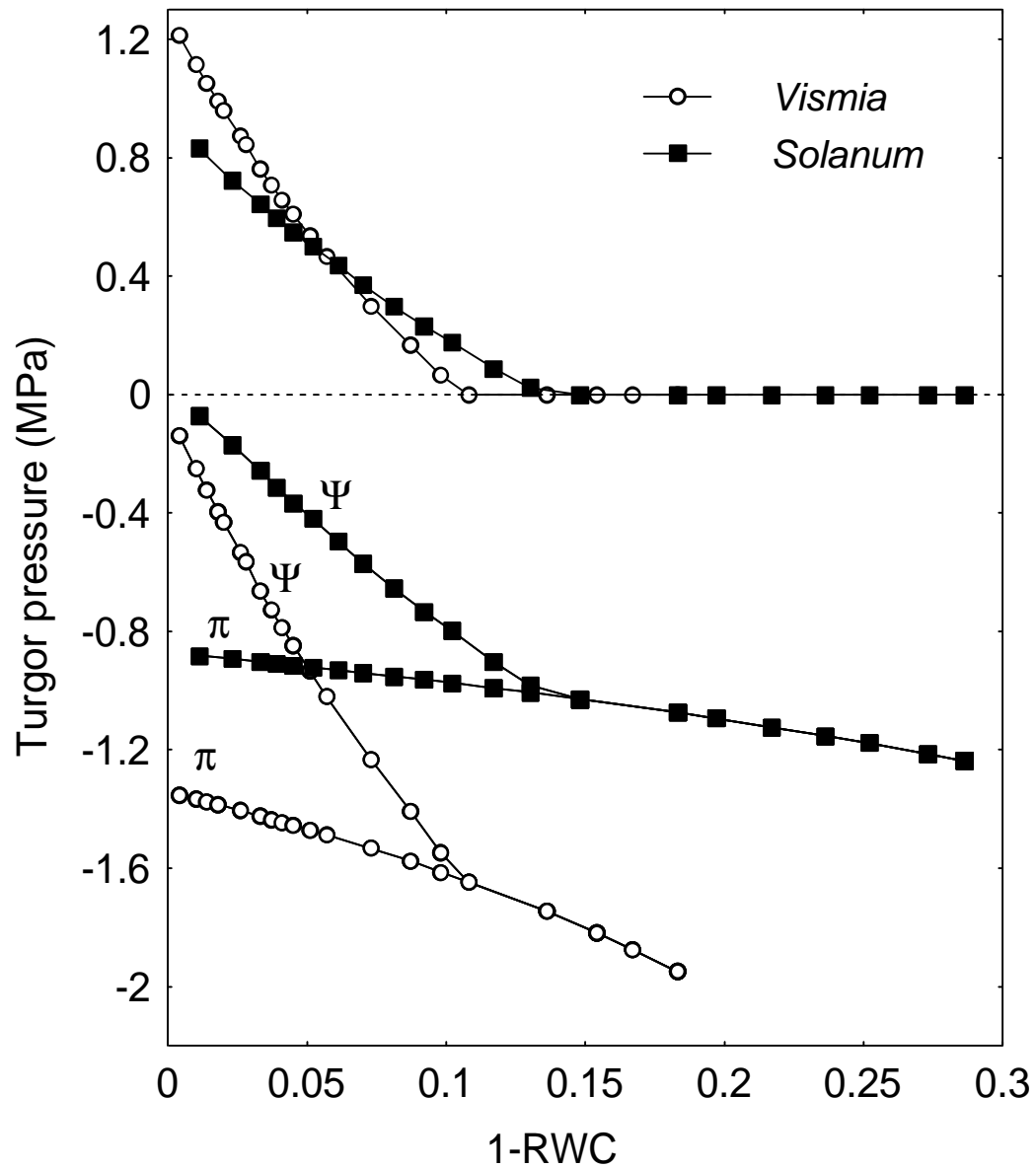


Figure 8.17. Relationships of relative water content (RWC) to turgor pressure, osmotic potential (π), and water potential (Ψ) for *Vismia* and *Solanum*.

CO₂ assimilation

There were significant species, watering regimes and species by watering regime main effect differences in the CO₂ assimilation rates (Fig. 8.2,

Table 8.2). Similarly, the effect of light and its interaction with all other effects were also significant. *Post hoc* contrasts indicated that in *Vismia* differences in the light response curve between watering regimes were attributed to the differences in CO₂ assimilation rates observed at the second (ca. 550 μmol m⁻² s⁻¹; F_{1,20}=5.2, < 0.04) and at the fourth (ca. 130 μmol m⁻² s⁻¹; F_{1,20}=16.7, < 0.001) irradiance levels. These light levels yielded lower CO₂ assimilation rates for water-limited plants (Fig. 8.2). For *Solanum*, a significant difference in *A* when compared to *Vismia* was observed only at the third (ca. 380 μmol m⁻² s⁻¹; F_{1,20}=4.9, < 0.04) and fifth (0 μmol m⁻² s⁻¹; F_{1,20}=7.7, < 0.01) irradiance levels with, respectively, higher CO₂ assimilation rate and *R_d* for water-limited plants (Fig 2).

Post hoc contrasts on differences between species, within each watering regime, revealed significantly greater assimilation rate and higher (more negative) dark respiration for water-limited *Solanum* at, respectively, the fourth (ca. 130 μmol m⁻² s⁻¹; F_{1,20}=11.7, < 0.003) and fifth (0 μmol m⁻² s⁻¹; F_{1,20}=49.7, < 0.001) irradiance levels (Fig. 8.2). On the other hand, in well-watered plants, *Vismia* displayed greater CO₂ assimilation rate at the highest irradiance level (ca. 800 μmol m⁻² s⁻¹; F_{1,20}=10.4, < 0.004), but lower (less negative) *R_d* (0 μmol m⁻² s⁻¹; F_{1,20}=12.9, < 0.002)

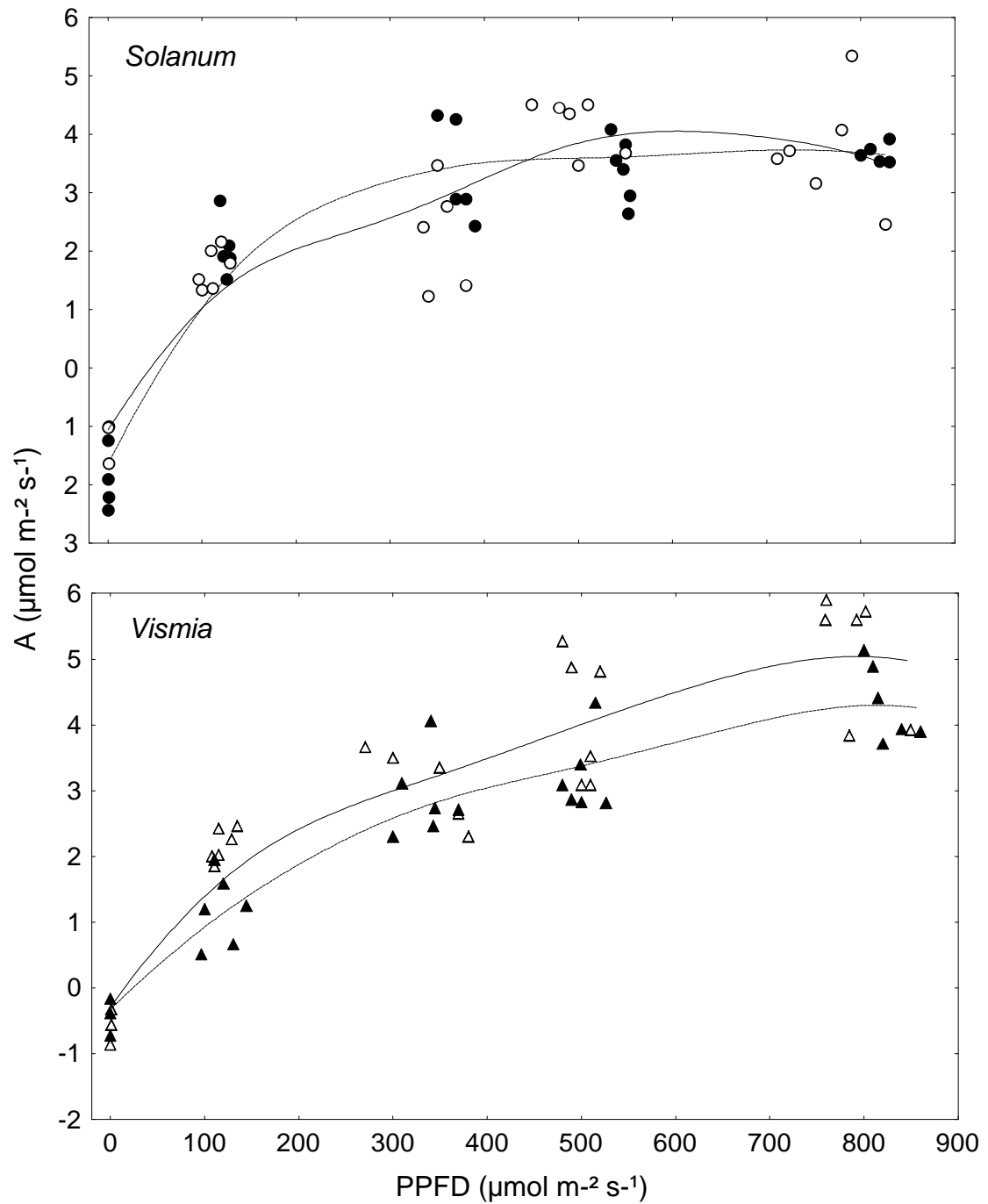


Figure 8.18. Light response curve of CO_2 assimilation of the youngest fully expanded leaves of *Solanum* and *Vismia* under well watered (open symbol, solid line) and water limited (closed symbol, dashed line) conditions. A= rate of net photosynthesis; PPFD= Photon flux density.

Table 8.2. Multivariate analysis of variance of CO₂ assimilation rate with repeated measures on light levels.

Source	df	MS	F	P
<i>Between subjects</i>				
Species (Sp)	1	3.75	9.34	0.006
Regime (Re)	1	2.07	5.15	0.034
Sp×Re	1	1.9	4.73	0.042
Error	20			
<i>Within subjects</i>				
Source	df	Pillai's trace	F	P
Light	4	0.9903	433.881	< 0.0001
Light×Sp	4	0.73	11.491	0.0001
Light×Re	4	0.5066	4.364	0.013
Light×Sp×Re	4	0.6023	6.437	0.0024
Error	17			

Leaf conductance

Both species increased stomatal opening in relation to light under both watering regimes (Fig. 8.3). All between-subjects and within-subjects effects were statistically significant (Table 8.3). *Post hoc* contrasts showed that in *Vismia* differences in stomatal conductance between watering regimes were significant for leaves at low light (ca. 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$; $F_{1,20} = 6.4$, < 0.02) and in the dark ($F_{1,20} = 13.6$, < 0.001); these same leaves also had higher conductance under well-watered conditions (Fig. 8.3). For *Solanum*, an unusual response pattern was observed; leaf conductance was always higher in water-limited plants under all light levels ($F_{1,20} > 5.5$, $P < 0.03$, Fig. 8.3). *Post hoc* contrasts comparing differences between species

revealed significantly greater leaf conductance values for water-limited *Solanum* under all light levels ($F_{1,20}= 13.2, < 0.002$, Fig. 8.3). No difference in stomatal conductance could be detected ($F_{1,20} < 4.2$, ns) between the two species under well-watered conditions (Fig. 8.3).

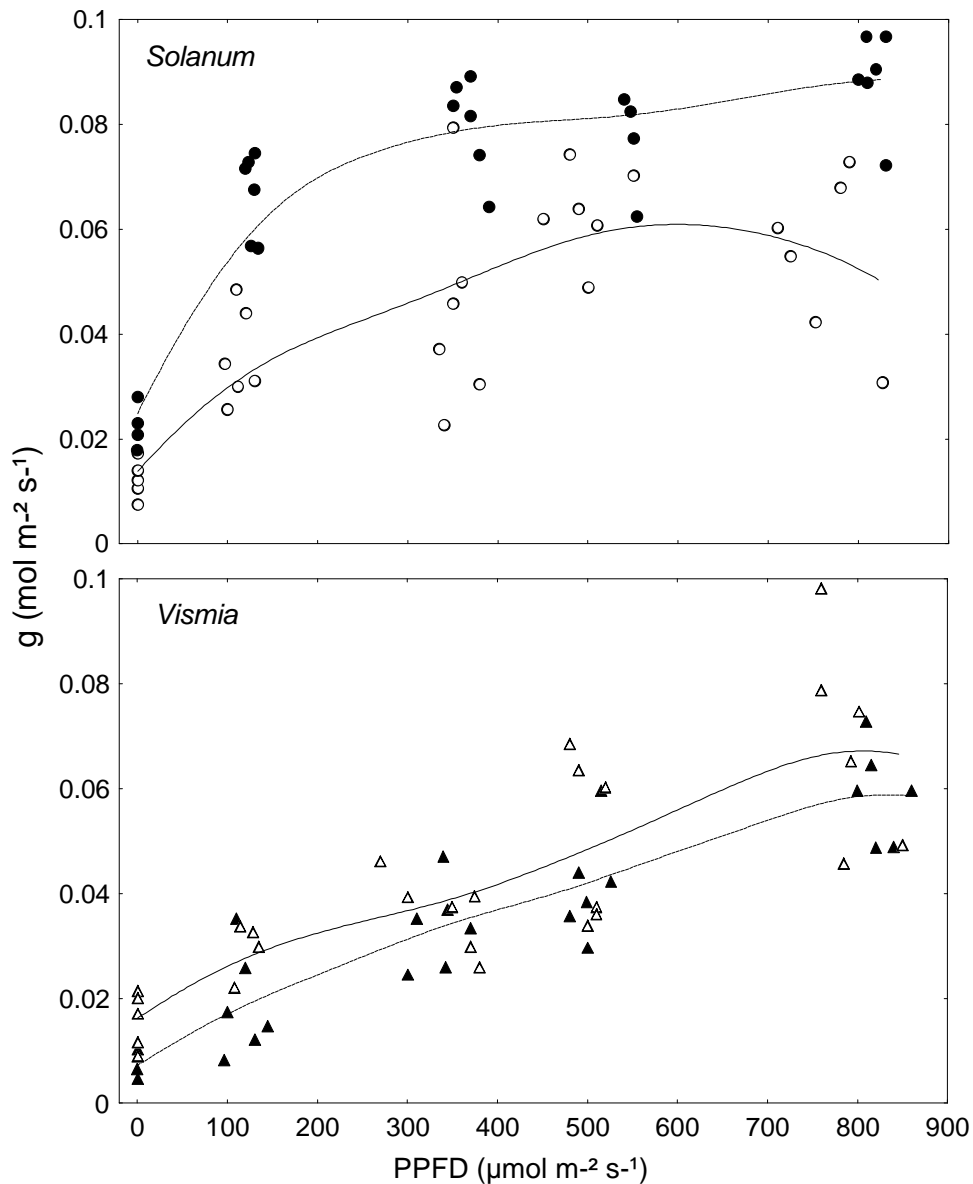


Figure 8.19. Light response curve of stomatal conductance of the youngest fully expanded leaves of *Solanum* and *Vismia* under well watered (open symbol, solid line) and water limited (closed symbol, dashed line) conditions. g = rate of stomatal conductance; PPFD= Photon flux density.

Table 8.3. Multivariate analysis of variance of stomatal conductance with repeated measures on light levels.

Source	df	MS	F	<i>P</i>
<i>Between subjects</i>				
Species (Sp)	1	0.01	87.7	0.0001
Regime (Re)	1	0.002	18.9	0.0003
Sp×Re	1	0.008	70.7	0.0001
Error	20	0.00012		
<i>Within subjects</i>				
Source	df	Pillai's trace	F	<i>P</i>
Light	4	0.9767	178.523	< 0.0001
Light×Sp	4	0.7959	16.577	0.00011
Light×Re	4	0.4386	3.32	0.035
Light×Sp×Re	4	0.4822	3.958	0.019
Error	17			

Photosynthesis parameters

Light-saturated photosynthesis (A_{\max} , Table 8.4, Figs.8.1 and 8.2) was higher in both species under well-watered conditions. Comparing species, A_{\max} was higher in *Vismia*, under both watering regimes. Dark respiration (R_d , Table 8.4 and Fig. 8.2) was higher (more negative) in *Solanum* under both watering regimes. Within species differences in R_d , assessed by *post hoc* contrasts, revealed that water-limited *Solanum* plants

had a significantly higher R_d , whereas, in *Vismia*, no significant difference ($P= 0.51$) could be detected. As a result of the higher R_d observed in *Solanum*, the light compensation point in this species, as R_d/α (Table 8.4), was considerably higher than in *Vismia*. Within species light compensation points provided a sensitive index of leaf response to the watering regimes. Drought stress always led to higher R_d/α values; these were 38 % and 15 % higher in water-limited *Vismia* and *Solanum*, respectively.

Table 8.4. Photosynthetic parameters of *Vismia guianensis* and *Solanum crinitum* under well-watered and water-limited regimes. Values are means (s.d.), n=6. Symbols and units; A_{max} is light saturated photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); α is apparent quantum efficiency ($\text{mol CO}_2 \text{ photon}^{-1}$); R_d is dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and R_d/α is light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$)

	Well-watered	Water-limited
<i>Vismia guianensis</i>		
A_{max}	5.10	4.33
α	0.025 (0.003)	0.017 (0.009)
R_d	0.505 (0.22)	0.412 (0.185)
R_d/α	20.44 (8.36)	28.18 (6.45)
<i>Solanum crinitum</i>		
A_{max}	3.72	3.67
α	0.028 (0.003)	0.035 (0.008)
R_d	1.23 (0.29)	1.78 (0.56)
R_d/α	43.65 (8.89)	50.17 (9.05)

If we take α as an index of photosynthetic efficiency, soil moisture deficits caused a 32 % decrease in the photosynthetic efficiency in *Vismia*, but not in *Solanum*, which unlike *Vismia*, displayed a 25 % increase in α under the water-limited regime (Table 8.4).

Intrinsic water-use efficiency expressed as the ratio A/g is shown in Figure 8.4. *Solanum* displayed significantly lower A/g under both watering regimes. For both species there was a tendency for A/g values to decrease with increasing water deficit; this trend, however, was not statistically significant for *Vismia* (Fig. 8.4).

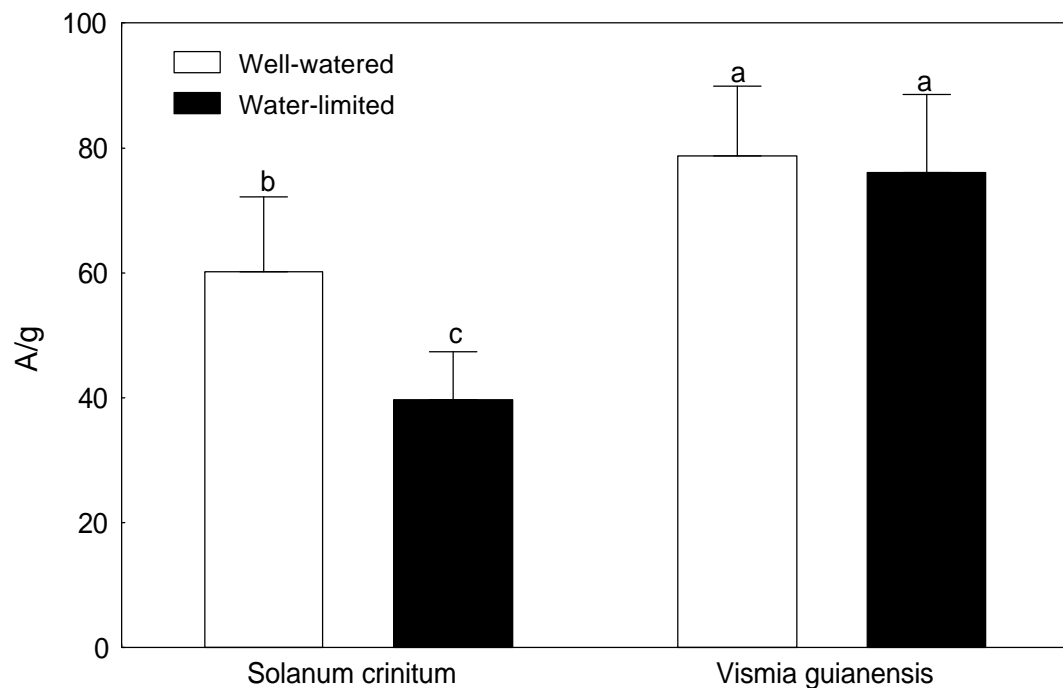


Figure 8.20. Intrinsic water-use efficiency expressed as the net photosynthesis (A) to stomatal conductance (g) ratio for *Solanum* and *Vismia* under well watered and water limited conditons. Different letters indicate significant differences for species and watering regime interactions (Tukey's HSD procedure). Values are means ('wiskers' = 1 s.d.), $n= 24$.

Discussion

Tissue water relations

Bulk tissue elastic properties have been claimed to be involved in the promotion of turgor maintenance (e.g., Tyree & Jarvis 1982, Robichaux et al. 1986, Dawson 1990). Plants with either inelastic or elastic tissue properties can possess different mechanisms for the maintenance of favorable turgor pressures as tissue water content falls and hence, presumably, have a greater capacity to maintain their physiological activities in situations of low moisture availability. In contrast, inelastic tissues permit a greater water potential gradient to develop between leaves and soil and would help the plant to draw-up water during water stress, and thereby increase turgor. On the other hand, plants with elastic tissue properties could undergo greater changes in cell volume during water stress, and still maintain a favorable turgor potential (Abrams 1988, Dawson & Bliss 1989).

The bulk tissue water relations (Table 8.1, Fig. 8.1), suggest that *Vismia* and *Solanum* have different physiological mechanisms for dealing with limited soil moisture. The significantly lower ϵ (i.e., relatively more elastic tissue) observed in *Solanum* (Table 8.1) gives this species a relatively larger tissue capacitance, allowing the occurrence of large changes in tissue water content for relatively small changes in Ψ (Jones 1992) (Fig. 8.1). This tissue elastic property may aid *Solanum* in maintaining physiological activity during moisture deficits, by maintaining turgor potential over greater changes in the volume of tissue water (Clayton-Greene 1983, Robichaux et al. 1986). This characteristic can become particularly important for this species as it has a relatively low A/g

(Fig. 8.4). In contrast, the relatively more rigid tissues (i.e., higher bulk modulus of elasticity) would aid *Vismia* in rapidly developing of a steep water potential gradient from the leaf to the soil (i.e., rapidly drop turgor potential) while losing only a small amount of tissue water (Fig. 8.1). This strategy would maintain a gradient for continued water uptake from the soil, without subjecting the plant to large tissue water deficits. Such mechanism could increase the plant's capacity to obtain more 'bound' water from a drying soil and hence contribute to the maintenance of higher tissue turgor pressures and a more favorable water balance (Dawson & Bliss 1989, Bowman & Roberts 1985). In addition, *Vismia* possesses higher osmotic concentrations at full hydration (Fig. 8.1) than *Solanum*. This could serve to either maintain turgor down to relatively low Ψ values, or to further enhance water uptake (Dawson 1990). Turgor loss point values calculated for *Vismia* and *Solanum* (Table 8.1) were remarkably similar to the ones reported by Wright (1991) for seven species of tropical shrubs from the genera *Psychotria* and *Piper*, respectively.

In seasonally dry environments, like in eastern Brazilian Amazonia, the strategy suggested for *Vismia* may be selectively advantageous during a prolonged dry season. As soils dry, competition for limited soil water will become of greater importance as it decreases. In contrast, under situations of periodic but "rapidly" developing water deficits, such as during an increase in the daily evaporative demand, the ϵ of *Solanum* may help buffer plants against short-term water stress by allowing them to undergo relatively greater amounts of tissue water loss while maintaining a positive turgor pressure. Because soil moisture stress in pot-grown plants is likely to develop more rapidly and uniformly than under field conditions (e.g.,

Wan *et al.* 1993), I believe that in the present study the simulated moisture stress treatment may have provided a relatively greater advantage to *Solanum* over *Vismia*, due to its water relation characteristics.

Although *Vismia* had significantly lower $\Psi\pi_{\text{tlp}}$ and $\Psi\pi_{\text{hyd}}$ than *Solanum* (Table 8.1, Fig. 8.1), we believe that the small magnitude of these differences does not justify different ecological groupings for these species in relation to drought. Based on their tissue water relation properties, however, response to drought is very different for these two species.

Gas exchange response

The light response of photosynthesis for *Vismia* and *Solanum* (Fig. 8.1, Table 8.2) revealed that the experimental level of soil moisture tested in this study (i.e., ca. 50 % of well-watered plants), though relatively low, was not severe enough to greatly affect the shape of the curves. The water-limited regime caused an average decrease in assimilation rate, over all light levels, of 23 % in *Vismia* ($F_{1,20} = 9.9, < 0.005$), but only 0.5 % in *Solanum* ($F_{1,20} = 0.004, \text{ns}$). This suggests that *Solanum* has a much greater capacity to maintain assimilation rates when soil moisture is limited. This feature was also confirmed in the light response curve of stomatal conductance (Fig. 8.2, Table 8.2). *Vismia* showed an overall decline in stomatal conductance, due to the moisture stress treatment, of only 25 % ($F_{1,20} = 8.3, < 0.009$). This average decrease in stomatal conductance was consistent with the one observed in the assimilation rate, suggesting, for this species, a relatively great importance of stomatal closure in causing the observed decrease in assimilation. We cannot explain the unusual g vs. PPFD response in *Solanum* when exposed to

moisture stress. Plants under the water limited conditions had, on average, a 60 % increase ($F_{1,20} = 81.3, < 0.001$) in g , over all photon flux densities (Fig. 8.2). The stomatal behavior was not consistent with the observed assimilation behavior. It is unlikely that the unusual stomatal conductance behavior displayed by *Solanum* plants could have been an artifact of the measuring system since leaf temperatures and external CO_2 concentrations during measurements were identical between treatments, ruling out the possibility of g was influenced by leaf temperature or external CO_2 concentrations. It may be that, due to their bulk tissue elastic properties, *Solanum* plants subjected to restricted soil water are well buffered from tissue dehydration and, as a consequence, sustain high tissue turgor potential, thus maintaining stomatal conductance. In this case, leaf water status, as opposed to soil water status, was probably more important in affecting stomatal conductance in this species. Although we have found that *Solanum* plants subjected to restricted water supply, did have lower leaf water potentials than well-watered plants, there is evidence in the literature that stomatal conductance can be relatively insensitive to leaf water potential, and may even increase with decreasing leaf water potential, suggesting leaf water potential rather than soil water potential controls stomatal conductance (Jones 1985). Our data suggest that assimilation in *Solanum* was directly influenced by water stress (decreased mesophyll biochemical capacity, electron transport, or other changes) even though g was not markedly changed. This lead to a decline in A/g , when exposed to water deficit as well as a decoupling of g from A ; this could mean that in *Solanum*, the photosynthetic machinery is more sensitive than are the stomata to water deficit.

Analysis of the photosynthetic parameters (Table 8.4), indicates that, unlike in *Vismia*, photosynthetic efficiency in *Solanum*, assessed by the α , was not negatively affected by the water limited treatment. This result agrees with the observed CO₂ assimilation response curve (Fig. 8.1). The light compensation point was positively affected by soil moisture stress both in *Vismia* and *Solanum*. The relative increase in the R_d/α , due to drought stress, was, however, higher in *Vismia*. This species owed its higher R_d/α , under low soil moisture, to a decrease in α , whereas in *Solanum*, an elevated R_d was responsible for the higher R_d/α observed under the water limited treatment. The light compensation point values, estimated in the present study for well watered and water limited *Vismia*, were similar to the ones reported by Riddoch et al. (1991) for a group of tropical “pioneer trees” from Nigeria, while those of *Solanum* were comparable to the R_d/α values determined, in that same study, for “weeds of gaps.” These are in accord with the life forms of the species from the present study.

Plant response to drought is not commonly viewed as being important for plants of Amazonia. However, drought can be quite severe during the prolonged, hot, dry season in many tropical areas of the world. Here, I show some of the very first data on the response of two important gap-invader species from Amazonia to drought, and the fact that they can differ quite dramatically in the mechanisms which allow them to sustain themselves during water deficits.

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ROOT AND SHOOT GROWTH IN RESPONSE TO SOIL DRYING IN SEEDLINGS OF FOUR AMAZONIAN WEEDY SPECIES

Introduction

Seedling survival in drought-prone environments may depend upon the species' ability to compensate for the negative effect of low water potentials in the soil and atmosphere by adjusting root and shoot morphological and physiological patterns (see Kramer 1983 and Morgan 1984 and references therein). In this context, an improved plasticity in promoting a shift in the allocation of assimilates from shoot to root and in adjusting the growth and distribution of the root system in response to soil drying are generally considered important acclimation mechanisms to drought (Molyneux & Davies 1983, Sharp & Davies 1979, Morgan 1984).

While it could be argued that for some crop plants (mainly the ones in which only the above ground biomass is harvested) a relatively high investment in the root system may not be very advantageous due to the growth and maintenance costs in root development, for wild plant species such investment could be advantageous. Hence, invasive plants that exhibit great plasticity in root growth and distribution in response to soil drying could be considered as well adapted to environments where limited soil water availability is a major constraint to plant growth.

In the experiment described in this chapter I have compared root penetration and growth, and biomass allocation patterns, in response to soil drying in seedlings of *Ipomoea asarifolia* (Desr.) Roem. & Schultz (Convolvulaceae), *Stachytarpheta cayennensis* (Rich) Vahl. (Verbenaceae), *Solanum crinitum* Lam. (Solanaceae) and *Vismia guianensis* (Aubl.) Choisy (Guttiferae). These species are considered important invasive species of anthropogenic and (or) naturally disturbed habitats in eastern Brazilian Amazonia (see Albuquerque 1980, Dantas 1989 and Dias Filho 1990), a region characterized by a marked dry season. My objective was to determine whether seedlings of these species show below and above ground responses to soil drying that could be characterized as enhanced ability to acclimate to water deficits.

Materials and methods

Plant material and growing conditions

Seeds from *Ipomoea asarifolia*, *Stachytarpheta cayennensis*, *Solanum crinitum* and *Vismia guianensis* were collected from plants invading pasture areas in Paragominas, PA (3°05' S - 47°21' W) in eastern Brazilian Amazonia. Seeds were germinated on filter paper in petri dishes and when radicles reached 5 to 10 mm in length, seedlings were transferred to soil columns (one seedling per column) to allow relatively unrestricted root development. The soil column was a polythene tube 100 cm long and 7.6 cm in diameter, filled with 2.3 kg of fritted clay (OilDri Corporation of America, Chicago, IL). This rooting medium was used because it was relatively easy to separate from roots and had high water-holding capacity, allowing gradual soil drying similar to what may occur under natural

conditions. Tubes were closed at the bottom with a plastic mesh to hold the growth medium and allow free drainage. Before seedling transplant, each soil column was saturated with 2.1 L of a nutrient solution (15 % N, 30 % P₂O₅, 15 % K₂O, 0.02 % B, 0.07 % Cu, 0.15 % Fe, 0.05 % Mn, 0.0005 % Mo and 0.06 % Zn; 3.5 g L⁻¹).

Tubes were placed in a greenhouse for the duration of the experiment. Minimum and maximum temperatures in the greenhouse were 25 ± 2.2° C (night) and 33 ± 2.1° C (day). A maximum photosynthetic photon flux density (PPFD) of approximately 1000 μmol m⁻² s⁻¹ was supplemented and photoperiod extended to 12 hours by 400 W high-pressure sodium vapor lamps. Relative humidity of the air was maintained at around 80 %.

Treatments and measurements

All seedlings received a 21-day pretreatment in which the soil columns were irrigated daily with either 100 ml of deionized water or, on alternating days, with 100 ml of nutrient solution (the same solution applied before planting). A transparent plastic cover, with a central opening to allow seedling development, was placed on the surface of each column to reduce moisture loss from the growth medium. Following the pretreatment, two treatments were applied for an additional 21 days to compare root development under well-watered and water-limited conditions. Seedlings in one treatment received 100 ml d⁻¹ of deionized water; seedlings in the second treatment were not watered. Each treatment was applied to seven seedlings of *Ipomoea*, *Stachytarpheta* and *Solanum* and to three seedlings of *Vismia*.

To determine the vertical distribution of roots within the columns, at the end of the 42-day experiment, plants were clipped at the soil surface and each column was cut into sections of either 5 cm (*Solanum* and *Vismia*) or 10 cm (*Ipomoea* and *Stachytarpheta*) in depth. Roots in each column section were extracted and washed. For each seedling, maximum rooting depth (to the maximum 5 or 10 cm), shoot mass, total leaf area, and root mass (vertical distribution of root dry mass in the column) were calculated for all species. Roots and shoots of each seedling were dried at 70°C for 48 h. Leaf area was measured using a leaf area meter (Model LI-3000. Li-Cor, Inc. Lincoln, NE) and conveyor belt assembly (Model LI-3050. Li-Cor, Inc. Lincoln, NE).

Experimental design and statistical analysis

Soil columns were arranged in the greenhouse in a completely randomized design with seven (*Ipomoea*, *Stachytarpheta* and *Solanum*) or three (*Vismia*) replicates. Each replicate was an individual column planted with a single plant and placed at a particular location inside the greenhouse. For each species, differences between treatments in maximum rooting depth, root/shoot ratio, root dry weight accumulation and biomass allocation patterns were determined by paired *t*-tests; homogeneity of variances was assessed by Levene's test (see Milliken & Johnson 1992). When necessary the data were log or square root transformed for the *t*-test. Transformed data were back transformed for presentation. All statistical analyses were performed by STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994).

Results

Root/shoot ratio

Soil drying increased root/shoot ratio by 45 % ($t = 4.1$, $P = 0.001$) in *Ipomoea* and by 38 % ($t = 6.0$, $P < 0.001$) in *Stachytarpheta* (Fig. 9.1). For *Solanum*, no significant difference ($t = 0.8$, $P = 0.41$) in root/shoot ratio could be detected between treatments; however, plants in unwatered soil displayed a mean root/shoot ratio 15 % higher than in watered soil (Fig. 9.1). Contrary to these species, root/shoot ratio in *Vismia* had a tendency to be higher in watered soil (Fig. 9.1); however, the difference between watering regimes was not statistically significant for this species ($t = 1.5$, $P = 0.37$).

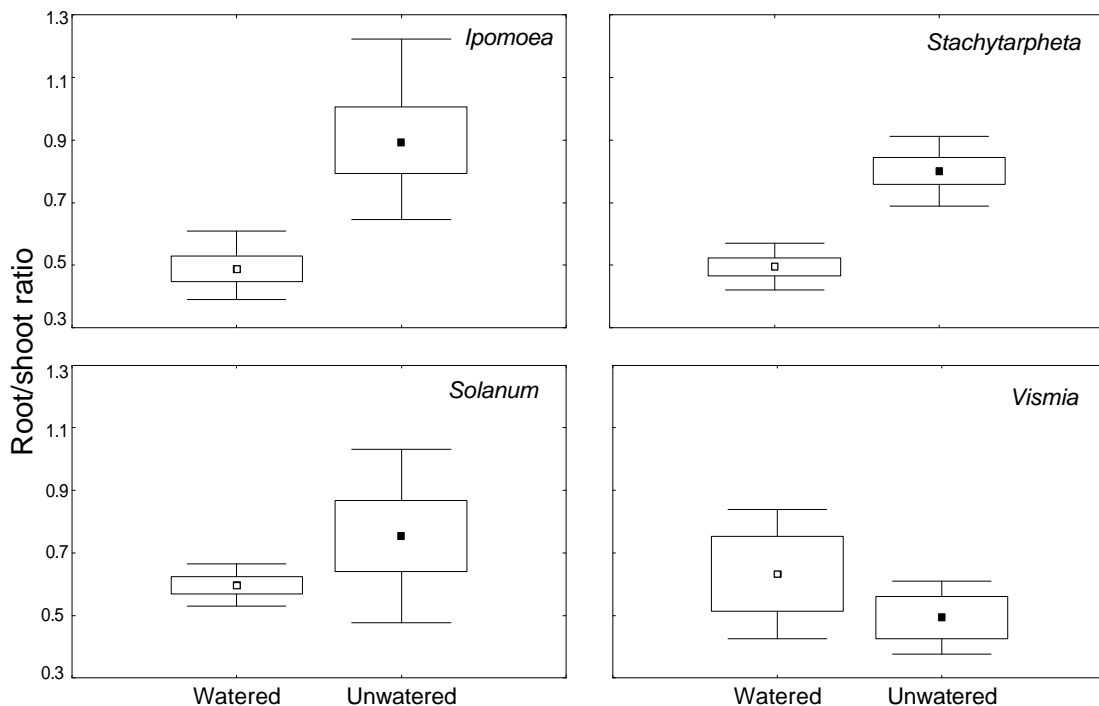


Figure 9.1. Box plots of root/shoot ratio as a function of watering regime in four Amazonian species. The mid-point is the mean, the box is ± 1 standard error and the error bar is ± 1 standard deviation; $n = 3$ for *Vismia* and $n = 7$ for the other species.

Rooting depth

No significant difference in maximum rooting depth could be detected between treatments for any of the species ($t \leq 1.15$, $P \geq 0.27$) (Fig. 9.2).

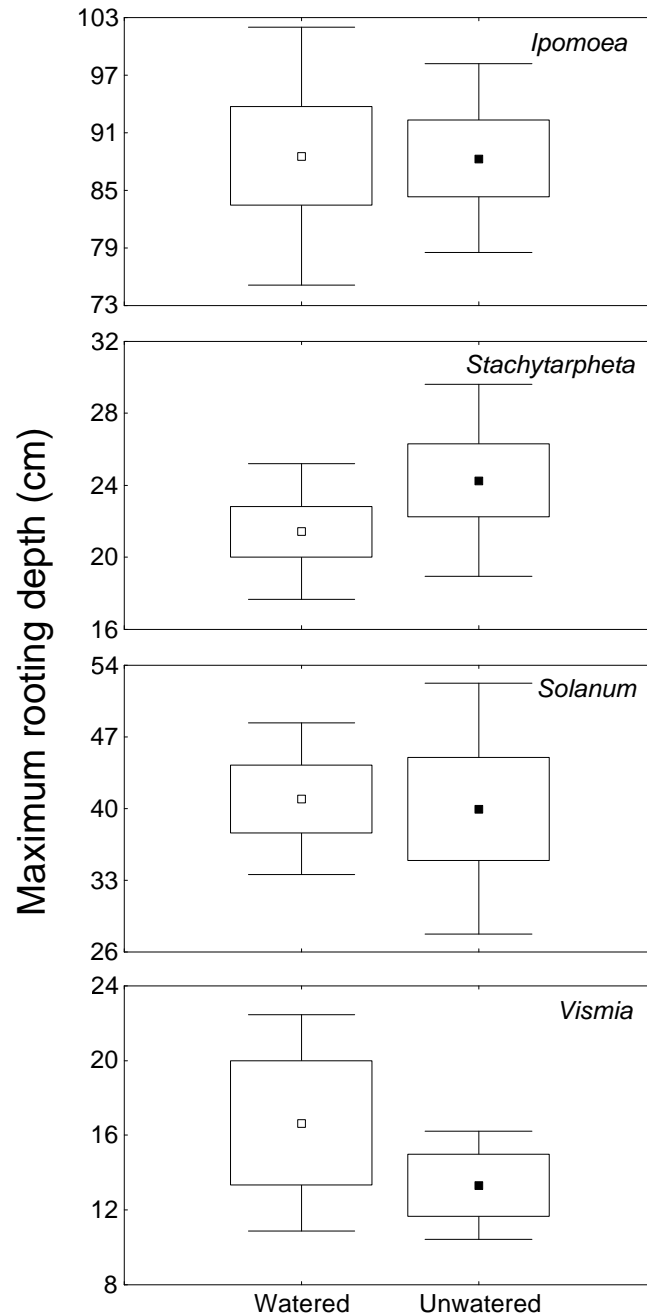


Figure 9.2. Box plots of maximum rooting depth of four Amazonian species in response to watering regime. Dot = mean, box = ± 1 s.e., error bar = ± 1 s.d.; $n = 3$ for *Vismia* and 7 for the other species.

However, a tendency for greater rooting depth in unwatered soil was suggested by the data from *Stachytarpheta*, while an opposite tendency was observed in *Vismia* (Fig. 9.2). Among species, rooting depth was maximum for *Ipomoea*, followed by *Solanum*, *Stachytarpheta* and *Vismia*.

Root growth

Root dry matter distribution in the profile was influenced by watering regimes in all studied species. In watered conditions, root development in *Ipomoea* was maximum at the 0-10 cm layer (Fig. 9.3), while in unwatered conditions, maximum root development had a tendency to be greater between the 60-70 and 70-80 cm layers (Fig. 9.3).

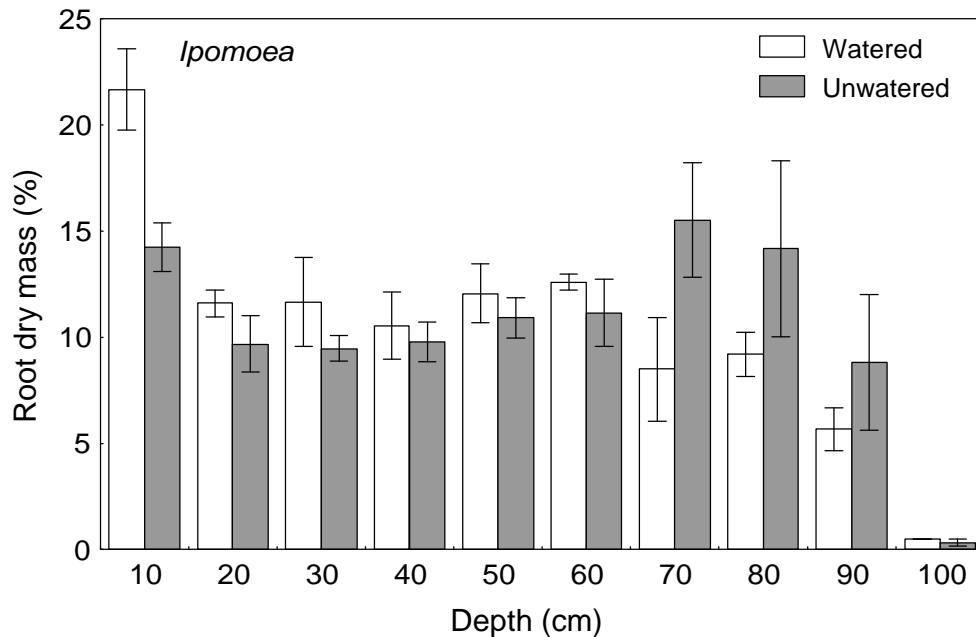


Figure 9.3. Percentage of total root dry mass in consecutive 10 cm soil layers in watered and unwatered columns for *Ipomoea*. Values are means of seven seedlings \pm standard error.

For *Stachytarpheta*, root dry mass in watered soil was maximum at the 0-10 cm layer, and significantly greater than for unwatered plants ($t=9.22$, $P < 0.001$) (Fig. 9.4). In unwatered soil relative root weight was equivalent at the 0-10 and the 10-20 cm soil layers and was significantly greater at 10-20 cm than for watered plants ($t=9.37$, $P < 0.001$) (Fig. 9.4). Also, no statistical difference between treatments could be detected at 20-30 cm and no roots grew beyond 30 cm.

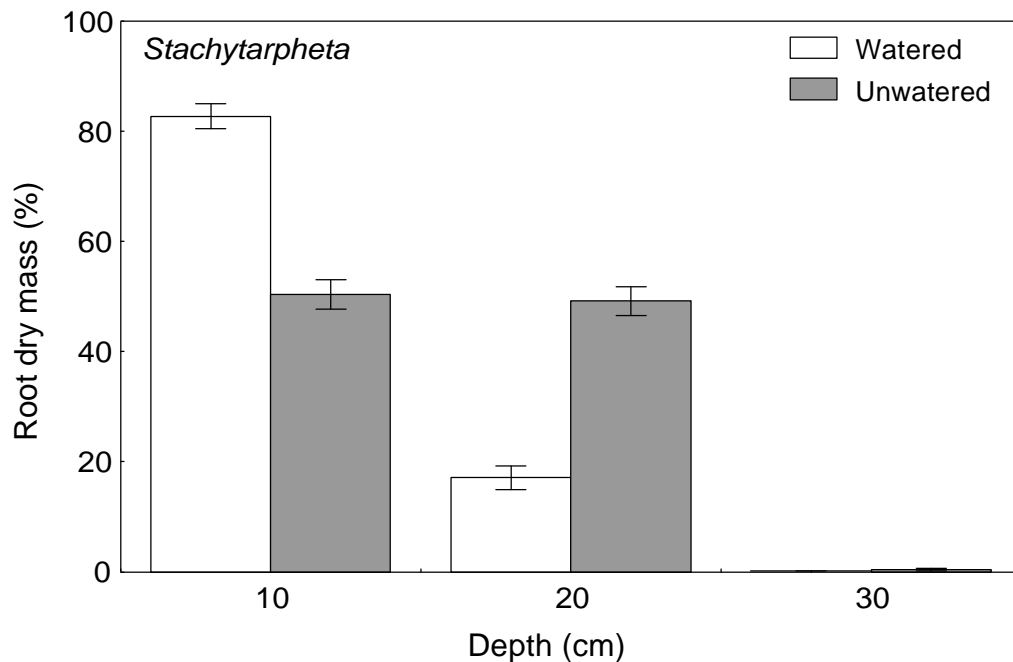


Figure 9.4. Percentage of total root dry mass in consecutive 10 cm layers in watered and unwatered columns for *Stachytarpheta*. Values are means of seven seedlings \pm standard error.

In *Solanum*, root dry matter in unwatered conditions had a tendency to be greater at 15-20 cm (Fig. 9.5), while in watered soil, root dry mass was similar at depths up to 30 cm, showing a tendency to decrease

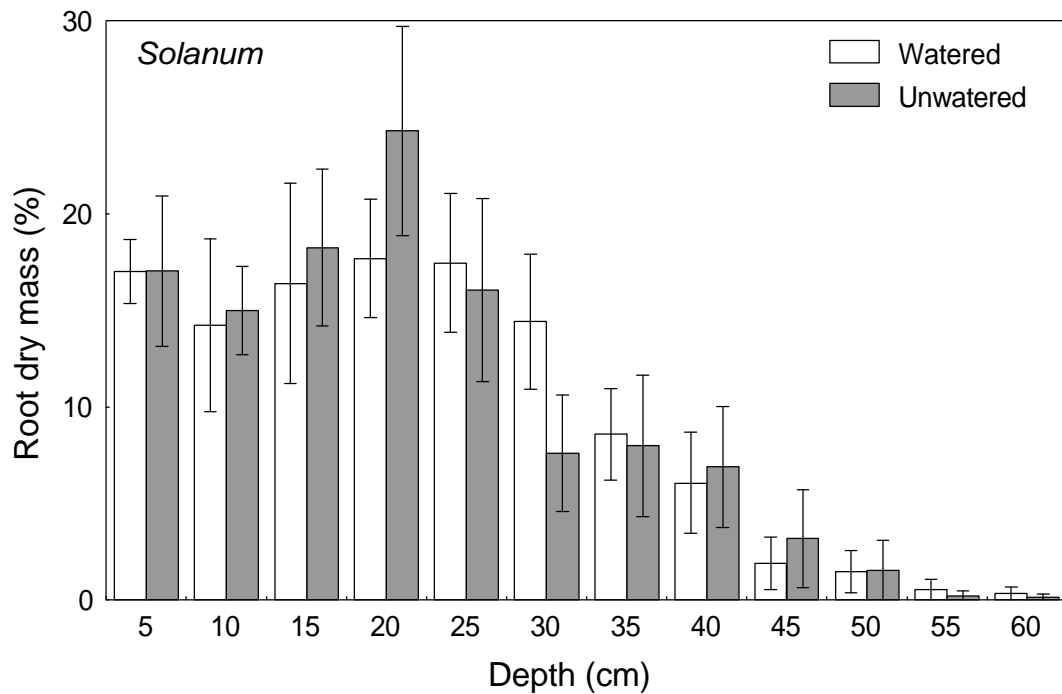


Figure 9.5. Percentage of total root dry mass in consecutive 5 cm layers in watered and unwatered columns for *Solanum*. Values are means of seven seedlings \pm standard error.

thereafter (Fig. 9.5). Otherwise the rooting depth distributions of *Solanum* appeared similar between the two treatments.

Root dry mass distribution in *Vismia* followed the same pattern observed in the other species (Fig 9.6). In watered soil, *Vismia* maximized root development in the surface layer (0-5 cm) and showed a tendency to decrease root development in the subsequent layers (Fig. 9.6). In unwatered soil, root development had a tendency to be maximum at the 5-10 cm layer (Fig. 9.6). *Vismia* developed no roots below 20 cm in either treatment.

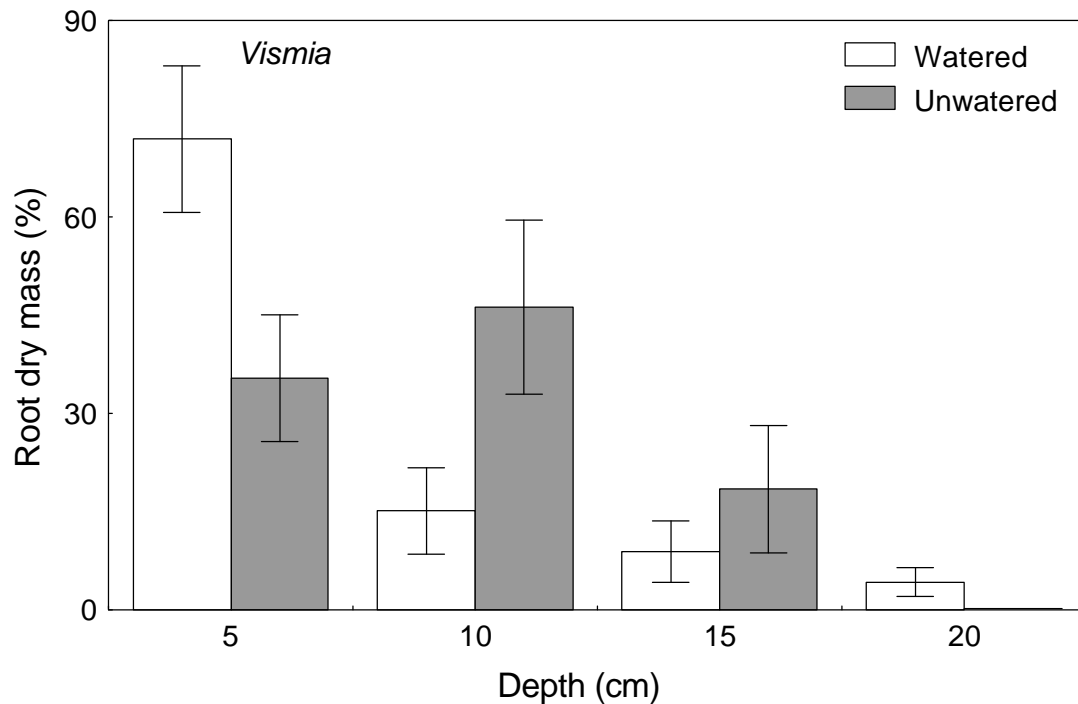


Figure 9.6. Percentage of total root dry mass in consecutive 5 cm layers in watered and unwatered columns for *Vismia*. Values are means of seven seedlings \pm standard error.

Biomass production and allocation pattern

Total dry matter was reduced by soil drying in *Ipomoea*, *Solanum* and *Vismia*, though not significantly ($P > 0.05$) in *Vismia* (Table 9.1). In *Stachytarpheta*, total biomass was unaffected by soil drying (Table 9.1). For *Ipomoea* and *Solanum*, the decline in total above-ground biomass was apparently the major cause for the significant reduction in total plant biomass in response to soil drying (Table 9.1). In contrast to the other species that had their below ground biomass reduced by soil drying, root

Table 9.1. Biomass of the four Amazonian species under two watering regimes after 42 days. Values are means (\pm s.d.); n= 3 for *Vismia* and 7 for the other species. The *P*-value denotes statistical differences between treatments according to the paired *t*-test.

	Watered	Unwatered	<i>P</i>
<i>Ipomoea</i>			
Leaf dry mass (g)	1.77 (0.07)	0.87 (0.04)	0.008
Stem dry mass (g)	2.71 (0.09)	0.86 (0.03)	< 0.001
Shoot dry mass (g)	4.48 (0.16)	1.74 (0.06)	0.02
Root dry mass (g)	2.16 (0.45)	1.54 (0.43)	0.001
Total biomass (g)	6.64 (0.16)	3.27 (0.06)	0.001
Number of leaves	12 (4.2)	9.8 (3.1)	0.2
Leaf area (cm ²)	680.8 (34)	296.7 (12)	0.005
<i>Stachytarpheta</i>			
Leaf dry mass (g)	0.20 (0.05)	0.16(0.03)	0.11
Stem dry mass (g)	0.05 (0.02)	0.04 (0.01)	0.10
Shoot dry mass (g)	0.25 (0.07)	0.19 (0.03)	0.10
Root dry mass (g)	0.12 (0.04)	0.16 (0.02)	0.08
Total biomass (g)	0.37 (0.11)	0.36 (0.05)	0.7
Number of leaves	19.4 (3.1)	8.0 (1.1)	< 0.001
Leaf area (cm ²)	54.5 (12.6)	37.9 (5.5)	0.008

Table 9.1 (Continued)

	Watered	Unwatered	<i>P</i>
<i>Solanum</i>			
Leaf dry mass (g)	2.08 (0.25)	0.41 (0.01)	0.002
Stem dry mass (g)	0.45 (0.06)	0.09 (0.004)	0.003
Shoot dry mass (g)	2.54 (0.3)	0.49 (0.02)	0.002
Root dry mass (g)	1.49 (0.16)	0.35 (0.03)	0.003
Total biomass (g)	2.01 (0.69)	0.92 (0.21)	0.002
Number of leaves	8.7 (1.0)	5.6 (0.9)	< 0.001
Leaf area (cm ²)	689.0 (76.7)	82.6 (3.4)	< 0.001
<i>Vismia</i>			
Leaf dry mass (g)	0.05 (0.03)	0.03 (0.02)	0.5
Stem dry mass (g)	0.007 (0.005)	0.006 (0.002)	0.6
Shoot dry mass (g)	0.06 (0.04)	0.04 (0.02)	0.5
Root dry mass (g)	0.03 (0.02)	0.02 (0.005)	0.3
Total biomass (g)	0.086 (0.059)	0.055 (0.024)	0.5
Number of leaves	18.0 (7.2)	15.3 (3.1)	0.6
Leaf area (cm ²)	20.6 (14.6)	10.2 (4.5)	0.3

dry mass in water-limited *Stachytarpheta* increased; however, this increase was not statistically significant (Table 9.1). A common response to soil drying in all species was a tendency to reduce both the total number and area of leaves. This may have ultimately contributed to the observed reduction in the total dry matter production in most water-limited plants.

All species varied in their biomass allocation patterns in response to the watering regimes (Tables 9.2 and 9.3, Fig. 9.7). *Ipomoea* and *Stachytarpheta* significantly increased their relative investment in root tissue (root weight ratio, RWR) in response to low water availability ($t \geq 4.1$, $P \leq 0.001$) (Table 9.2, Fig. 9.7). However, in *Solanum* and *Vismia*, no significant difference in RWR could be detected between watering regimes ($t \leq 0.6$, $P \geq 0.37$) (Table 9.2, Fig. 9.7).

Table 9.2. Summary of paired *t*-test for differences between watering regimes in root weight ratio (RWR), leaf weight ratio (LWR) and stem weight ratio (SWR) of four Amazonian invading species.

Species	RWR	LWR	SWR
<i>Ipomoea asarifolia</i>	**	ns	***
<i>Stachytarpheta cayennensis</i>	***	***	**
<i>Solanum crinitum</i>	ns	ns	ns
<i>Vismia guianensis</i>	ns	ns	ns

*** $P = 0.001$, ** $P = 0.01$, ns = not significant.

In *Stachytarpheta*, the amount of biomass allocated to leaves (LWR) was significantly higher ($t = 5.1$, $P = 0.001$) in watered soil (Table 9.2, Fig. 9.7). For the remaining species, no significant difference in LWR could be detected between treatments (Table 9.2, Fig. 9.7). Low water availability decreased allocation of biomass to support tissues (SWR) in *Ipomoea* and *Stachytarpheta* ($t \geq 3.6$, $P \leq 0.004$), whereas no treatment effect ($t \leq 0.8$, $P \geq 0.48$) could be detected in *Solanum* and *Vismia* (Table 9.2, Fig. 9.7).

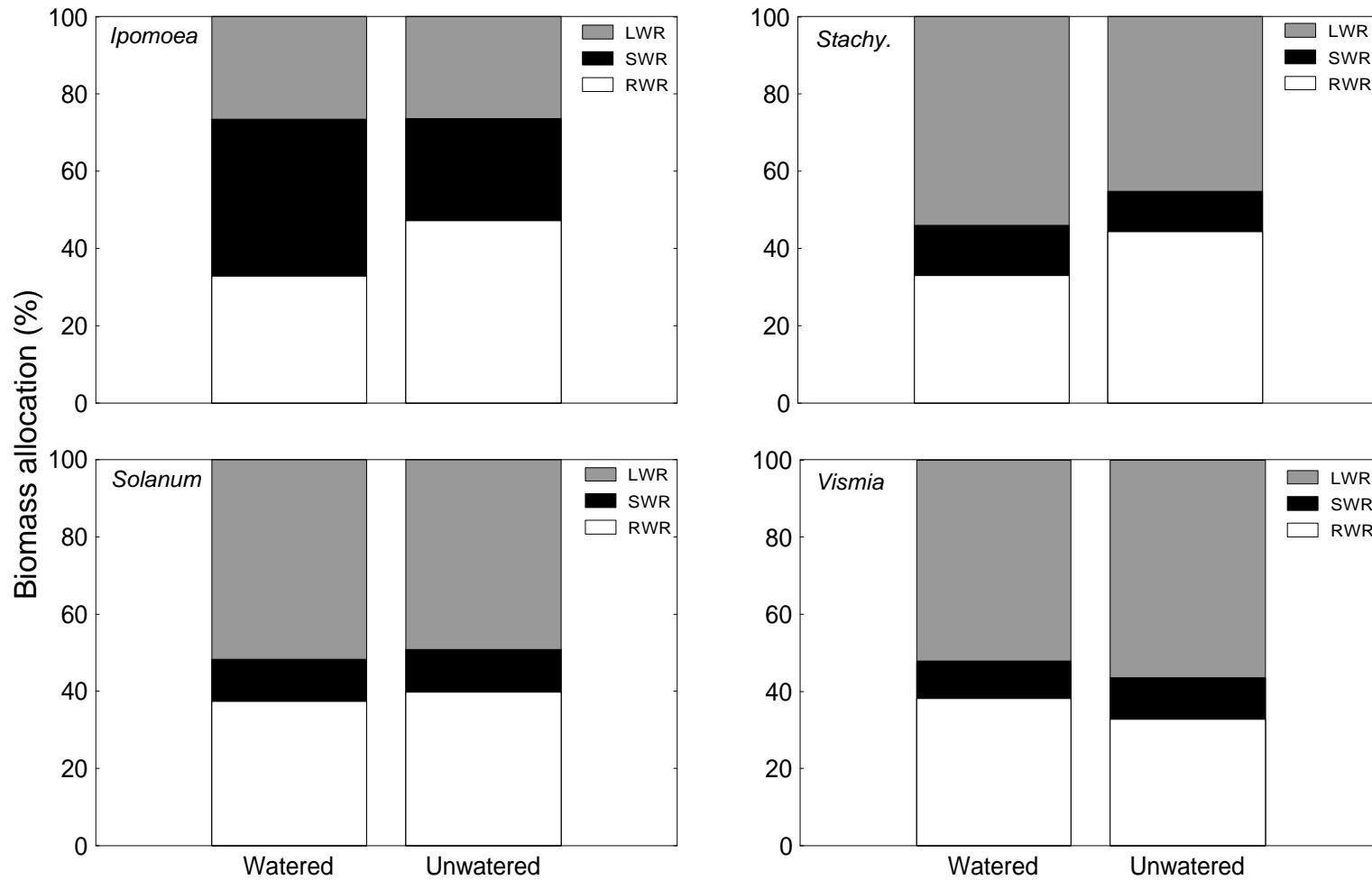


Figure 9.7. Mean proportion of biomass allocated to roots (RWR), stems (SWR) and leaves (LWR) as a function of watering regime in four Amazonian species.

Water limitation significantly decreased plant leafiness, i.e., leaf area per unit weight of whole plant (LAR) in *Stachytarpheta*, *Solanum* and *Vismia* (Table 9.3). However, no significant difference in LAR could be detected for *Ipomoea* (Table 9.3). In all the four species studied, specific leaf area (SLA) was significantly lower in unwatered soil (Table 9.3).

Table 9.3. Leaf area ratio (LAR = leaf area per total plant dry weight, cm² g⁻¹) and specific leaf area (SLA = leaf area per leaf dry weight, cm² mg⁻¹) of well-watered and water-limited plants. Values are means (\pm s.d.), n= 7 for *Ipomoea*, *Stachytarpheta* and *Solanum*, and n= 3 for *Vismia*. For each species, means within columns are significantly different at the $P = 0.05$ level (*), at the $P = 0.01$ level (**), or at the $P = 0.001$ level (***), in the paired t -test.

Watering regime	LAR	SLA
<i>Ipomoea</i>		
Watered	101.6 (18.3)	0.384 (0.043) *
Unwatered	89.7 (11.6)	0.342 (0.010) *
<i>Stachytarpheta</i>		
Watered	148.3 (16.9) ***	0.275 (0.027) **
Unwatered	105.8 (4.5) ***	0.234 (0.010) **
<i>Solanum</i>		
Watered	171.8 (3.4) ***	0.333 (0.020) ***
Unwatered	99.6 (18.1) ***	0.202 (0.019) ***
<i>Vismia</i>		
Watered	171.8 (3.5) **	0.448 (0.047) *
Unwatered	99.6 (18.1) **	0.331 (0.040) *

Discussion

The present results showed that some patterns of root and shoot growth were significantly affected by drying soil in these species. A reduction in shoot growth relative to root growth is a common response to soil drying (Kramer 1983). Thus, plants exposed to drought stress usually show an enhanced allocation to roots (i.e., increase in root weight ratio, RWR) (e.g., Dale & Causton 1992) and, as a consequence, an increase in their root to shoot ratios (e.g., Hoogenboom et al. 1986, Khalil & Grace 1992, Motzo et al. 1993, Nash & Graves 1993, Wan et al. 1993, Weerathaworn et al. 1992). Of the four species studied, only *Vismia* did not show a tendency to increase its root/shoot ratio and RWR in response to soil drying (Figs. 9.1 and 9.7, Table 9.2). It is possible that the relatively low growth rate of this species at the early stages of seedling development, also observed in another experiment (see Chapter 5), may have in part limited its capability to efficiently adjust to soil drying by promoting a rapid shift in biomass allocation to roots. In the present investigation, the ability of the studied species to increase RWR in response to soil drying was in fact positively related to their known growth rate at early stages of seedling development (see Chapters 4, 5 and 6 for growth rate comparisons) and also to their seed mass (see Chapter 1). This finding is consistent with the view that fast-growing species and (or) species with comparatively larger seeds generally have a higher degree of plasticity in root morphology (e.g., Baker 1972, Evans & Etherington 1991, Lambers & Poorter 1992) and as such have the capacity to respond relatively faster to drought.

The significantly higher specific leaf area (SLA) in the well-watered plants of all species (Table 9.3) is consistent with the results of Jones et al.

(1980), Khalil & Grace (1992), Retuerto & Woodward (1993) and Van Loo (1992) who found that water deficit reduces SLA. Also, the reduction in the leaf area ratio (LAR) in response to soil drying observed in the present study (Table 9.3) is a common response reported in the literature for water stressed plants (e.g., Khalil & Grace 1992, Retuerto & Woodward 1993).

By significantly increasing RWR and (or) decreasing SLA and LAR in response to reduced water supply, all four species revealed the ability to optimize water use in situations when low soil water potential would be concurrent with high evaporative demand. However, among the species studied, *Stachytarpheta* was apparently more efficient in significantly adjusting all of the above traits in response to drought (Fig. 9.7, Tables 9.2 and 9.3).

Results from other studies on the effect of soil drying on rooting depth are variable. Some report an increase (e.g., Box et al. 1989 for wheat, Hoogenboom et al. 1986 for soybean, Leidi & Gutierrez 1993 for cotton seedlings, and Sharp & Davies 1985, for corn) or, depending on the species, either an increase, a decrease, or no significant effect of soil drying on root depth (Evans & Etherington 1991, Reader et al. 1993). In the present study, no significant increase in rooting depth in response to soil drying could be detected for any of the species studied (Fig. 9.2). However, although not statistically significant ($P= 0.08$), the mean maximum rooting depth of water-limited *Stachytarpheta* was 12 % higher than that of well-watered plants (Fig. 9.2). Also, depth of root penetration was not significantly reduced in any of the species in unwatered soil. Because of the vulnerability of the surface soil to drying, the ability to

sustain root growth in drying soil that was observed in all the studied species would be of great importance for promoting seedling establishment of these species in natural conditions.

Although water content of the growth medium was not monitored in this experiment, it could be observed during root sampling at the end of the experiment that moisture content in the unwatered soil was, as expected, less at the top layers and increased with depth, while in watered soil, moisture was distributed more uniformly. All of the four species studied were capable of altering their root distribution profile to take advantage of this soil moisture availability pattern. In general, root dry matter accumulation was maximized at the upper layers in the watered soil and at deeper layers in the unwatered soil (Figs. 9.3 to 9.6). Similar patterns of redistribution of root growth in response to drying soil have also been observed in corn (Sharp and Davies 1985), sycamore seedlings (Khalil & Grace 1992) and peanut (Meisner & Karnok 1992). Interestingly, in unwatered *Stachytarpheta* the relative root dry weight density was similar between the 0-10 and the 10-20 cm layers (Fig. 9.4). However, during root sampling, in unwatered columns unlike in watered conditions roots in the 0-10 cm soil layer had a much higher proportion of suberized biomass than in the subsequent layers (data not shown). This increase in root suberization at the shallowest (driest) soil layer, as suggested elsewhere (see Nobel & Sanderson 1984), could probably reflect a mechanism to prevent water movement from the roots to the dry soil.

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MOWING EFFECTS ON THE FECUNDITY OF *STACHYTARPHETA CAYENNENSIS*

Introduction

In tropical agricultural areas, recruitment of weed species through the establishment of seedlings is important (e.g., Staver 1991). The process of recruitment of new individuals from seed requires a sequence of steps in order to be successful. These steps include seed production, dispersal, germination, seedling establishment and growth. In this context, production of seeds is a critical phase that, especially for a species lacking vegetative reproduction, will determine to a great extent how successful the recruitment of new individuals will be.

Stachytarpheta cayennensis (Rich) Vahl. is an erect Verbenaceae shrub recognized as an important perennial weedy species of pastures and crop areas in Brazil and, in particular, in Brazilian Amazonia (Dias Filho 1990, Lorenzi 1991). Reproduction in *Stachytarpheta* occurs only sexually through seeds that are produced generally in pairs inside a dry fruit that develops in cavities along erect spikes (Fig. 10.1). Although native to tropical America, this species also occurs as a weed in Australia (Kleinschmidt & Johnson 1987, McFadyen 1984), Hawaii (Haselwood & Motter 1983) and India (Nair et al. 1982).

A common weed management practice usually conducted in pastures invaded by *Stachytarpheta* and related weed species in Brazilian

Amazonia is the mechanical or manual mowing of the area by the beginning of the rainy season, when most weed species have just started their reproductive phase. This initial mowing is usually complemented by another by the end of the rainy season (i.e., three to five months later) (see Dias Filho 1990). Even though most perennial weed species are known to withstand this mowing management (Dias Filho 1990), it is believed that, compared to unmowed plants, the fecundity of mowed weeds can be decreased due to a reduced production of reproductive structures (e.g., inflorescence and seeds).

Although mowing is a common practice in the management systems of agricultural areas in Amazonia and other tropical areas, no published information is known to exist on the effects of defoliation on the fecundity of individual weed species. Such knowledge would help evaluating the biological and economic effectiveness of mowing in controlling these species and also determining how adapted they are to defoliation.

The objective of this study was to determine how a simulated mowing regime (a single defoliation at 12 cm from the soil surface, at the beginning of the species' reproductive phase) affects fecundity (i.e., the number and size of flowering spikes and the number of seeds) in the tropical weed *S. cayennensis*, grown under controlled environmental conditions.

Materials and methods

Plant material and growing conditions

Stachytarpheta cayennensis seeds were collected from plants growing in pasture areas 12 km from Paragominas, PA (3° 05' S - 47° 21' W) in

Eastern Brazilian Amazonia. Seeds were germinated on filter paper in petri dishes and then planted individually in 1750 ml plastic pots in a mixture of peat:vermiculite:perlite (1:1:1). Plants were grown in a greenhouse at temperatures of $24 \pm 2.2^{\circ}\text{C}$ (minimum) to $33 \pm 2.1^{\circ}\text{C}$ (maximum) and a maximum photosynthetic photon flux density (PPFD) of approximately $900 \mu\text{mol m}^{-2} \text{s}^{-1}$. Pots were watered every other day to field capacity and fertilized every two weeks with 30 ml of a water soluble fertilizer solution (15 % N, 30 % P_2O_5 , 15 % K_2O , 0.02 % B, 0.07 % Cu, 0.15 % Fe, 0.05 % Mn, 0.0005 % Mo and 0.06 % Zn; 3.5 g L^{-1}).

Treatments and sampling

Conventional mowing was simulated on *Stachytarpheta* plants by clipping the plants at 12 cm from the soil surface at the beginning of the reproductive stage, i.e., five to six weeks after germination. Mowed plants were compared to unmowed plants grown under the same conditions.

Number of primary branches off the main stem and flowering spikes (Fig. 10.1) were assessed for each plant every 20 days for 60 days, starting at 50 days after mowing. At the last evaluation date (i.e., 110 days after mowing), the number of seeds per spike and spike length were also recorded for all plants.

Experimental design and statistical analysis

Pots were arranged in the greenhouse in a completely randomized design with seven replicates. Each replicate was an individual pot planted with a single plant and placed at a particular location inside the greenhouse.

Differences between treatments in the number of spikes per plant and per branch through time were analyzed by analysis of variance with

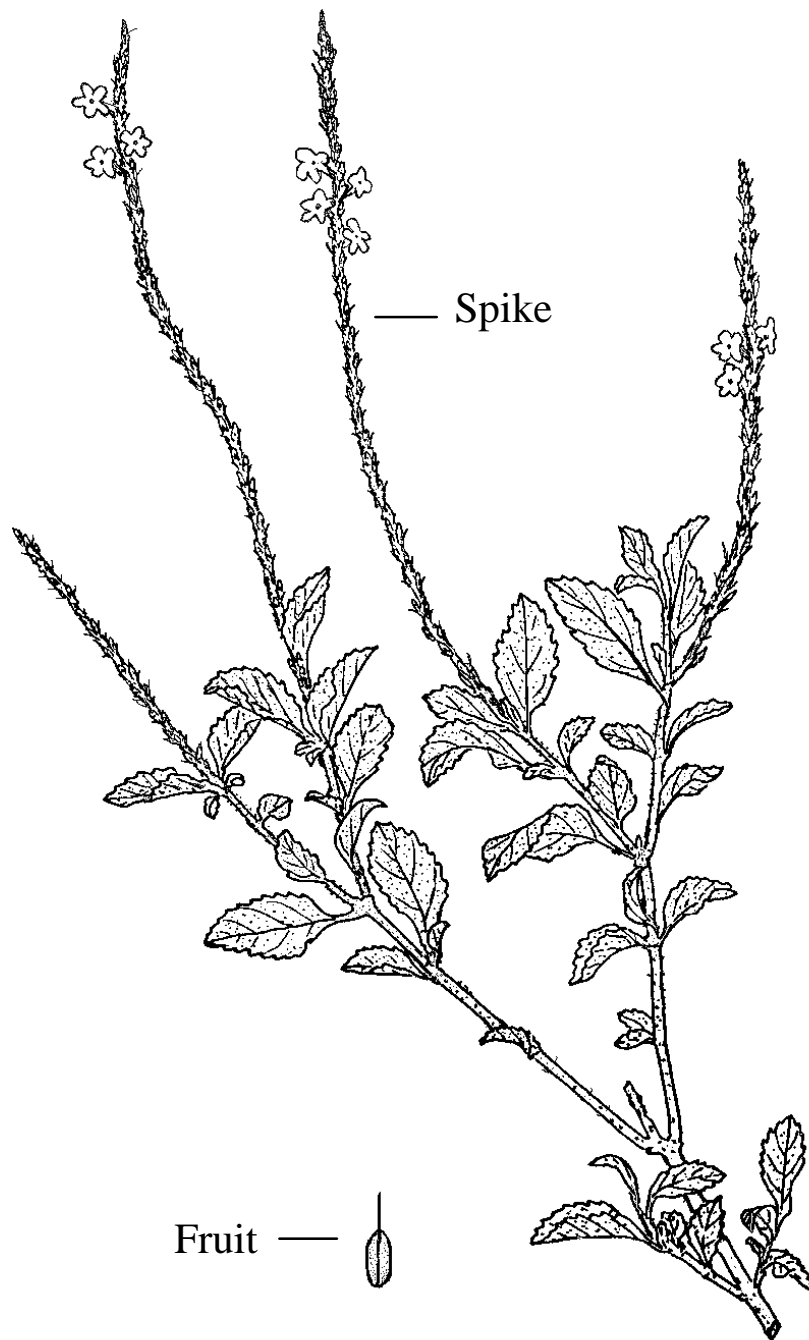


Figure 10.21. Detail of a branch (with flowering spikes) and a fruit of *Stachytarpheta cayennensis*.

repeated measures (see von Ende 1993). The within-subject or repeated measures effect was Time, and the between-subject main effect was Mowing intensity. Homoscedastic residuals, assessed by Box M test, were confirmed both for logarithmically transformed values of number of spikes per branch ($P= 0.1$) and untransformed values of number of spikes per plant ($P= 0.3$). No severe departures from the normality assumption were identified by examining half-normal probability plots of z-transformed within-cell correlations for both data. Compound symmetry of the covariance matrix of each analysis of variance was tested by the Mauchly's sphericity test. The Huynh-Feldt correction (see von Ende 1993) was considered for both analyses. Differences in the number of seeds and branches per plant were evaluated by Kruskal-Wallis ANOVA. Differences in the number of seeds per branch and per spike and in the mean spike length per plant were assessed by Mann-Whitney U test. The statistical package STATISTICA for Windows release 4.5 (STATISTICA for Windows 1994) was used for all computations of the data.

Results and discussion

The indicators of *Stachytarpheta* fecundity were differentially affected by mowing. Mowing significantly increased the number of spikes per branch (Table 10.1, Fig. 10.2) and the number of seeds per branch and per spike (Mann-Whitney U Test, $P= 0.001$, for both variables) (data not shown).

The number of primary branches per plant was 45 % lower (Kruskal-Wallis ANOVA, $H= 10.4$, $P= 0.001$) in mowed plants, and did not change from day 50 to 110 after mowing (data not shown). Mean spike length per plant was slightly higher for mowed plants (17.3 cm vs. 16.6 cm),

however, this difference was only marginally significant (Mann-Whitney U test, $P= 0.06$). No significant effect of mowing could be detected on the number of spikes per branch (ANOVA, $F_{1,12}= 1.96$, $P= 0.19$). However, a tendency for a lower number of spikes in mowed plants was observed throughout the evaluation period (Fig. 10.3).

Table 10.1. Analysis of variance of number of spike per branch with repeated measurement on time. Treatment (mowed and unmowed) is the fixed main effect.

Sources	df	MS	F	<i>P</i>	H-F
<i>Between-subjects</i>					
Treatment (Tr.)	1	48.1	5.7	0.03	----
Error	12	8.43			
<i>Within subjects</i>					
Time (T)	3	3.58	45.7	----	< 0.001
T × Tr.	3	0.36	4.6	----	0.008
Error	36	0.078			

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

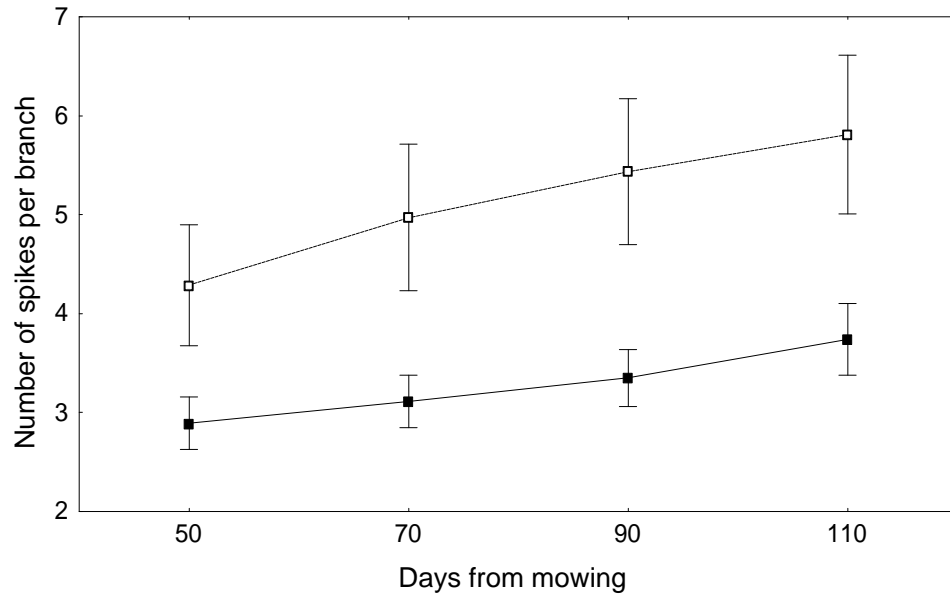


Figure 10.2. Change over time in the number of flowering spikes per plant (mean \pm s.e., $n=7$) for two mowing intensities: mowed (open squares) and unmowed (closed squares).

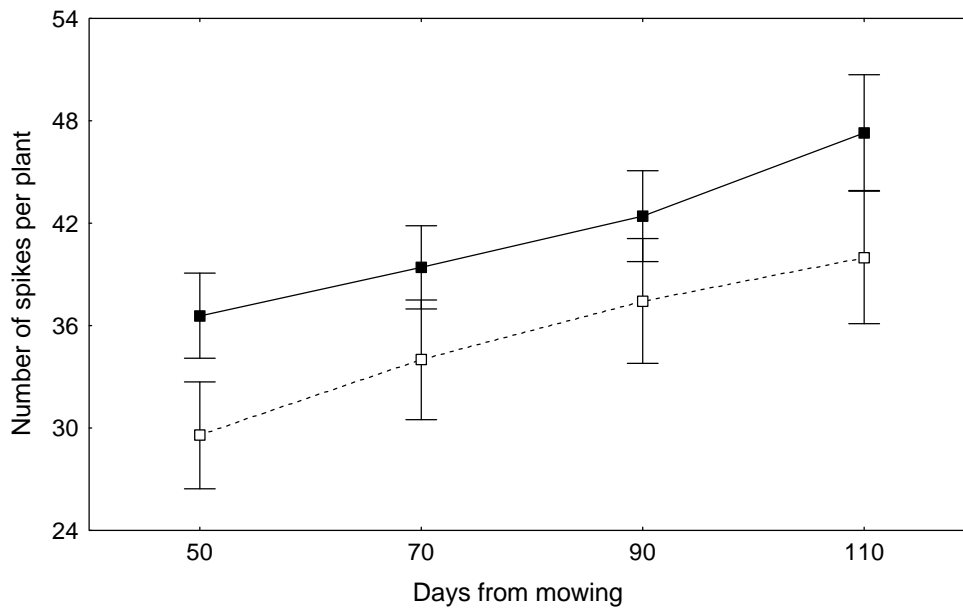


Figure 10.3. Change over time in the number of flowering spikes per plant (mean \pm s.e., $n=7$) for two mowing intensities: mowed (open squares) and unmowed (closed squares).

The total number of seeds per plant was not affected significantly by mowing (Kruskal-Wallis ANOVA, $H= 0.04$, $P= 0.85$), however, seed number in mowed plants had a tendency to be higher than in unmowed ones (Fig. 10.4). So, although mowing significantly increased the number of spikes per plant and the number of seeds per branch and per spike, seed number per plant was not significantly affected. This response was a consequence of the negative effect mowing had on the number of branches per plant.

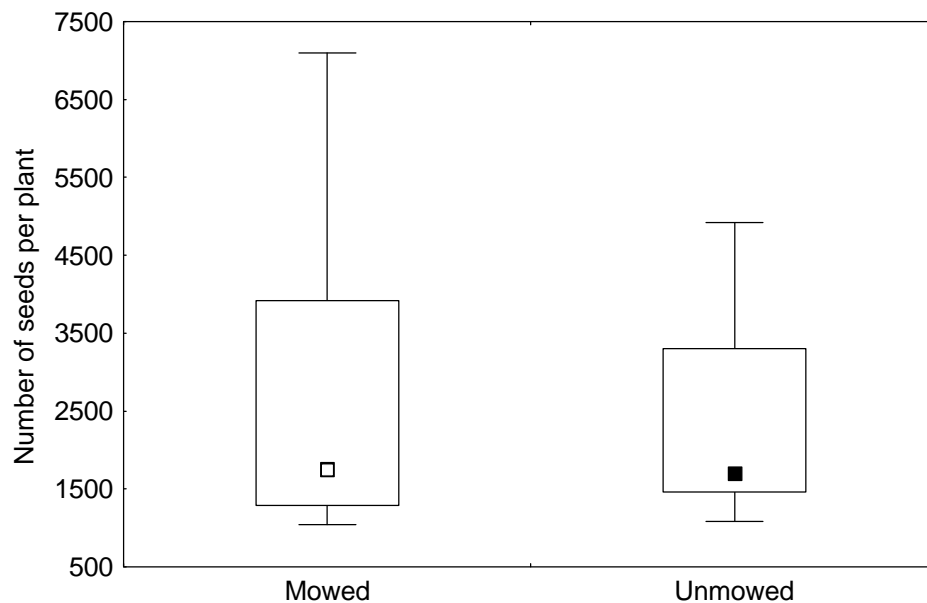


Figure 10.4. Box plot of the number of seeds per plant for two mowing intensities. For each box plot the middle point is the median, the box represents the quartiles (25th and 75th percentiles), and the whisker is the range (minimum and maximum values).

Other studies have reported inconsistent results on the effects of defoliation (i.e., mowing and grazing) on the reproductive output of plant species. In the legume shrub *Stylosanthes hamata*, a single heavy grazing followed by mowing (Wilaipon & Humphreys 1976) or a defoliation to 13

cm (Fisher 1973) significantly increased seed yield. Also, grazing increased seed yield in *Trifolium subterraneum* (Steiner & Grabe 1986). Conversely, in the grasses *Bouteloua gracilis* (Coffin & Lauenroth 1992) and *Panicum virgatum* (George et al. 1990) and in the legume *Aeschynomene americana* (Chaparro et al. 1991), grazing significantly reduced seed production.

These contrasting results may be explained both by the distinctive response to defoliation of individual species and also by the particular intensity and frequency of defoliation used. So, although a single and not intense defoliation may increase reproductive output by removing apical dominance, and, thus, by providing more sites for the development of reproductive structures, a more frequent and intense defoliation regime could also be capable of contributing to the reduction of the available carbon and energy for the development of reproductive structures. For example, although in the study of Wilaipon & Humphreys (1976) seed yield of *S. hamata* was increased by a single defoliation, in the same study intermittent grazing and mowing decreased seed yield of that species. In the present study the defoliation regime was relatively not severe, and simulated a common management observed in pastures areas in Brazilian Amazonia (Dias Filho 1990): a single manual or mechanical mowing of *Stachytarpheta*, at the beginning of its reproductive phase, followed by at least a four-month period without mowing. The results suggested that fecundity in *Stachytarpheta* under this regime is not ultimately affected, because mowed plants had the ability to compensate for a significant reduction in the number of branches, caused by defoliation, by increasing the number of spikes and seeds per branch. This compensatory

development of reproductive structures allowed mowed *Stachytarpheta* to maintain seed output to a level similar to that of unmowed plants.

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SUMMARY AND PRACTICAL IMPLICATIONS

The need for data with which to help predict the potential of occurrence and possible range extension (or contraction) of weedy species in Brazilian Amazonia was the major motivation for the research work conducted for this thesis. The research contributed to these objectives by providing one of the first in-depth investigations of the ecophysiological responses of four important wild weedy plants from Brazilian Amazonia to an array of environmental conditions. A summary of the major results from the present research, together with their practical implications for active or abandoned agricultural areas in Amazonia, is presented below.

Seed ecology

Results from “exploratory” trials on the seed biology of the species studied are summarized in Table 11.1. Also, some seed ecology attributes summarized from the findings of Chapters 2 and 3 are presented in Table 11.2. These results revealed a unique feature of *Ipomoea* seeds. Seeds of this species are divided into two groups, one (the greatest proportion of seeds) possessing a strong innate dormancy (hard seededness), another possessing an opportunistic germination behavior (i.e., capable of germinating within 10 to 24 h of continuous exposure to “ideal” conditions). This opportunistic germination behavior, together with the findings that germination in this species is not inhibited by darkness and that *Ipomoea* is capable of emerging from relatively great depths (Table

11.2, Chapter 2) are of significance to the research questions being addressed in this dissertation (see page 8).

Table 11.1. Some seed characteristics of the species studied.

Species	Time to first germination ¹	Time to maximum germination ²	Hard seededness ³
<i>Ipomoea</i>	10-24 h	5 d	Yes
<i>Stachytarpheta</i>	3-5 d	14 d	No
<i>Solanum</i>	12-17 d	25-40 d	Yes
<i>Vismia</i>	8-10 d	20 d	No

¹Time to first germination of untreated (not scarified) seeds.

²Time required for more than 50 % germination in a lot of untreated seeds under continuous “ideal” conditions.

³Determined by acid scarification.

Table 11.2. Summary of seed germination or emergence response of the species studied to selected environmental variables¹.

Species	Light	Water stress	Nitrate	Planting depth
<i>Ipomoea</i>	×	--	-	×
<i>Stachytarpheta</i>	+++	-	+ (Dark)	---
<i>Solanum</i>	+	---	+++	-
<i>Vismia</i>	++	-	- (Light)	--

¹Results summarized from Chapters 2 and 3. A “+” indicates a positive response, a “-” indicates a negative response, an “×” indicates no significant response. The number of signs indicates the intensity of the response.

The lack of dark-dormancy and the ability for hypocotyl extension (i.e., emergence from greater planting depths) in *Ipomoea* agrees with the knowledge that under natural conditions this species is prone to originate from areas protected from direct sunlight such as along fences, windrows and dead trunks or in sites covered by slash (Dias Filho 1990), making it more difficult to apply conventional control practices. Also, under natural conditions, the observed opportunistic germination behavior of this species could potentially promote its germination at the earliest possible time after sporadic rainfall events at the beginning of the rainy season, conferring on *Ipomoea* a possible competitive advantage over other later germinating species. Although it could be argued that such early germination is deleterious, by prematurely exposing seedlings to dry spells, the large seedlings that emerge from the large *Ipomoea* appear to tolerate many of the stresses encountered in early development. Early development of *Ipomoea* would be improved in relation to other, smaller-seeded, plants as the stored seed energy reserves could sustain the seedling longer, until the photosynthetic capacity could be developed, and could also promote faster initial seedling development.

As seed production in *Ipomoea* is known to occur throughout the year (Dias Filho 1990), the higher proportion of seeds with coat imposed dormancy in this species could be viewed as an adaptive mechanism to increase the probabilities of successful seedling recruitment by preventing germination of the majority of seeds during conditions unfavorable to growth, such as aseasonal rain events during the dry season. These characteristics have to be taken into consideration in developing a control strategy or in evaluating the invasive potential of this species.

Among the other species studied, only *Solanum* showed a strong innate seed dormancy (Table 11.1). However, unlike *Ipomoea*, all *Solanum* seeds had this attribute, and acid-scarified seeds germinated only after seven to eight days following scarification instead of less than one day as observed in *Ipomoea*.

The “delayed” germination behavior of *Solanum* together with the presence of hard-seededness (Table 11.1) could be viewed as adaptations to prevent seed germination inside the digestive systems of animals and also to prevent seeds from germinating too early at the beginning of the wet season. The observed germination response of *Solanum* to water stress (Chapter 3) reinforces the view that this species is “protected” from germinating when soil moisture conditions are not adequate.

Like *Solanum*, *Vismia* seeds also had a relatively “delayed” germination (Table 11.1) that could also be viewed as an adaptation to animal dispersal and to seedling recruitment in sites with unpredictable rainfall regimes.

A potential restriction to the invasive potential of *Ipomoea* is the lack of a special seed dispersal mechanism (besides rain water and involuntary transportation by man [Dias Filho 1990]), which is not offset by increased seed longevity in the soil (see Chapter 2). So, besides lacking the ability to efficiently invade new areas, this species also seems to lack the capacity to reinfest previously invaded areas through recruitment from a soil seed bank. These features suggest that eradication of this species is possible in a relatively short time, provided seed production of established plants could be prevented (by periodic mowing, for example) and emerging seedlings controlled.

Contrary to *Ipomoea*, *Stachytarpheta* had a comparatively remarkable ability to retain seed viability in the soil. This suggests that once allowed to produce seeds in a certain area, eradication of this species could be difficult. However, long term experiments (e.g., > 2 yr) are necessary to confirm this.

A negative relationship was observed between the measured mean time to first germination (Table 11.1) and seed mass (Table 1.1) of the species studied. This characteristic could be viewed as a mechanism by which germination of the smaller seeds (with relatively less energy reserves for seedling development) is delayed until “ideal” environmental conditions have been maintained for a relatively long period of time. In a seasonal environment like eastern Brazilian Amazonia, this germination characteristic could be of great survival value for seedlings with a slow development rate.

Results from Chapter 3 (see also Table 11.2) demonstrated that seeds of both *Vismia* and *Solanum* seem to respond to a wide range of environmental conditions known to occur in disturbed areas in eastern Brazilian Amazonia. Both species were able to germinate in the dark, and the nitrate ion significantly stimulated germination of *Solanum* under both light and dark environments, although a moderate negative effect of this ion could be detected in germination of *Vismia* in the light. Seed germination in *Vismia* was very insensitive to water stress and emerged better at the soil surface, while *Solanum* was less tolerant of decreasing osmotic potentials and emerged better at depths of up to 4 cm than at the soil surface. The findings that these two successional species were able to germinate in the dark and that nitrate significantly stimulated dark

germination of *Solanum* contrast with that of Uhl & Clark (1983) who reported an absolute light requirement (and no nitrate effect) for the germination of a group of successional species from Venezuelan Amazonia, including one species from the genus *Vismia* and one from *Solanum*.

Since *Solanum* fruits are known to be consumed by grazing ruminants, the ability of this species to germinate in the dark and its great plasticity for hypocotyl extension could be viewed as having a considerable survival value for seeds dispersed by these animals, probably aiding in seedling emergence from within dung pats. In addition, as the survival of seeds through the digestive tract and in the dung of ruminants is related to the presence of hard seed coats (Gardener et al. 1993a, 1993b), and germination of weed species with a strong hard-seededness can actually be improved by ruminant digestion (Gardener et al. 1993a), the presence of hard-seededness in *Solanum* (Table 11.1) may be a characteristic that aids dispersal by grazing ruminants. These characteristics could have great practical implications for the spread of this species into active pasture areas.

Vismia had a greater ability than *Solanum* to establish when seeds were at the soil surface, and to germinate at lower osmotic potentials (Table 11.2, Chapter 3). These characteristics suggest that this species is more prone to invade bare soils spots in overgrazed pastures or in abandoned agricultural areas in Brazilian Amazonia than *Solanum*. In these environments, soil moisture stress is known to be relatively severe (see Nepstad 1989) and thus could restrict germination of *Solanum* more than that of *Vismia*. However, in these areas, *Solanum* seed at the soil

surface could find appropriate microhabitats for germination and emergence along nurse logs and beneath slash. In addition, since seeds of these species are known to be dispersed mainly by bats (Dias Filho 1990), and as a consequence, are likely to be deposited into new areas mostly at the soil surface, it could be hypothesized that recruitment directly from the seed rain (i.e., recently dispersed seeds) may be of a greater significance for *Vismia*, while recruitment from the soil seed bank would be more important for *Solanum*. The presence of hard-seededness and the ability to emerge from greater depths observed in *Solanum* seeds could further reinforce this hypothesis.

The capacity of *Solanum* seed to respond positively to nitrate could help increase the competitive ability of this species in agricultural areas by synchronizing germination at periods when conditions for establishment would likely be most favorable, such as at the end of a drying cycle of the soil (e.g., at the beginning of the rainy season or after the recurrence of rains following a short dry spell) or after soil cultivation. During these events, the concentration of nitrate ions in the soil solution is known to increase due to the changing activity of soil microorganisms. Also, the use of fertilizers containing nitrate could stimulate recruitment of this species into agricultural areas.

The longevity observed in buried *Solanum* seed (Fig. 3.4) indicates that this species can build up in the soil seed bank (i.e., capable of dispersing in time), and that soil cultivation may actually enhance its persistence in agricultural environments by promoting seed burial. On the other hand, the rapid decline observed in the viability of seed at the soil surface (Fig. 3.4) suggests that a fallow period may be successful as a

control technique for *Solanum*. The results from Chapter 3 also suggest that in areas with a longer wet season *Solanum* seed population, at the soil surface may undergo a sharper decline than in areas with a marked and longer dry season.

Seedling morphology and ecophysiology

The ability of invading plant species to modify their patterns of development appropriately in response to changes in the light environment can be a major factor in their adaptation to agricultural habitats like tropical pastures. In these environments, weed seedlings may have to start their development under conditions of permanent shade or, sometime during their development, be shaded by fast growing tropical grasses or other pasture weeds.

It has been demonstrated that, for tropical tree seedlings, the magnitude of responses in growth and leaf adjustment can vary considerably among species with differential tolerances to shade (Thompson et al. 1992). Results from Chapter 4 showed that both *Stachytarpheta* and *Ipomoea* expressed comparable responses in growth and leaf adjustments to low light (Table 4.1, Fig. 4.3), suggesting a similar ability for dealing with this low resource condition. These characteristics together with the light compensation point derived for each species (Table 4.4) might be indicative of a similar capacity of *Stachytarpheta* and *Ipomoea* to tolerate shade quite well.

Important effects of the light environment on the structure of *Ipomoea* were also found (Chapter 4; Table 4.1, Figs. 4.1 and 4.2). These effects may either increase or decrease the competitive ability of these species in an agricultural environment. For example, high-light *Ipomoea*

produced twice as much stem as low-light plants ($t= 3.5$, $P= 0.002$). Because under natural conditions stem nodes from this species can root when in contact with the soil, and if separated from the plant, survive as independent plants (Dias Filho 1990), high-light *Ipomoea* could have a competitive advantage over plants grown under low light. Multiple stems in high-light grown *Ipomoea* can also be advantageous in competitive situations by occupying of larger spaces.

The light environment may also play an important role in determining the competitive ability of *Stachytarpheta*, by shortening the time required for the onset of flowering and increasing the relative amount of biomass allocated to reproductive structures in unshaded plants relative to shaded ones (Fig. 4.2). Because *Stachytarpheta* is only capable of reproducing by seed, not vegetatively, the light environment may directly affect this weed's infestation potential. Also, as low-light grown *Ipomoea* and *Stachytarpheta* plants allocated a higher proportion of their biomass to leaf area or mass and a smaller proportion to roots than did high-light plants, plants developed under shade may be relatively more vulnerable to edaphic stress factors, such as drought or low nutrient availability. Conversely, a preferential allocation to roots may further give a competitive advantage to plants developed under full sunlight by enhancing survivorship and promoting resprouting following mowing, fire or herbivory.

An important result of Chapter 4 was that, irrespective of light environment during growth, leaf nitrogen content and CO₂ assimilation were inversely related to the allocation of biomass to reproductive structures in *Stachytarpheta*. Based on this, it could be hypothesized that

this species might be more vulnerable to stresses like mowing or fire at the initial stages of flowering because of a reduced vigor as expressed by lower carbon gains, which could, in turn, restrict its resprouting ability. Under natural conditions this limitation could be further enhanced because plants in the field, unlike the ones in the present study, could experience more limiting edaphic conditions. Such information might also have important practical implications for planning the most appropriate time for the control of this species.

If we regard relative growth rate at early stages of seedling development as an indication of establishment potential and competitive ability, *Ipomoea* seedlings could be considered more competitive than *Stachytarpheta*, at least in the short term, under both high and low light environments (Fig. 4.3). Also, the much larger initial seedling size of the large-seeded *Ipomoea* may make this species less dependent on high-resource levels and rapid growth rates for early seedling survival. Moreover, both species had their growth potential much reduced in low light (Fig. 4.3). Seedling size in *Ipomoea* could also be seen as a potential advantage to deal with low-resources such as reduced light, by enhancing the chances of a successful establishment of this species under such conditions. Furthermore, the growth form of each species, a fast growing herbaceous vine (*Ipomoea*) and a relatively slow growing shrub (*Stachytarpheta*), could also be regarded as an indication of the better adaptation of *Ipomoea* to cope with a low-light environment during establishment by facilitating the light seeking capacity of this species. Finally, the above observations are further corroborated by the fact that germination in *Ipomoea* is not affected by light, unlike that in

Stachytarpheta, which has photoblastic seeds (Table 11.2, Chapter 2). Hence, the germination syndrome in *Ipomoea* seems to be indicative of a better adaptation of seedlings to start development under low light conditions, while the opposite could be inferred for *Stachytarpheta*.

Results from Chapter 5 indicated that the light environment has important effects on biomass distribution and growth of *Vismia*. As high-light plants allocated significantly more biomass to roots (Table 5.1) and had a higher relative growth rate than low-light plants (Fig. 5.2), *Vismia* was very responsive to the light resource and would be able to take advantage of the light environment normally found in forest margins, gaps and overgrazed pasture areas in Brazilian Amazonia. Based on these results it appears that plants developed under full sunlight may have an enhanced survivorship in active pasture areas, as a preferential allocation to roots would facilitate resprouting following death of above ground tissue caused by mowing, fire or livestock trampling. Also, as high-light grown *Vismia* allocated a smaller proportion of its biomass to leaf area and a larger proportion to roots than did low-light plants, it could be hypothesized that plants developed under shade may be relatively more vulnerable to edaphic stress factors, such as drought or low nutrient availability due to a comparatively greater transpirational area and a reduced potential for soil nutrient and moisture capture. Moreover, because *Vismia* is known to be capable of vegetative reproduction from root sprouts (Dias Filho 1990), low-light conditions may reduce its invasive potential by significantly decreasing the amount of biomass allocated to root tissue.

The photosynthetic data in response to growth under low or high light show that, at least in the short term, low-light grown *Vismia* is capable of satisfactorily responding to increasing irradiance levels. This suggests that *Vismia* is capable of retaining its full photosynthetic capacity despite growth in shade. On the other hand, high-light grown plants may be to some extent impaired if there is a decrease in the irradiance environment.

In Chapter 6 it was shown that similarly to *Vismia*, *Solanum* has the ability to develop morphogenetic and growth adjustment responses that, in part, can offset loss of photoassimilate under low light and, as a consequence, maintain growth to satisfactory levels. However, a corollary of these adjustments to low light appears to be a higher investment in above ground tissues relative to roots, and such adjustments might render low-light *Solanum* more vulnerable to stresses that directly affect its above ground tissues such as fire, herbivory or mowing. On the other hand, a reduced allocation to roots may lessen this species' ability to cope with edaphic constraints like reduced soil water or nutrient availability.

Although *Solanum* seedlings seem to be shade-tolerant, being able to acclimate to low light, apparently this species would be more competitive in open (i.e., unshaded) areas due to an increased allocation to roots. This is further corroborated by the fact that this species is capable of generating new individuals through root sprouts (Dias Filho 1990).

Results from Chapter 7 suggested that, contrary to *Stachytarpheta*, *Ipomoea* 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 clear, however, whether under more

natural conditions, with 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, i.e. associated with moister areas, (Dias Filho 1990) suggests that this might also be the case. Conversely, *Ipomoea* 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 this weed's resprout ability. Based on its stomatal response to soil moisture, the use of herbicides that require open stomata for improved absorption would be less effective on *Ipomoea* under the above conditions.

Given the known moisture regime of pasture areas in Brazilian Amazonia (see Nepstad 1989), and the gas exchange response of *Stachytarpheta* in relation to soil moisture, this species if left uncontrolled appears to have the potential to become a more persistent and competitive weed than *Ipomoea* in areas dominated by large fluctuations in light and water availability.

An important goal of Chapter 8 was to assess possible physiological mechanisms that promote turgor maintenance and thus enable *Vismia* and *Solanum* plants to survive as invaders of drought prone habitats in eastern Brazilian Amazonia. As expected both species appear to be able to cope with drought quite well. However, the data in Chapter 8 suggested that these species have different mechanisms for accommodating limited soil water availability. The more negative osmotic potential (π), larger bulk tissue elastic modulus (ϵ) and higher intrinsic water-use efficiency (A/g) measured in *Vismia* (Table 8.1, Figs. 8.1 and 8.4) may indicate that this

species is relatively more drought tolerant than *Solanum*, having the ability to maintain turgor down to lower values of tissue water potential. However, with more elastic tissue properties and a moderate decrease in the osmotic potential as tissue water content decreases (Fig. 8.1, Table 8.1), *Solanum* may be more competitive for soil water than *Vismia*. At the same time, it may be that because of its ability to sustain growth under limited soil water *Solanum* could also be potentially more susceptible to drought damage, if this less conservative stomatal behavior could not be balanced by an adequate water uptake from the soil. This may in part explain the low drought tolerance attributed to *Solanum* by Nepstad (1989) based on high seedling mortality in transplant experiments in eastern Brazilian Amazonia. However, seedling transplants usually do not quickly develop an extensive rooting system, when compared to untransplanted seedlings in the field (M. B. Dias Filho, unpublished observation). In fact, root growth and development characteristics in response to soil drying (Chapter 9) suggest that this species may be able to partially compensate for its less conservative stomatal behavior. Because A/g , π and ϵ are lower in *Solanum*, this species may be better at coping with short-term water stress, and hence can be classified as a superior “stress-tolerator,” while *Vismia* seems better able to cope with chronic, long-term water stress and hence can be thought of as a superior “stress-avoider” or a generalist species with respect to water stress. This species-level of classification is an extension of the ideas of Dawson & Ehleringer (1993), but for the special case of tropical disturbed habitats.

In Chapter 9 it was demonstrated that all four species studied showed to some extent morphological acclimation to soil drying. They were able to maintain root growth and also to alter the root distribution

profile in response to drying soil. Only *Vismia* did not show a significant shift in biomass allocation (greater partitioning into root tissue) in response to soil drying. However, despite its comparatively low plasticity, very small seedling size and shallow rooting depth, all water-limited *Vismia* seedlings were able to survive throughout the experimental period. Such behavior suggests the presence of very efficient traits that may improve this species' ability to adjust and to partially offset the damaging effects of soil drying. This agrees with the response of this species to soil water limitation discussed in Chapter 8.

The finding that in *Ipomoea* and *Solanum* seedlings, root growth, expressed as the relative dry matter distribution in the soil profile (Figs. 9.3 and 9.4), and maximum rooting depth (Fig. 9.2) were comparatively higher than for the other two species studied, was compatible with the previous knowledge that these species are relatively not very conservative in their use of water (see Chapters 7 and 8). A fast and vigorous root growth, as suggested by the data in Chapter 9, would allow seedlings of these species to compensate for that water use characteristic by being relatively better equipped to exploit and/or compete for soil water.

Stachytarpheta was particularly efficient in modifying its below and above ground biomass patterns (i.e., showing a great plasticity) in response to soil drying. Under natural conditions such ability could help reduce its transpirational demand relative to water absorption and thus improve this species' establishment capability in drying soil. This correlates with the observation that, in Brazilian Amazonia, *Stachytarpheta* is known to exploit seasonally dry, open habitats (Dias Filho 1990). Because *Stachytarpheta* is the only species studied that reproduces exclusively from

seeds (no vegetative reproduction), this species might be under greater selective pressures for traits that promote seedling survival in drought-prone environments (e.g., plasticity in root development) and as such would show a comparatively superior acclimation to soil drying. In other studies (e.g., Reader et al. 1993, Sydes & Grime 1984) a positive correlation between plasticity in root development and dependence on regeneration by seed has also been demonstrated.

In Chapter 10, the effect of a simulated mowing regime on the fecundity of *Stachytarpheta* was determined. The results obtained have important practical implications for the management of *Stachytarpheta* in agricultural areas and to the knowledge of the biology of this species. They suggested that a single mowing at the beginning of the reproductive phase would not contribute to the control of *Stachytarpheta*, as fecundity is not significantly reduced. In addition, it was shown in Chapter 10 that *Stachytarpheta* seems to be adapted to defoliation, being able to compensate for this stress by increasing the output of the remaining reproductive structures. Finally, it could be hypothesized that this species is capable of succeeding as a weed in areas under that particular mowing management system.

The results from the experiments described in this dissertation have identified ecophysiological characteristics which indicate that all four species studied are equipped with traits that can render them noxious weedy species in tropical regions. Moreover, based on the environmental and management conditions known to exist in cultivated pastures and certain crop areas in eastern Brazilian Amazonia, the potential of these species to become persistent weeds and to extend their ranges could be

tentatively classified in the following sequence: *Stachytarpheta* \geq *Vismia* > *Solanum* > *Ipomoea*.

The species' ecophysiological responses to environmental conditions, together with additional aspects of their biology identified in this research or previously known, should provide the basis for predicting their potential of occurrence and for planning ecologically sound weed management and control strategies of these and other species with similar characteristics.

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