Industrial Crops and Products 34 (2011) 1235–1237

Contents lists available at ScienceDirect

Industrial Crops and Products

journal homepage: www.elsevier.com/locate/indcrop

Short communication

Shade delayed flowering and decreased photosynthesis, growth and yield of Sacha Inchi (*Plukenetia volubilis*) plants

Z.Q. Cai [*]

Laboratory of Tropical Plant Resource Science, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China

ARTICLE INFO

Article history:
Received 24 January 2011
Received in revised form 13 March 2011
Accepted 17 March 2011
Available online 17 April 2011

Keywords:
Flowering
Fruit
Growth
Photosynthesis
Plukenetia volubilis

ABSTRACT

We examined variation in the flowering phenology of Sacha Inchi (*Plukenetia volubilis*) plants monitored during an 8-month period with reference to a light gradient (20%, 52%, 75% and 100% of full sunlight), and related these results to photosynthetic features, growth and fruit yield. With strong phenotypically plastic response to light, relative growth rate and photosynthetic capability continually increased with increasing irradiance and their maximum values were much similar to those of the pioneer species. Shade did not increase the apparent quantum yield and reduce the light saturation point and respiration rate. Thus, it was suggested that *P. volubilis* is a high-light demanding species. Shade delayed initial flowering date and decreased flower and fruit parts. An earlier initiation of flowering was associated with higher flower biomass and plant total biomass, in turn; the latter was positively correlated with fruit biomass across light gradients. These results suggested that an optimized crop management practice should be adopted to ensure that *P. volubilis* be grown under conditions with minimal shading.

1. Introduction

Plukenetia volubilis, commonly known as Sacha Inchi, is an oilseed woody vine originated from Amazonian tropical rain forest and belonging to the Euphorbiaceae family. The seeds of Sacha Inchi have high protein (27–30%) and oil (40–60%) content (Hamaker et al., 1992; Cai et al., 2011) and have shown high economical value. Its oil is one of the richest plant sources of Omega fatty acids, essential for human life (Cai et al., 2011). *P. volubilis* plants flower about five months after being planted, blooming and fruiting throughout the growing season. The male flowers are small, white, and arranged in clusters. Two female flowers are located at the base of the racemose inflorescence. The fruits are capsules with 4–7 lobes with one seed per lobe. In tropical forests, *P. volubilis* regenerates in the shade of an overstory canopy, but for commercial production, it is normally cultivated on cleared land devoid of overhead shade. The objective of this study was to investigate variation in the flowering phenology of *P. volubilis* monitored over a long-term period (8 months) with reference to a light gradient, and relate these results to growth, fruit yield and photosynthetic traits.

2. Materials and methods

2.1. Plant materials

Seeds (1.13 g dry weight per seed) of *P. volubilis*, introduced from South America, were sown in Xishuangbanna Tropical Botanical Garden (21°56′N, 101°15′E, 600 m asl), Chinese Academy of Sciences in August 2009. When the seedlings were approximately 15 cm tall, uniform seedlings were selected and were grown in forest surface soil at intra- and inter-row spacing of 1.0 and 1.0 m, respectively, in shade houses. As a liana species, *P. volubilis* plants were supported by steel wires with a height of 1.8 m. Each of four irradiance treatments (20, 52, 75% sunlight, and open site) were created using layers of neutral-density screen on a steel frame. Five to six plants in each treatment were harvested and oven dried to determine the initial biomass at the beginning of the experiment (September 2009). At each light level, 5–7 plants were randomly selected and the date of first bloom was recorded for each plant. As the plants of the studied species grow very fast and some branches will reach out of the shade houses if the treatments lasted for a very long time, the focus was on plant acclimation responses to irradiance in the first growing season.

2.2. Leaf and whole-plant traits

At the end of the experiment (May 2010), gas exchange measurements were made on the uppermost, matured leaves using a

---

[*] Tel.: +86 6918715070; fax: +86 6918715070.
E-mail address: czq@xtbg.org.cn

0926-6690/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.indcrop.2011.03.021

Table 1
Days to initial flowering (DIF, d), leaf stomatal density and photosynthetic variables and whole-plant morphological traits in plants of *P. volubilis* along a light gradient.

RLI	DIF	SD_{ab}	SD_{ab}	A_{max}	AQE	R_d	LCP	LSP	SLA	LAR	Total biomass	RGR
20%	176b	315a	38.2a	16.7a	0.058a	0.62a	9.9a	291a	357.4c	158.4c	253.2a	17.0a
52%	179b	347ab	43.5a	17.2a	0.060a	0.71a	11.8a	306a	325b	122.3b	312.7a	17.8a
75%	155a	356ab	43.9a	21.0b	0.059a	0.91a	15.9a	382b	319.6ab	124.7b	702.9b	20.9b
100%	151a	373b	61.1b	23.7b	0.0057a	1.18a	21.0a	431c	233a	57.9a	934.3c	22.2b

Abbreviations: RLI, relative light intensity (%); SD_{ad}, stomatal density in in adaxial epidermis (no. mm^{-2}); SD_{ab}, stomatal density in in abaxial epidermis (no. mm^{-2}); A_{max}, light-saturated photosynthetic rate ($\mu mol\ m^{-2}\ s^{-1}$); AQE, apparent quantum efficiency; R_d, dark respiration rate ($\mu mol\ m^{-2}\ s^{-1}$); LCP, light compensation point ($\mu mol\ m^{-2}\ s^{-1}$); LSP, light saturation point ($\mu mol\ m^{-2}\ s^{-1}$); SLA, specific leaf area ($cm^2\ g^{-1}$); LAR, leaf area ratio ($cm^2\ g^{-1}$); RGR, relative growth rate ($mg\ g^{-1}\ d^{-1}$). Values of individual treatments are means of four to seven replications. Values within columns followed by the different letter are significantly different at the $P \leq 0.05$ level.

portable Li-6400XT photosynthesis system (Li-Cor, Lincoln, USA) in open system mode at mid-morning. Photosynthetic light–response curves (A-PPFD) were determined at irradiances between 2000 and 0 $\mu mol\ m^{-2}\ s^{-1}$ using a built-in LED-B light source. Photosynthetic variables were calculated using the non-rectangular hyperbola model. Stomatal densities were counted using impressions made on both abaxial and adaxial epidermis with clear nail polish using a microscope. Six to seven plants were harvested for each light level. The plants were separated into leaves, stems, coarse roots (diameter ≥ 1 mm), fine roots (diameter < 1 mm), flowers (both male and female parts) and fruits; and were dried to a constant mass and weighed. Then, the biomass fraction of each component was calculated. Flower and fruit biomass were used to assess flower and fruit abundance because of the large number of flowers. Subsamples of leaf were scanned to analyze for leaf area; and specific leaf area (SLA, $cm^2\ g^{-1}$ leaf), leaf area ratio (LAR, cm^2 leaf g^{-1} plant) and relative biomass growth rate (RGR, $mg\ g^{-1}\ d^{-1}$) was calculated.

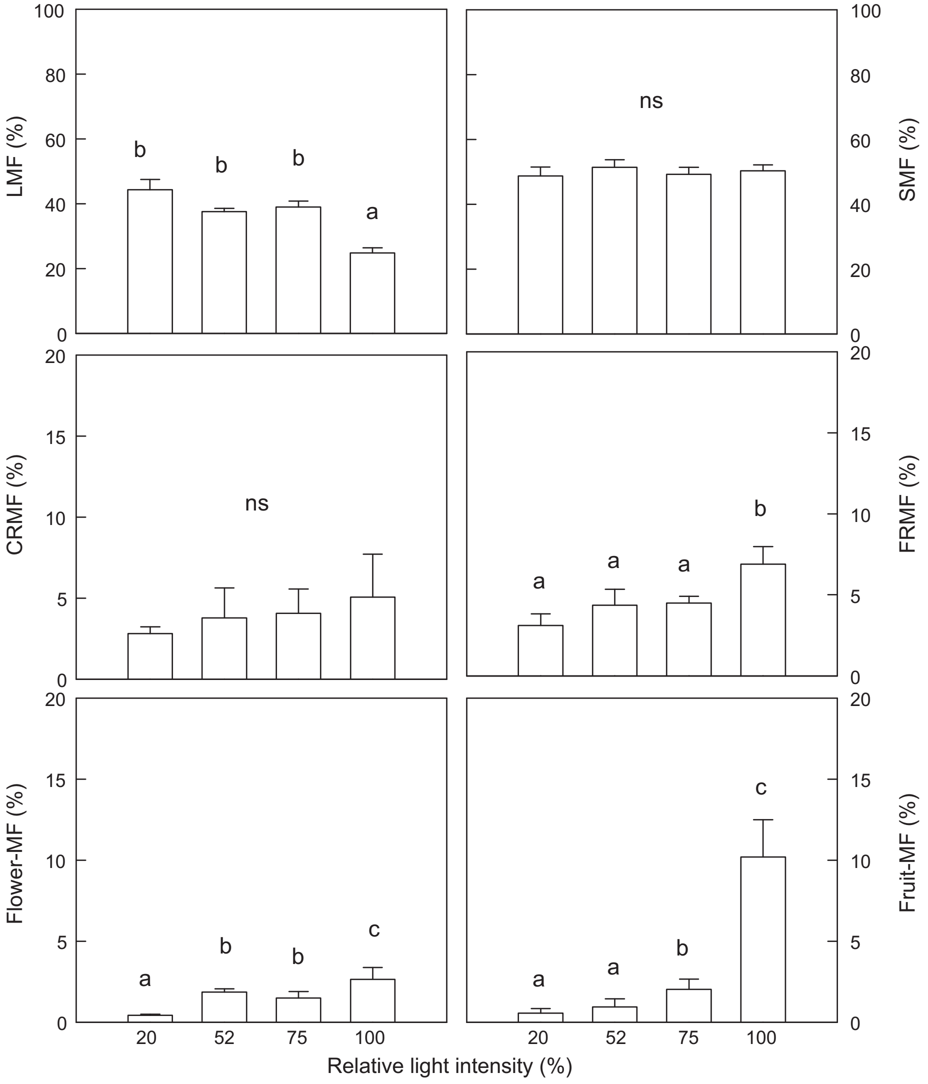

Fig. 1. Responses of biomass allocation to light in plants of *P. volubilis*. Different letters indicate significant differences ($P < 0.05$) among light levels. LMF, leaf mass fraction; SMF, stem mass fraction; CRMF, coarse root mass fraction; FRMF, fine-root mass fraction; Flower-MF, flower mass fraction; Fruit-MF, fruit mass fraction. Each value is the mean of five to six replicate plants. ns, not significant ($P > 0.05$).

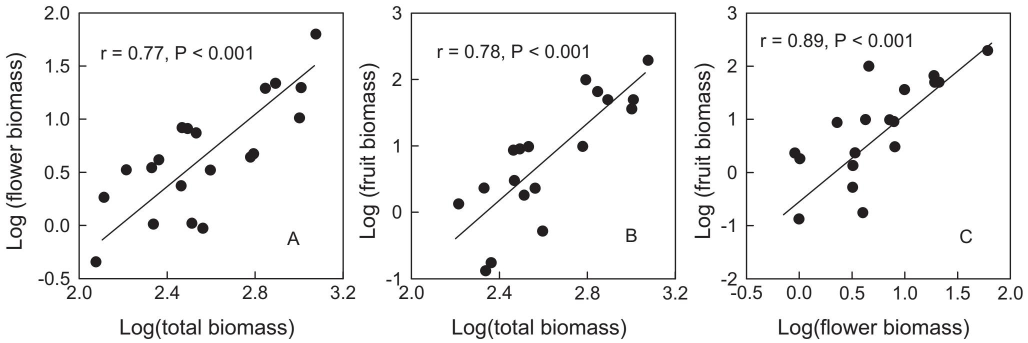

Fig. 2. Relationships between plant total biomass and (A) flower mass and (B) fruit mass, and between flower mass and fruit mass (C) in plants of *P. volubilis* across the light gradients.

2.3. Statistical analyses

Differences in values of each morphological and physiological variable to the light environments were tested by one-way ANOVA, followed by a Tukey HSD post hoc test.

3. Results and discussion

P. volubilis plants grown in relatively low light (20–52% of full sunlight) required more time to achieve initial flowering than those in high light (75–100% of full sunlight) (Table 1). The leaves of *P. volubilis* plants are amphistomatic; stomatal densities in the abaxial epidermis increased with increasing light intensity. The light-saturated photosynthetic rate (A_{max}) of plants grown in the open site was 1.4 times that of plants grown in 20% of full sunlight. Although it has been suggested that *P. volubilis* is able to establish and survive in a low-light understory (Semino et al., 2008), it can be described as a shade-persistent, high-light demanding species (cf. Dalling et al., 2001): (1) their maximum photosynthetic capability and relative growth rate (RGR) are much similar to those of the pioneers (Table 1) (Poorter, 1999; Cai et al., 2009); (2) with strong phenotypically plastic responses to variation in light, photosynthetic capability, RGR and total biomass continually increased with increasing irradiance, which differed from the results of most shade studies. The findings of these studies indicated that RGR usually reached its optimum at intermediate (16–50%) light levels above which it declined (Poorter, 1999; Cai et al., 2009). Similar to many other woody plants (Poorter, 1999), shade significantly increased specific leaf area and leaf area ratio. Shade had no effect on the apparent quantum efficiency (AQY), dark respiration rate (R_d) and light compensation point (LCP) (Table 1); high AQY and low R_d and LCP values are considered to promote carbon fixation in low-light conditions. Thus, it was suggested that *P. volubilis* is strongly adapted to high-light conditions.

In accordance with results of soybean (Jiang and Egli, 1993), long-term exposure to shade diminished reproductive potential directly by decreasing initiation of flowering, flower and fruit parts of *P. volubilis* (Fig. 1). The fruit and flower mass fraction at open site were more than 9 and 5 times greater, respectively, than those in the lowest sunlight. High flower and fruit production of *P. volubilis* plants in high light involved an increase in supply of photosynthetic carbon fixation (Routhier and Lapointe, 2002): an increased photosynthetic input because they received saturating irradiances throughout the day; plant total biomass increased in high light. The effect of shade was more severe on fruit yield than on photosynthetic capability and flower part of *P. volubilis* plants, indicating an effect on bud differentiation and fruit set. The effect of shade on fruit yield of *P. volubilis*, seemingly not an effect of reduced photosynthesis, indicated that factors such as flower initiation, fruit set, or other morphogenetic characteristics may play important roles. Both flower biomass and fruit biomass were positively correlated with total plant biomass across light levels (Fig. 2). Earlier flowering individuals in high light had higher plant biomass and fruits, indicating that earlier flowering did not imply fewer resources allocated from maternal plants, and thus fewer resources available for fruit production.

In summary, *P. volubilis* plants grown in high light exhibited better growth compared with plants grown in the shade, which mainly attributed to its superior physiological performance (photosynthetic rates). Long-term exposure to shade delayed inhibition of flowering and reduced biomass (or numbers) of flower and fruit parts. The light-demanding and rapid-growth characteristics of *P. volubilis*, and its high yield in high light suggested that a clear-cutting or a close-to-open canopy silvicultural system would be a practical alternative for the management of this species in commercial production.

Acknowledgements

The author thanks D.Y. Jiao, L.L. Li, and Y.L. Qin who assisted with this study. Funding was provided by grants for Academy-Locality Cooperation project and for the excellent young scientists of Chinese Academy of Sciences (KSCX2-EW-Q-17).

References

Cai, Z.Q., Wang, H., Yang, J., Cai, C.T., 2009. Growth, photosynthesis and root reserpine concentrations of two *Rauvolfia* species in response to a light gradient. Ind. Crops Prod. 30, 220–226.

Cai, Z.Q., Yang, Q., Tang, S.X., Dao, X.S. Nutritional evaluation in seeds of a woody oil crop, *Plukenetia volubilis* Linneo. Acta Nutr. Sin. 33, in press.

Dalling, J.W., Winter, K., Hubbell, S.P., Hamrick, J.L., 2001. The unusual life history of Alseis blackiana, a shade-persistent pioneer tree? Ecology 82, 933–945.

Hamaker, B.R., Valles, C., Gilman, R., Hardmeier, R.M., Clark, D., García, H.H., Gonzales, A.E., Kohlstad, I., Castro, M., 1992. Amino acid and fatty acid profiles of the Inca peanut (*Plukenetia volubilis* L.). Cereal Chem. 69, 461–463.

Jiang, H., Egli, D.B., 1993. Shade induced changes in flower and pod number and flower and fruit and abscission in soybean. Agron. J. 85, 221–225.

Poorter, L., 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Funct. Ecol. 13, 396–410.

Routhier, M., Lapointe, L., 2002. Impact of tree leaf phenology on growth rates and reproduction in the spring flowering species *Trillium erectum* (Liliaceae). Am. J. Bot. 89, 500–505.

Semino, C.A., Rojas, F.C., Zapata, E.S., 2008. Protocolo del cultivo de Sacha Inchi (*Plukenetia volubilis* L.). La Merced, Peru, PhD thesis, pp. 1–87.