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Original article

Biomass allocation and photosynthetic responses of lianas and pioneer tree seedlings to light

Tarin Toledo-Aceves*, Michael D. Swaine

School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK

ARTICLE INFO

Article history:

Received 18 October 2007

Accepted 21 March 2008

Published online 27 May 2008

Keywords:

Acclimation

Biomass allocation

Growth

Photosynthesis

Plasticity

Shade tolerance

Woody climber

ABSTRACT

Lianas are frequently considered as light demanding plants due to their proliferation in gaps and forest edges. Since lianas are exposed to a very heterogeneous light environment, they could be expected to express morphological and physiological plasticity in response to changes in the light environment, as high as that found in pioneer trees. We compared the biomass allocation and photosynthetic responses of seedlings of three species of lianas and two species of pioneer trees to increased light availability. Seedlings were transferred from medium ($4\text{--}5 \text{ mol m}^{-2} \text{ d}^{-1}$) to high irradiance ($12\text{--}15 \text{ mol m}^{-2} \text{ d}^{-1}$) in a controlled environment. In general the three liana species allocated fewer resources to the stem in comparison with the trees. The difference in the response between irradiance regimes was similar among the species, with no strong differences between trees and lianas probably due the early stage of the plants. With increase in irradiance plants accumulated more biomass, allocated more resources to the roots and less to the leaves, reduced the leaf area ratio (LAR) and specific leaf area (SLA). The photosynthetic rates recorded were not related to the rates of growth as measured by the increase in dry biomass (RGR_m). Regardless of the life form, plants under higher irradiance increased their light compensation point (L_{cp}) and attained light saturation (L_{sp}) at higher levels of irradiance, while the saturated photosynthetic rate (A_{max}) did not show a clear pattern, and dark respiration (R_d) and quantum yield (Q) were not affected by the transference. The understanding of liana and tree seedlings responses to the light environment may have important implications in the dynamics of tropical forest regeneration.

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1. Introduction

Lianas (woody climbers) are a conspicuous component of tropical forests (Gentry, 1991). They can represent about 30% of all woody stems in gaps after 4 years of gap succession (Uhl et al., 1988). Since their abundance is higher in gaps and in forest edges than in the forest understorey (Putz, 1984; Schnitzer and Carson, 2001), lianas are generally considered

gap-dependant pioneer species (Schnitzer and Bongers, 2002). However, there is a wide range of shade tolerance within the group (Sánchez and Valio, 2002).

Lianas are exposed to a very heterogeneous light environment, both spatially and temporally. At an early stage, many must maximize their carbon gain under the low light conditions of the forest understorey. Further growth will normally lead to higher irradiance, but because of their ability to grow

* Corresponding author. CONABIO, Bioinformatics, Avenida Liga Periférico-Insurgentes Sur 4903, 14010 México DF, Mexico. Tel.: +52 55 5004 4947; fax: +52 55 5004 4931.

E-mail address: t.tarin@lycos.com (T. Toledo-Aceves).

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doi:10.1016/j.actao.2008.03.003

laterally as well as vertically, they may achieve this more readily than trees. Species of highly variable environments are expected to display high plasticity (Bazzaz and Carlson, 1982), which represents an advantage related to the competitive ability of species (Lambers et al., 1998). There is evidence for lianas possessing a wide physiological plasticity (Carter and Teramura, 1988; Avalos and Mulkey, 1999; Sánchez and Valio, 2002). Comparing data from different studies, Castellanos (1991) reported that lianas have lower rates of net photosynthesis than trees and non-woody climbers. However, these results are difficult to compare because there are considerable procedural variations between studies, such as the type of measurements, habitat and growth conditions.

Seedling responses to light availability involve physiological and anatomical changes at the leaf and whole plant level (Strauss-Debenedetti and Bazzaz, 1996; Montgomery, 2004). Typically, plants grown in the shade have higher leaf area ratio (LAR), specific leaf area (SLA) and lower light compensation point (Lcp) and light saturation point (Lsp) than plants grown in high light. Other adaptive phenotypic responses to shading include maximization of the carbon gain through long leaf life spans and low respiration rates in low light (Mooney and Ehleringer, 1997; Lambers et al., 1998). In contrast, sun-grown plants possess traits conferring greater growth potential: greater net assimilation rate (NAR) and higher Lsp and Lcp than plants grown under low irradiance (Walters and Reich, 1996; Lambers et al., 1998; Veneklaas and Poorter, 1998). The ability to acclimate to a new condition can vary from trait to trait, so that phenotypic plasticity can be large for one trait and small for other traits (Lambers et al., 1998).

Most of the studies that analyze seedling response to the light environment have been focused on tree seedlings, while other life forms, such as climbers, have received little attention despite their ecological and economic importance. Lianas can play an important role in forest regeneration, especially in forest managed for timber extraction. After colonising gaps lianas can remain installed for several years, delaying or arresting the forest succession (Putz, 1991; Schnitzer and Bongers, 2002; Parren, 2003; Grauel and Putz, 2004). Their morphological and physiological responses to changes in the light environment are therefore of relevance for the management of forests.

The objective of this study was to compare the patterns of biomass allocation and photosynthetic responses of lianas and pioneer tree seedlings in response to changes in light availability. We hypothesized that since lianas are exposed to a very heterogeneous light environment, they are expected to display high morphological and physiological plasticity in response to the increase of light. To test these predictions, liana and tree seedlings were transferred from medium to high light in a controlled environment and their photosynthetic and morphological responses were measured. Plasticity is expressed as spatial and temporal responses to an environmental change. When the responses to changing conditions occur in an already expressed phenotype the adjustment is called acclimation (Avalos and Mulkey, 1999). In this study we considered acclimation as an indicator of the flexibility of the species to respond to the change in light availability and includes the changes following the production of new leaves and stems.

2. Methods

2.1. Study species

The lianas *Acacia kamerunensis* Gand. (Mimosaceae), *Loeseneriella rowlandii* N. Hallé (= *Hippocratea africana*) (Celastraceae) and *Afrobrunnichia erecta* (Asch.) Hutch. & Dalziel (Polygonaceae) and the light demanding trees *Swietenia* sp. (Meliaceae) and *Ceiba pentandra* (L.) Gaertn (Bombacaceae) were used. Species will be referred to from now on by their genus name. All species with the exception of *Swietenia* coexist in tropical forests in Ghana (Hall and Swaine, 1981). *Swietenia*, also known as true mahogany is in the same family as the *Khayas* of Africa, to which the genus is closely related. For *Swietenia*, the species was not determined but information from species of the same genus is used in some comparisons and the complete name is provided when it is the case. *Ceiba* is widespread in Ghana, but absent from wettest forests, and extending to the driest forests (Hall and Swaine, 1981). *Acacia* is widespread in Ghana except in the wettest and driest forest (i.e. rainfall between ca. 1200 and 1700 mm); *Loeseneriella* is widespread and rather like *Ceiba*, absent from wettest forests; *Afrobrunnichia* is less common, with a similar range to *Acacia* but extending into wettest forests (Hall and Swaine, 1981). *Swietenia macrophylla* is considered a mid-successional species, found in late secondary or primary vegetation (Marengo et al., 2001; Ramos and Grace, 1990). *Ceiba* is a pioneer species, requiring large gaps to establish (Hall and Swaine, 1981; Siepel et al., 2004). Both trees have important commercial value (Whitman et al., 1997). In Ghana, seedlings of *Acacia* can be found in the forest understorey but can grow rapidly only in forest gaps, *Loeseneriella* regenerates in shade and displays low rates of growth in forest gaps (Toledo-Aceves and Swaine, 2008a) and *Afrobrunnichia* is found inside and at edges of forest gaps (Hall and Swaine, 1981).

2.2. Experimental design

The experiment was conducted in a temperature-controlled greenhouse at University of Aberdeen (Scotland, UK). The photoperiod was 12 h for the first 6 months and increased to 14 h in the last 2 months to compensate for the reduction of natural light during the winter (mean temperature 20–22 °C, minimum temperature 17 °C). A high-pressure sodium lamp was used as supplement to the natural light for this purpose. Plants were grown from seed in polythene pots (15 cm diameter × 20 cm depth) and watered to maintain the soil at field capacity. Liana seedlings were supported with a stick.

At germination and during the first 3 months, all the plants were grown under 4–5 mol m⁻² d⁻¹, medium light (M) equivalent to approximately 10–15% of full daylight in Ghana (based on measurements taken with a data logger in 2003 and 2004). Twenty-five plants were grown per species. After 3 months ten plants were transferred to 12–15 mol m⁻² d⁻¹, high light (MH) equivalent to approximately 30–50% of full daylight, simulating the irradiance in large canopy gaps (Chazdon and Fetcher, 1984). The transference from M to MH simulates a canopy opening, reflecting the temporal heterogeneity in light availability that predominates in the forest. Another ten plants of each species were left growing under the initial

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