

The Effect of Light Regime on Source–Sink Relations in the Shade-Enduring *Ajuga reptans* Plant

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Abstract—A quantitative approach to the evaluation of source–sink relations in *Ajuga reptans* plants grown under the forest canopy (shade plants) and on an open plot (sun plants) was worked out in terms of growth characteristics, CO₂ exchange, and carbon balance. Shade plants developed leaves with the relative and specific areas twice exceeding those of sun plants. Sun plants assimilated more carbon, using a significant part of it for the development of numerous runners. During a day, shade and sun plants produced 0.03 and 0.67 g of substrate, respectively. At the same time, forest (shade) plants spent 48% of assimilates for the respiration, in comparison with plants from the open plot that spent almost 70% of assimilates for respiration as they were greater in size. It was concluded, that light controls source–sink relations, which is a way of realization of the life strategy and a coordination mechanism of functional integrity of the plant organism. Light not only controls photosynthesis (source activity) but morphophysiological characteristics of plants with their hierarchical structure of sinks too.

Key words: *Ajuga reptans* - ¹⁴C partition - assimilates - source–sink relations - carbon balance - growth - CO₂ exchange - illumination

INTRODUCTION

The investigation of the source–sink system and regulation of source–sink relations provides for the important information about genotype-determined morphophysiological characteristics of plants and their variability under the influence of the environment [1–3]. It is accepted, that source–sink relations play a key role in the integration of physiological processes in the plant adaptation to growth conditions [4]. From these standpoints, studying the influence of various environmental factors on source–sink relations causes a special interest.

Light is one of the main ecological factors controlling photosynthesis, growth, and development of plants. The photosynthetic rate and the capacity for carboxylation reduce at adaptation to the shade conditions [5, 6]. Leaf blades become thinner, and the size of chloroplasts increases. More substances are directed to the formation of the leaf blade, and translocation of assimilates to roots and reproductive organs decreases, which indicates the change in the source–sink relations. The source–sink relations in shade-enduring plants after their transfer to full sun conditions are poorly investi-

gated. Earlier we have studied the characteristics of the photosynthetic apparatus of *Ajuga reptans* plants growing under forest canopy and cultivated on an open plot [7, 8]. It was established that, at adaptation to high irradiance, the specific leaf weight and leaf mesostructure changed, the chlorophyll content was reduced, and the assimilation number increased. Under light saturation, the net assimilation rate of sun-plant leaves reached 4–5 mg CO₂/(dm² h) that was 25–30% higher than the net assimilation rate of shade-plant leaves. The rate of CO₂ uptake at the light intensity of adaptation radiation (IAR) was 40–45% of that at saturated light intensity. Leaves of sun plants were characterized by an increased rate of respiration and by active alternative pathway [9]. The respiration rate of runners and roots varied from 0.8 to 1.2 mg CO₂/(g h).

It was assumed, that these structural and functional changes in the source leaves during adaptation to irradiance conditions should affect the source–sink relations in the whole plant. The goal of the present work was a comparative morphophysiological investigation and estimation of the source–sink relations in sun and shade plants in terms of growth indices, distribution of the biomass and ¹⁴C-assimilates, as well as carbon balance. We investigated *A. reptans* plants grown under forest canopy (shade plants) and cultivated on an open plot (sun plants).

Abbreviations: IAR—intensity of adaptation radiation; NAR—net assimilation rate; P_g —gross photosynthesis; P_n —net photosynthesis; P_{IAR} —photosynthetic rate at IAR; PP_n —productivity of net photosynthesis; R —respiratory losses; RGR—relative growth rate; SR—specific radioactivity; SSR—source–sink relations; SSS—source–sink system.

MATERIALS AND METHODS

Plants from natural cenoses of *Ajuga reptans* L. growing in the vicinity of Syktyvkar (a subzone of Middle Taiga) were studied. The irradiance under the canopy of spruce-aspen oak-grass forest at the period of the greatest development of foliage (July) did not exceed 5% of the maximum one. Young plants displaced from the forest to a collection plot were used in experiments during the following growth season.

Estimation of CO₂ exchange of leaves and other organs was carried out with an Infralit-4 infrared gas analyzer (Germany) in differential mode. An error of the average rate of CO₂ exchange did not exceed 10%. The technique for the measurement was described previously in detail [7]. Components of daily balance of plant dry weight were calculated by the method based on CO₂ exchange and growth characteristics, as it was described previously [10, 11]. The daily photosynthetic productivity (PP_n , g/(plant day)) was calculated from the equation:

$$PP_n = 0.68P_{IAR}At,$$

where P_{IAR} is P_n value at the IAR (mg CO₂/(dm² h); A is the leaf area, dm²; t is the length of the photoperiod, h; and 0.68 is a coefficient for the conversion of the amount of CO₂ fixed into glucose equivalent.

Losses of the respiratory substrate (R , g/(plant day)) were calculated from the equation:

$$R = 0.68rWt,$$

where r is the dark respiration rate at average daily temperature, mg CO₂/(g h); W is plant dry weight, g; and t is a duration, h.

The amount of substrate assimilated expressed in glucose equivalents (ΔS , g/(plant day)) was calculated from the equation:

$$\Delta S = PP_n - (R_1 + R_2 + R_3),$$

where R_1 , R_2 , and R_3 are overnight respiratory losses in leaves, and daily losses in stems and roots, respectively.

Gross photosynthesis (P_g , g/(plant day)) was estimated as the sum of the assimilated substrate (ΔS) and respiratory losses (R).

The net-assimilation rate (NAR, g/(dm² day)) was calculated from the formula:

$$NAR = Y_g \Delta S / A,$$

where Y_g is the growth efficiency coefficient (0.7 g/g) and A is the plant leaf area, dm². The variable Y_g was introduced to express NAR in the equivalents of dry biomass, as it is accepted in the classical growth analysis.

The relative growth rate (RGR, g/(g day)) was calculated from gasometric data as a product of NAR and the relative leaf area (LAR, dm²/g) according to the formula:

$$RGR = Y_g (\Delta S / A) (A / W).$$

Table 1. Morphometrical parameters of *Ajuga reptans* plants grown under different conditions (July 1996)

Index	Habitat	
	forest	plot
Plant weight, g dry wt	0.9 ± 0.1	25.0 ± 3.5*
Roots/shoot	0.12 ± 0.03	0.12 ± 0.03
No. runners per plant	2.5 ± 0.8	17.1 ± 1.5*
Runner weight, g dry wt	0.20 ± 0.04	1.6 ± 0.3*
No. leaves per plant	29.1 ± 3.3	93.2 ± 6.8*
Weight of leaves, g dry wt/plant	0.5 ± 0.1	11.4 ± 2.4*
Area of leaves, dm ² /plant	2.4 ± 0.4	24.3 ± 5.3*
Relative leaf area, dm ² /g of plant dry wt	2.5 ± 0.5	1.0 ± 0.2*
Specific leaf area, dm ² /g dry wt of leaves	4.0 ± 0.7	2.0 ± 0.4*
Specific leaf weight, g dry wt/dm ²	0.20 ± 0.01	0.47 ± 0.03*
Relative leaf weight, g/g dry wt of plant	0.51 ± 0.11	0.46 ± 0.12

* Significantly different at $P \leq 0.05$ ($n = 20$).

For estimation of growth characteristics, 20 plants were collected in each treatment. Plants were divided into shoots and roots, weighed, and dried at 70°C. The error of the average weight of the organ biomass varied from 10 to 15%.

For studying post-photosynthetic dynamics of assimilated carbon, plants were exposed to the ¹⁴CO₂-enriched atmosphere during 20 min in a transparent chamber. Labeled CO₂ was produced from Ba¹⁴CO₃ by the addition of 0.1 N HCl. The initial CO₂ concentration in the chamber was 0.09%, which exceeded the atmospheric concentration almost three times. Samples for the analysis (3–5 plants) were collected periodically within a month and a half after the exposure. They were dried and ground, and their specific radioactivity was determined with an US-4 α-β radiometer (Doza, Russia) in five replicates. The losses of labeled carbon from the whole plant were the measure of the respiratory substrate oxidation [12, 13].

Figures and tables give mean values and their standard errors.

RESULTS

Plant growth and biomass accumulation. Table 1 shows the comparative morphophysiological characteristics of *A. reptans* plants growing under different light conditions. For the second year after their transfer from the forest, plants cultivated on an open plot produced a compact mat and substantially surpassed forest plants in their biomass, leaf area, and the number of leaves and

Table 2. The dynamics of the specific radioactivity of *Ajuga reptans* organs, cpm/(min 100 mg dry wt) $\times 10^3$ (July 1996)

Time after exposure, days	Leaves of maternal rosette	Runners	Inflorescences	Roots
0	14.2 \pm 1.0	1.7 \pm 0.2	0.9 \pm 0.1	0.8 \pm 0.1
1	12.5 \pm 0.8	6.1 \pm 0.5	1.7 \pm 0.1	2.7 \pm 0.2
3	7.7 \pm 0.6	6.4 \pm 0.4	3.2 \pm 0.3	3.4 \pm 0.2
10	5.5 \pm 0.4	5.7 \pm 0.4	2.7 \pm 0.2	2.7 \pm 0.3
30	3.7 \pm 0.3	4.5 \pm 0.3	2.6 \pm 0.2	2.4 \pm 0.1

* Plants were exposed to $^{14}\text{CO}_2$ atmosphere ($n = 5$).

stolons (runners). The specific leaf weight (SLW) of sun plants more than twice exceeded SLW of shade plants. Forest plants were characterized by a greater relative leaf area and specific leaf area. There were no significant differences in the ratios of leaf weight to plant weight and root weight to shoot weight.

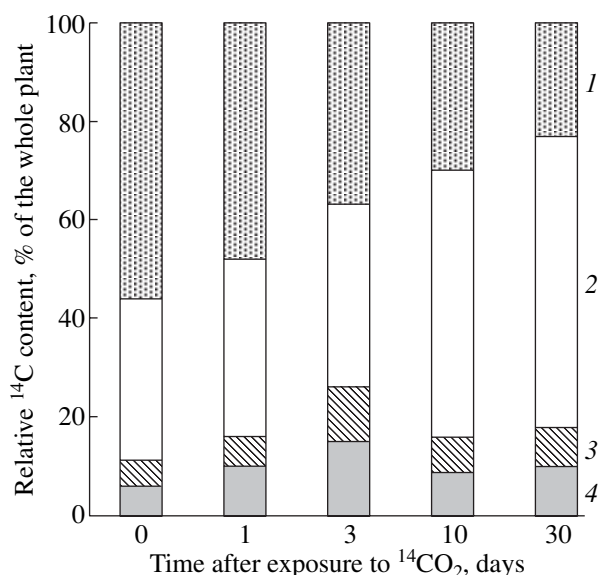
Specific radioactivity of organs and ^{14}C partitioning within the plant. As Table 2 shows, the label was detected in all parts of cultivated plants immediately after their exposure to $^{14}\text{CO}_2$, but the concentration of ^{14}C -products in the maternal rosette leaves was by the order higher. On the next day, an appreciable increase of ^{14}C in runners, inflorescences, and roots was observed. This corresponded to the loss of ^{14}C -label from maternal rosette leaves. By the 10th day, the specific radioactivity in leaves decreased three times from the initial. Further, the level of SR in leaves changed

insignificantly, and, by the end of the experiment, plant organs almost did not differ in their radioactivity calculated per dry weight unit.

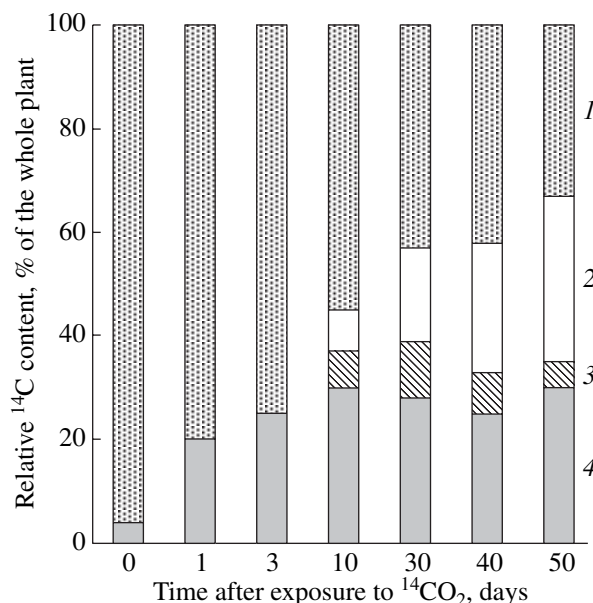
The analysis of the relative label distribution showed (Fig. 1) that a significant part of the label was redistributed from leaves to stolons (runners). Thus, in a day after plant exposure to $^{14}\text{CO}_2$, about 30% of the label was localized in runners, but in a month, its relative content in runners increased twice.

For more exact estimation of a maternal rosette role in the supply of the developing runners with a growth substrate, in the following experiment, young plants (without runners) were exposed to the ^{14}C atmosphere. It is clear from Fig. 2, that leaves retained a significant part of a label until the beginning of the active growth of buds producing runners. The formation of runners was accompanied by redistribution of ^{14}C within a plant. By the end of the experiment, the relative content of label in runners reached 40%. It is necessary to note, that by this time less than 20% of the originally assimilated labeled carbon remained in plants (Fig. 3).

Carbon balance and relative growth rate of plants. In the range of saturated light, the net-assimilation rate in leaves of plants cultivated on the plot reached 4–5 mg $\text{CO}_2/(\text{dm}^2 \text{ h})$ that was 25–30% higher than the net-assimilation rate in leaves of forest plants. The rate of CO_2 uptake at adaption radiation (P_{IAR}) was 40–45% of that at the saturation light intensity. The respiration rate of leaves was 2.0 and 1.5 mg $\text{CO}_2/(\text{g h})$, respectively. For runners and roots, it varied within 0.8–1.2 mg $\text{CO}_2/(\text{g h})$.

**Fig. 1.** The dynamics of label partitioning in *Ajuga reptans* plant organs after $^{14}\text{CO}_2$ assimilation by sun plants at flowering (June 18, 1996).

(1) Leaves of the maternal plant; (2) runners; (3) inflorescences; (4) roots.

**Fig. 2.** The dynamics of label partitioning in *Ajuga reptans* plant organs after $^{14}\text{CO}_2$ assimilation by young plants without runners (July 24, 1997).

(1) Leaves of the maternal plant; (2) runners; (3) inflorescences; (4) roots.

Based on the CO_2 exchange, quantification of components of plant carbon balance was made. The calculations showed (Table 3) that, during the photosynthesis, shade and sun plants produced 0.03 and 0.67 g of substrate per day, respectively. At the same time, forest plants spent 48% of assimilates for respiration, in comparison with plants from the open plot that spent almost 70% of assimilates for respiration. Absolute losses of a respiratory substrate in leaves, runners, and roots in the sun plants were the order higher than in the shade plants. Although rather close the values of the net-assimilation rate are, the relative growth rate of shade plant was twice higher than in sun plants.

DISCUSSION

We demonstrated that light plays an important role in the establishing the source–sink relations in *A. reptans* plants. In natural habitats under the forest canopy, an ecotype is formed whose strategy is directed to the investment of assimilated carbon into the leaf surface production, providing for the supply of a plant with a carbon substrate under light deficiency conditions (5% of maximum radiation). The data concerning the RLA and SLA testify to this (Table 1). Such a strategy inevitably leads to the limited formation of vegetative runners. The number of runners in shade plants in a forest was seven times less, and their relative weight expressed as a percentage of the total biomass was two-fold lower, than in sun plants on an open plot.

Plants cultivated on a plot under high-light conditions assimilated more carbon (Table 3), although they had two-fold smaller RLA and SLA (Table 1). The apparent photosynthesis rate of thicker leaf blades of sun plants with developed palisade tissue was on the average 25% higher than in the leaves of shade plants [7]. An additional carbon was directed to the formation of numerous runners, which then formed the system of separated rosettes. Not only apical buds, but also all other buds on the runners developed actively in sun plants, as distinct from plants in natural habitats [14, 15]. Subsequent separation of young rooted rosettes as a result of destruction of the plagiotropic part of over-ground runner parts led to the formation of separated plantlets (ramets), with shortened shoots and two or three rosette leaf pairs. The formation of runners strongly depended on assimilates coming from the source leaves of the maternal rosette.

The data obtained with ^{14}C showed that the carbon reserved in maternal rosette leaves was actively translocated to the runners. ^{14}C was transported through the runner and used for the formation of daughter rosettes. It is important that even young rosettes, which did not yet have the runners, deposited carbon for their further formations (Fig. 2). *A. reptans* plants cultivated on an open plot produced more vegetative runners in comparison not only with plants from natural habitats on the northern boundary of an area (a subzone of Middle

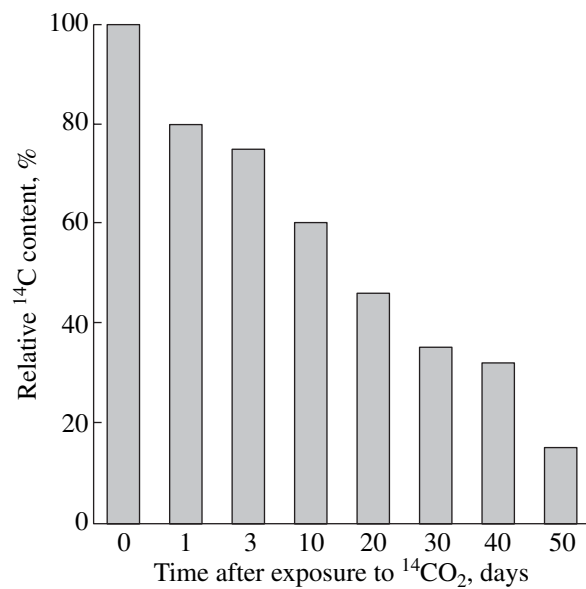


Fig. 3. The long-term dynamics of label content in *Ajuga reptans* plants, % of the originally assimilated $^{14}\text{CO}_2$.

Taiga), but also with the plants growing in the center of the area in broad-leaved forest of Middle Russia.

It seems likely that, in plants close in their morphology to *A. reptans*, light plays not only trophic but also a signal role. Under the forest canopy, where the ratio of red to far-red light is low [5], a spectral light composition apparently regulates the initiation of runner buds.

At the initial stages of growth, runners and daughter ramets accept a significant part of assimilates from source leaves of a maternal plant. Therefore, the formation of numerous runners by well-illuminated plants receiving light enriched with red light gives an essential

Table 3. Growth characteristics and dry weight balance of *Ajuga reptans* plants grown under different light conditions (July 1996)

Index	Habitat	
	forest	plot
Productivity of net photosynthesis, PP_n , g/(plant day)	0.0240 ± 0.0001	$0.44 \pm 0.01^*$
Respiratory losses, R , g/(plant day)	0.0150 ± 0.0002	$0.45 \pm 0.01^*$
Gross photosynthesis, P_g , g/(plant day)	0.0310 ± 0.0002	$0.67 \pm 0.01^*$
Net assimilation rate, NAR, g/(dm ² day)	0.005 ± 0.001	0.006 ± 0.002
Relative growth rate, RGR , g/(g day)	0.012 ± 0.001	$0.006 \pm 0.002^*$
R/P_g	0.480 ± 0.001	$0.670 \pm 0.005^*$

* Significantly different at $P \leq 0.05$ ($n = 20$).

load on the photosynthetic apparatus through a demand for assimilates.

Thus, the data obtained allow to conclude that the formation of a source–sink system as a way of realization of the life strategy and the mechanism of functional integrity of a growing organism, is under the light control. Light regulates not only the process of photosynthesis (source function), but morphophysiological parameters of plants with the certain hierarchical structure of sinks too.

In conclusion, ecophysiological studies create a necessary basis for understanding the interaction mechanisms of plants with the environment and revealing the complex effects of light in their life.

REFERENCES

1. Mokronosov, A.T., *Fotosinteticheskaya funktsiya i tselostnost' rastitel'nogo organizma, 42-e Timiryazevskoe chtenie* (Photosynthetic Function and Integrity of the Plant Organism, the 42nd Timiryazev Lecture), Moscow: Nauka, 1983.
2. Golovko, T.K., Respiration in the Source–Sink System of Plants, *Doctoral (Biol.) Dissertation*, Moscow: Inst. Plant Physiol., 1993.
3. Golovko, T.K., Respiration in the Source–Sink System of Plants, *Fiziol. Rast.* (Moscow), 1998, vol. 45, pp. 632–640 (*Russ. J. Plant Physiol.*, Engl. Transl.).
4. Kursanov, A.L., *Transport assimilyatov v rastenii*, Moscow: Nauka, 1976. Translated under the title *Assimilate Transport in Plants*, Amsterdam: Elsevier, 1984.
5. Tang, Y., Light, *Plant Ecophysiology*, Prasad, M.N.V., Ed., New York: Wiley, 1996, pp. 3–40.
6. Lambers, H., Chapin, F.S., and Pons, T.L., *Plant Physiological Ecology*, New York: Springer-Verlag, 1998.
7. Dymova, O.V. and Golovko, T.K., Light Adaptation of Photosynthetic Apparatus in *Ajuga reptans* L., a Shade Tolerant Plant as an Example, *Fiziol. Rast.* (Moscow), 1998, vol. 45, pp. 521–528 (*Russ. J. Plant Physiol.*, Engl. Transl.).
8. Golovko, T.K., Dymova, O.V., and Pystina, N.V., Adaptation of the Photosynthetic Apparatus in Shade-Tolerant Plants, *Vestn. Nizhegorod. Univ.*, 2001, pp. 77–79.
9. Golovko, T.K. and Pystina, N.V., The Alternative Respiration Pathway in Leaves of *Rhodiola rosea* and *Ajuga reptans*: Presumable Physiological Role, *Fiziol. Rast.* (Moscow), 2001, vol. 48, pp. 846–853 (*Russ. J. Plant Physiol.*, Engl. Transl.).
10. Golovko, T.K. and Garmash, E.V., CO₂ Exchange and Growth of *Rhaponticum carthamoides* under the Conditions of the Middle Taiga Subzone of Northeastern Europe: 2. Photosynthesis/Respiration Ratio as an Index of the Productivity and Adaptive Responses of Plants, *Fiziol. Rast.* (Moscow), 1997, vol. 44, pp. 864–872 (*Russ. J. Plant Physiol.*, Engl. Transl.).
11. Dymova, O.V. and Golovko, T.K., Morphological and Physiological Aspects of *Ajuga reptans* Growth, *Reproduktivnaya biologiya rastenii na evropeiskom Severo-Vostoke* (Reproductive Biology of Plants from the Zone of Northeastern Europe), Syktyvkar: Komi Nauch. Tsentr, Ross. Akad. Nauk, 1998, no. 158, pp. 72–83.
12. Ryle, G.J.H., Cobby, J.M., and Powell, C.E., Synthetic and Maintenance Respiratory Losses of ¹⁴CO₂ in Uniculm Barley and Maize, *Ann. Bot.* (London), 1976, vol. 40, pp. 571–586.
13. Golovko, T.K. and Tabalenkova, G.N., Utilization of Assimilates in Growth and Respiration in *Lolium multiflorum* Lam. Plants, *Fiziol. Rast.* (Moscow), 1994, vol. 41, pp. 713–719 (*Russ. J. Plant Physiol.*, Engl. Transl.).
14. Smirnova, O.V., *Struktura travyanogo pokrova shirokolistvennykh lesov* (Grass Cover Structure in Deciduous Forests), Moscow: Nauka, 1987.
15. Teteryuk, L.V., Dymova, O.V., and Golovko, T.K., *Morfofiziologicheskie i populyatsionnye adaptatsii Ajuga reptans L. na severnoi granitse areala* (Morphological and Physiological Adaptation in the Population of *Ajuga reptans* on the Northern Boundary of the Area), *Ekologiya* (Yekaterinburg), 2001, no. 3, pp. 209–215.