BIOLOGIA PLANTARUM 42 (4): 631-636, 1999

BRIEF COMMUNICATION

Carbon translocation as affected by shade in saplings of shade tolerant and intolerant species

R.P. SOUZA and L.F.M. VÁLIO

Departamento de Fisiologia Vegetal, Instituto de Biologia, Caixa Postal 6109, Universidade Estadual de Campinas, Campinas, CEP 13083-970, São Paulo, Brazil.

Abstract

Carbon translocation was affected by shade in different tropical tree species differing in successional status and degree of shade tolerance. Plants of the early-successional shade-intolerant species *Cecropia pachystachya* and *Schizolobium parahyba* and of the late-successional shade-tolerant species *Myroxylon peruiferum* and *Hymenaea courbaril* were grown under full sun (FS) and natural shade treatments (NS) and assessed for [^{14}C]-sucrose translocation. Most of the ^{14}C was retained in the fed leaf after a 24 h translocation period. Under FS, the growing apical part of the plant was the most intense sink for most species. Shade affected growth and sink intensity differently in early and late successional species. Growth was more markedly affected in the early species. Whereas these continued to invest carbon into the growing apical part of the plant under shade conditions, the late successional species invested relatively more into other sinks.

Additional key words: allocation pattern, ^{14}C-sucrose, *Cecropia pachystachya*, growth, *Hymenaea courbaril*, *Myroxylon peruiferum*, *Schizolobium parahyba*, tropical tree species.

It has been recognized that the patterns of photoassimilate partitioning, and hence growth patterns, may be correlated with life-history traits and successional status of species. Hara *et al.* (1991) has suggested that whereas early-successional species tend to allocate more to growth in height, late-successional species tend to make greater investment into lateral branches and foliage. Under conditions of low productivity on the shaded florest floor, the manner by which plants distribute the limited amounts of

---

Received 11 February 1999, *accepted* 4 May 1999.

Abbreviations: FS - full sun; NS - natural shade; PAR - photosynthetically active radiation.

Fax: (+55) 19 2893124

assimilates may be an important factor in determining their chances of survival and establishment (Kohyama 1987). Shade has been shown to affect the distribution pattern of carbon in several cultivated species (Starck 1973, Mor and Halevy 1980, Heindl and Brun 1983, Corelli-Grappadelli *et al.* 1996). Both decreased photon flux density (Starck 1973, Farrar and Farrar 1987, Gawronska and Dwelle 1989) and red/far-red ratio (Kasperbauer and Karlen 1986, Keiller and Smith 1989) appear to play a role. The objective of this study was to evaluate carbon translocation as affected by shade in tree species differing in successional status and degree of shade tolerance in order to ascertain the existence of different strategies among them.

The study was carried out with the early-successional shade-intolerant species *Cecropia pachystachya* Trec. and *Schizolobium parahyba* (Vell.) Blake and the late-successional shade-tolerant species *Myroxylon peruiferum* L.f. and *Hymenaea courbaril* L. These species will be designated only by their genus name throughout. Plants were grown from seeds germinated under controlled conditions (constant light, PAR 14 μmol(photon) m^{-2} s^{-1}, 25 °C). Seedlings were transplanted into trays and kept in a greenhouse until establishment. Once established, the seedlings were transplanted into 3.5 dm^3 polyethylene bags filled with forest soil and were submitted either to full sun (FS) or natural shade (NS) treatments under field conditions. The field experiments were carried out at Santa Genebra Reserve, an area of semideciduous tropical vegetation situated in Campinas, SP, Brazil (22°44'45"S, 47°06'33"W, 670 m altitude). FS treatment consisted of exposing plants to full sun radiation in an open area adjacent to the forest whereas in the NS treatment plants were kept inside the forest under the shade imposed by the closed canopy. Irradiance under the shade treatment was *ca.* 0.4 to 2.4 % of full sun. Red/far-red ratio was *ca.* 0.23 to 0.74 under the forest and *ca.* 1.22 to 1.44 outside. In the FS treatment, the bags were kept inside ditches in soil to avoid excessive heating of the root system. FS plants were watered daily, while NS plants were watered always when necessary. After 135 - 145 d, plants were treated with [^{14}C]-sucrose in order to assess the carbon translocation pattern.

Uniformly labelled [^{14}C]-sucrose solution (0.01 cm^3; 18.5 kBq; specific activity 0.30 GBq $mmol^{-1}$) was applied, through a microcapillary, into the petiole of the youngest completely expanded leaf using five plants of each treatment. Two non-treated plants were kept as control. [^{14}C]-sucrose feeding was done at 09:00 and a 24-h translocation period was allowed. After this time, plants were harvested and separated in the following parts: fed leaf, shoot above fed leaf, leaves below fed leaf, stem below fed leaf and roots. The plant parts were then oven-dried (80 °C, 48 h) and, after determination of dry mass, they were ground to fine powder. Samples ranging from 1 mg to 100 mg of each plant part were suspended in 10 cm^3 scintillation fluid and then 400 mg of *CAB-O-SIL* (*Fluka*, Buchs, Switzerland) was added to each vial. The scintillation fluid consisted of 1 dm^3 toluene + 50 cm^3 ethanol + 5 g 2,5-diphenyloxazole scintillation grade + 100 mg 1,4-bis-[2-(4-methyl-5-phenyloxazolyl)]-benzene scintillation grade. Radioactivity was counted in a liquid scintillation counter (*Beckman Instruments*, Fullerton, USA). An external standard ratio using non-radioactive material from similar plant parts was used to correct for quenching. Results were converted to percentages of the total recovered activity. The relative sink intensity of the plant parts was determined by dividing the percentage radioactivity by the dry mass of the respective part (Palit 1985). The relative contribution of each plant part as a sink was calculated as the percentage of sink intensity of the plant part in relation to total sink intensity.

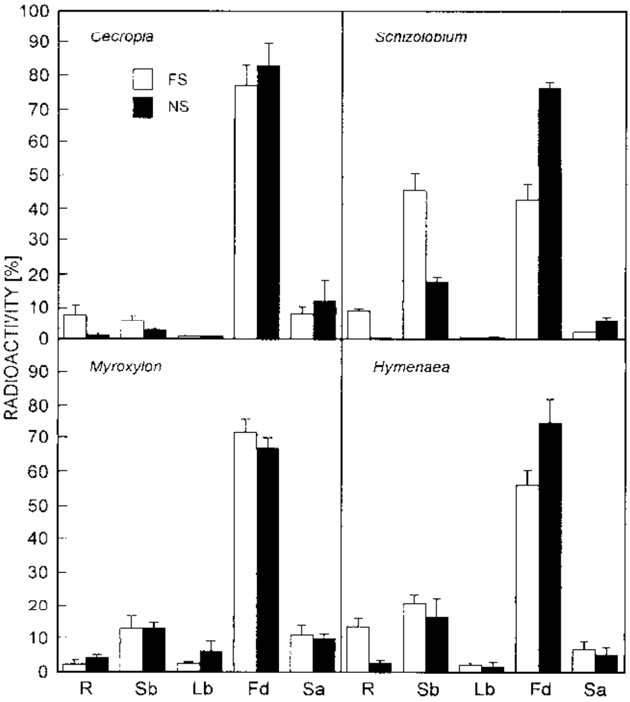

Fig. 1. Distribution of radioactivity in plants of *Cecropia pachystachya*, *Schizolobium parahyba*, *Myroxylon peruiferum* and *Hymenaea courbaril* 24 h after feeding [^{14}C]-sucrose to the youngest expanded leaf. Plants grown under full sun (FS) and natural shade (NS). R - root, Sb - stem below the fed leaf, Lb - leaves below fed leaf, Fd - fed leaf, Sa - shoot above fed leaf. *Vertical bars* indicate SE.

The distribution pattern of radioactivity (Fig. 1) showed that for most species, either under FS or NS treatments, large amounts of the ^{14}C (60 % to 80 % depending on species) was retained in the fed leaf. Only in *Schizolobium*, under FS treatment, a greater translocation was observed, with high radioactivity detected in the stem below the fed leaf. In fact, in *Schizolobium* under FS treatment, the stem below the fed leaf appeared to be an important sink, as indicated by its calculated sink intensity value (Table 1). For all other species, the shoot above the fed leaf, *i.e.*, the growing apical part of the plant, was the most intense sink, at least under FS treatment (Table 1). Retention of the bulk of photosynthates in the source leaves seems to be a common feature among different plant species (Mor and Halevy 1980, Mann 1983, Palit 1985, Fetene *et al.* 1997) as well as the predominant translocation to the apical growing part of the plants (Larson and Dickson 1986, Palit 1985, Corelli-Grappadelli *et al.* 1996).

Table 1. Dry mass (d.m.), sink intensity (SI) and relative contribution as a sink (RCS) of the different plant parts of *Cecropia pachystachya*, *Schizolobium parahyba*, *Myroxylon peruiferum* and *Hymenaea courbaril* grown under full sun (FS) and natural shade treatments (NS). Values are means ± SE; $n = 5$. For SI and RCS calculation, see text.

Species and plant part	Dry mass [g]		SI [% rad. g^{-1}(d.m.)]		RCS [%]	
	FS	NS	FS	NS	FS	NS
Cecropia						
Shoot above fed leaf	0.37 ± 0.06	0.04 ± 0.01	22.3	301.0	60.3	78.7
Fed leaf	0.38 ± 0.04	0.04 ± 0.00	-	-	-	-
Leaves below fed leaf	1.45 ± 0.11	0.13 ± 0.02	0.5	7.1	1.5	1.9
Stem below fed leaf	0.68 ± 0.08	0.05 ± 0.01	8.9	55.6	24.1	14.5
Root	1.49 ± 0.20	0.07 ± 0.02	5.2	18.6	14.1	4.9
Schizolobium						
Shoot above fed leaf	0.99 ± 0.05	0.02 ± 0.00	2.1	283.0	10.1	79.0
Fed leaf	1.03 ± 0.07	0.07 ± 0.02	-	-	-	-
Leaves below fed leaf	1.42 ± 0.14	0.03 ± 0.01	0.3	15.3	1.6	4.3
Stem below fed leaf	2.81 ± 0.23	0.30 ± 0.06	16.2	59.3	75.3	16.5
Root	3.24 ± 0.26	0.17 ± 0.05	2.8	0.7	13.0	0.2
Myroxylon						
Shoot above fed leaf	0.04 ± 0.01	0.02 ± 0.00	271.3	493.0	71.9	58.1
Fed leaf	0.04 ± 0.01	0.03 ± 0.00	-	-	-	-
Leaves below fed leaf	0.21 ± 0.03	0.07 ± 0.02	12.0	88.1	3.2	10.4
Stem below fed leaf	0.15 ± 0.02	0.06 ± 0.01	85.9	215.8	22.8	25.4
Root	0.27 ± 0.03	0.08 ± 0.02	8.2	52.1	2.1	6.1
Hymenaea						
Shoot above fed leaf	0.27 ± 0.04	0.24 ± 0.03	26.0	21.7	64.8	37.9
Fed leaf	0.37 ± 0.06	0.23 ± 0.03	-	-	-	-
Leaves below fed leaf	2.26 ± 0.42	0.40 ± 0.14	1.0	4.2	2.4	7.3
Stem below fed leaf	2.95 ± 0.56	0.67 ± 0.05	7.1	24.5	17.8	42.7
Root	2.25 ± 0.53	0.39 ± 0.06	6.0	6.9	15.0	12.1

The shade treatment had a strong influence on growth, especially of the early-successional species *Cecropia* and *Schizolobium*. In these species, growth, as analysed by dry mass accumulation, was more seriously affected than in the late-successional species *Myroxylon* and *Hymenaea* (Table 1). These results agree with the claims of smaller phenotypic plasticity for shade tolerant species (Grime 1983). Shade also had an influence on the distribution pattern of radioactivity (Fig. 1) and, partially due to the reduced values of dry mass, on the sink intensity too (Table 1). In *Schizolobium* and *Hymenaea*, a markedly greater retention of radioactivity could be observed in the fed leaf in detriment of translocation to other plant parts (Fig. 1). In *Cecropia* and *Myroxylon*, the distribution pattern of radioactivity seemed to be less affected by the shade treatment (Fig. 1). However, when the reduced dry mass values under shade were taken into account, marked changes in sink intensity values could be observed for all species (Table 1). In *Cecropia*, the shoot above the fed leaf remained the most intense sink under shade, but with a greater relative contribution, which increased from 60.3 % under FS to 78.7 % under NS. In *Schizolobium*, whose most intense sink under FS was the stem, the shoot above the fed leaf became the most intense sink under shade, with a relative contribution of 79 %. In *Myroxylon*, although the shoot above the fed leaf still remained the most intense sink under NS, its relative contribution decreased in comparison to the FS treatment, dropping from 71.9 % to 58.1 %. All the other plant parts - leaves and stem below fed leaf and roots - showed slight increases in their relative contribution as sinks. Finally, in *Hymenaea*, a marked change could be observed. Under shade, the shoot above the fed leaf ceased to be the most important sink. In this case, the stem below the fed leaf became the most intense sink, making evident the shift in sink priority due to shading, as observed by Corelli-Grappadelli *et al.* (1996) for peach plants.

So, the early and late successional species studied here seem to show a different response pattern to the shade treatment. Whereas the early successional species continue to invest carbon into the growing apical part of the plant in detriment especially of the roots, the late successional species proportionally decrease the investment into the growing apical part, investing relatively more into other sinks, probably aimed at their growth or simply their maintenance under conditions of severe shade. This difference in the response pattern to shade may be an important factor in determining successional status and shade tolerance of woody species (King 1991). As proposed by Hara *et al.* (1991), an allocation pattern favouring apical bud, and hence height growth, may be important for overtopping other plants in their early stages of succession in sunny environments. Under shade, this pattern favouring growth in height can be adaptative in competition if there is an early improvement in light conditions (Kohyama 1987). However, under persistent shade beneath dense tree canopies, where vertical gradients in irradiance are not pronounced, height growth and ability to compete for light is likely to be of secondary importance in relation to the capacity of tolerating shade (Grime 1983). For shade tolerators, the maintenance of the actual assimilate system, at the expense of height growth, may be more advantageous for survival and regeneration under shade.

References

Corelli-Grappadelli, L., Ravaglia, G., Asirelli, A.: Shoot type and light exposure influence carbon partitioning in peach cv. Elegant Lady. - J. hort. Sci. **71**: 533-543, 1996.

Farrar, S., Farrar, J.: Effects of photon fluence rate on carbon partitioning in barley source leaves. - Plant Physiol. Biochem. **25**: 541-548, 1987.

Fetene, M., Benker, C., Beck, E.: The pathway of assimilate flow from source to sink in *Urtica dioica* L., studied with ^{14}C under ambient atmospheric conditions. - Ann. Bot. **79**: 585-591, 1997.

Gawronska, H., Dwelle, R.B.: Partitioning of photoassimilates by potato plants (*Solanum tuberosum* L.) as influenced by irradiance. I. Partitioning patterns in cultivar Russet Burbank grown under high and low irradiance. - Amer. Potato J. **66**: 201-213, 1989.

Grime, J.P.: Plant Strategies and Vegetation Processes. - John Wiley & Sons, Chichester 1983.

Hara, T., Kimura, M., Kikuzawa, K.: Growth patterns of tree height and stem diameter in populations of *Abies veitchii*, *A. ariesii* and *Betula ermanii*. - J. Ecol. **79**: 1085-1098, 1991.

Heindl, J.C., Brun, W.A.: Light and shade effects on abscission and ^{14}C-photoassimilate partitioning among reproductive structures in soybean. - Plant Physiol. **73**: 434-439, 1983.

Kasperbauer, M.J., Karlen, D.L.: Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. - Physiol. Plant. **66**: 159-163, 1986.

Keiller, D., Smith, H.: Control of carbon partitioning by light quality mediated by phytochrome. - Plant Sci. **63**: 25-29, 1989.

King, D.A.: Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. - Funct. Ecol. **5**: 484-492, 1991.

Kohyama, T.: Significance of architecture and allometry in saplings. - Funct. Ecol. **1**: 399-404, 1987.

Larson, P.R., Dickson, R.E.: ^{14}C translocation pathways in honeylocust and green ash: woody plants with complex leaf forms. - Physiol. Plant. **66**: 21-30, 1986.

Mann, J.D.: Translocation of photosynthate in bulbing onions. - Aust. J. Plant Physiol. **10**: 515-521, 1983.

Mor, Y., Halevy, A.H.: Promotion of sink activity of developing rose shoots by light. - Plant Physiol. **66**: 990-995, 1980.

Palit, P.: Translocation and distribution of ^{14}C-labelled assimilate associated with growth of jute (*Corchorus olitorius* L.). - Aust. J. Plant Physiol. **12**: 527-534, 1985.

Starck, Z.: The effect of shading during growth on the subsequent distribution of ^{14}C-assimilates in *Raphanus sativus*. - Bull. Acad. pol. Sci. **21**: 309-314, 1973.