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Influence of Girdling on Photosynthesis Regulation in Grapevine

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ABSTRACT. The effect of leaf, internodes or cluster girdling on source leaf photosynthesis in grapevine (*Vitis vinifera*, var. Rkatsiteli L.) has been investigated. It was revealed that girdling of a leaf inhibited its photosynthetic activity, while girdling of internodes caused abating of the effect. Relations between photosynthetic activity of the experimental leaves with starch accumulation and stomatal conductivity were established. Ringing of the cluster also resulted in photosynthesis decreasing of the labeled source leaf, but results with full removal of the cluster were similar to the control. Difference in assimilates distribution between girdled and removed cluster variants was also noted. Possible explanations of the results are discussed. The principal role of the sink demand for assimilates in source functioning and transport regulation is concluded. *© 2007 Bull. Georg. Natl. Acad. Sci.*

Key words: *girdling, photosynthesis, stomatal conductivity, starch, assimilates transport.*

The question of leadership among the source and sink organs still remains debatable. Some investigators reject the attractive abilities of sink organs and rely on the universality of passive, symplastic unloading of the phloem [1]. According to them the phloem-loading zones are regarded as leading in phloem functioning, growth and productivity. Opposed to this is the model of phloem transport regulation by two active sinks (top and root) [2]. In this case sugar conversion and storing in the unloading zone may have the leading role in the regulation of phloem transport.

Taking into account the adaptivity of living processes in plant, it may be supposed that source and sink activities are mainly regulated endogenously, but partially it also depends on environmental conditions. Differences in assimilates export among plants with different type of ecological strategy may serve as a conformation to this [3].

The objective of the present study was to investigate the question of source-sink leadership in grapevine. This wood plant attracts attention by its characteristic rhythm of assimilates transport. In particular, it was established that during daytime mainly the accumulation of photoassimilates takes place in leaves of grapevine, while at night transport processes from the leaves to sink organs are activated [4]. The noded shoot of grapevine is also interesting. Here each internode is supplied with a particular, acropetally positioned leaf. Thus, internodes represent some space for transporting and storing of photoassimilates. In the process of active vegetation the function of leaves is not only supplying sink organs with assimilates, but also making some storage pool of assimilates in the internodes for morphogenesis. Determining the "capacity" of the internodal space and the character of its filling with assimilates would be interesting for the establishment of source-sink relations between leaves and sink organs.

The middle size shoots of grapevine (*Vitis vinifera* L., var. Rkatsiteli) were selected as experimental material, in the intensive growth phase of berries.

In order to establish source-sink relations between leaves and sink organs, as well as to determine the capacity of internodes and character of their filling with photoassimilates the experimental shoots were ringed, involving either only the source leaf (with LPI 8), or one, two, and three internodes with fixed leaves (respectively with LPI 8, 9, 10). In the other series of experiments all leaves, except the source one (LPI 8) were removed from the girdled internodes, to exclude their influence on assimilate transport from the source leaf. Changes in the photosynthetic activity of the last one were studied in both series of experiments.

One series of experiments was done with cluster. The cluster was either ringed or removed from the plant. Photosynthesis of the source leaf (with LPI 13-14) and transport of photoassimilates were observed in this case.

The photosynthetic activity of leaves was studied radiometrically, using labeling with $^{14}CO_2$ [5]. Experimental leaves were exposed in chamber and fed with $^{14}CO_2$ for 10min. Concentration of CO_2 was 1%, radioactivity – 1.5MBq, per liter of air. Labeled leaves were dried at 105°C and their activity was registered using end-window counter E-25 BFL and radiometer PP-8 (Russia). In all experiments photosynthesis was studied 3 days after girdling.

In shoot ringing experiments stomatal conductivity (using porometer Rotronic, Hygroscop BT, Austria) and starch content of the source leaves (colorimetrically after [6]) were also investigated.

While studying the transport of photoassimilates, the source leaf was labeled with $^{14}CO_2$ and 24h later the distribution of the label in the fixed shoot was measured.

The mean values of three biological replications with their standard deviations are demonstrated in the Tables.

In our early experiments defoliation was used to change the source-sink balance of the plant [7]. Lessening of the assimilative surface by defoliation caused increasing of the metabolic loading of retained leaves, as they had "to work" for the removed ones, recovering the increased demand for assimilates.

Girdling, when the phloem is damaged, causes a change of the source-sink relations, as opposed to defoliation, i.e. demand for assimilates of the source organ diminishes by means of its isolation from the sink. According to the obtained results it is clear that girdling of a leaf, when the symplastic transport of assimilates from leaf to stem ceased, photosynthesis of the experimental leaf abated (Table 1). This may be explained by the feedback inhibition of the process, which is connected with assimilates (starch) accumulation. The stomatal conductivity of the experimental leaf decreased correspondingly, pointing to reduction of gas exchange (Table 1). These results are corroborated by early experiments on leaves girdling, when photosynthetic activity and starch accumulation of leaves ringed for two, five and seven days were investigated [8].

In the case of ringing one, two or three internodes, when space appears for translocation of photoassimilates, partial unloading of the source leaf from metabolites took place. This caused appropriate diminishing of the extent of photosynthesis inhibition and starch content (compared with the ringed leaf) and an increase of stomatal conductivity (Table 1). However, stimulation of the leaf photosynthesis was limited, not reaching the control level. The same must be said about stomatal conductivity and starch content (Table 1). These results may be explained by the ceasing of the demand for assimilates from the sink (cluster) after girdling.

As in other wood plants, in grapevine there is laterally situated sink tissue like cambium. Partial recovery of the source leaf's photosynthesis in internode-ringed variants, compared with girdled leaf, may be due to utilization of assimilates by cambium.

From the obtained data it is clear that the space of two internodes is enough for establishing a new dynamic equilibrium between synthesis and utilization of starch. In the variant of one-girdled internode recovery of photosynthesis was less than in the two-girdled internodes. When three internodes were ringed, photosynthesis remained the same as in the two-girdled-internodes' variant. The difference in photosynthesis between defoliated and undefoliated internodes should be noted (Table 1). When the girdled internodes were not defoliated, the extent of photosynthesis activation of the source leaf was less, compared with the defoliated variant. This may be explained by the competition between the labeled

Table 1

Influence of girdling on photosynthetic activity, stomatal conductance and starch content of a source leaf

Variant		Defoliated internodes			Undefoliated internodes
		Photosynthesis, count·10^{-3}· min^{-1}·g^{-1}	Stomatal conductivity, cm·sec^{-1}	Starch, %	Photosynthesis, count·10^{-3}· min^{-1}·g^{-1}
Control		121	0.26	5.2	82
Girdled	Leaf	62	0.05	10.2	39
	One internode	71	0.14	9.1	53
	Two internodes	80	0.18	8.8	56
	Three internodes	84	0.19	8.7	59

Table 2

Influence of cluster girdling on source leaf photosynthesis and assimilates translocation

Variant	Photosynthesis count·10^{-3}· min^{-1}·g^{-1}	Stomatal conductivity cm·sec^{-1}	Distribution of radioactivity, % from total activity				Translocation, %
			Leaf	Stem		Cluster	
				Upward	Down ward		
Shoot with cluster	79	0.32	48.3	-	26.2	25.5	51.7
Shoot without cluster	51	0.32	56.4	-	42.6	-	43.6
Girdled cluster	48	0.12	42.5	17.7	39.8	-	57.5
Removed cluster	69	0.32	57.1	-	42.9	-	42.9

source leaf and other leaves for assimilates translocation towards the internodes, as they are also sources of assimilates. Owing to this, the labeled source leaf released less intensively and accordingly recovery of photosynthesis was low (Table 1).

The nature of the "demand-signal" for assimilates still remains unclear, but according to some speculations it may be sugars [9]. Besides this, plants possess a number of other signaling molecules, activating protective reactions [10]. Signals are supposed to be transmitted by the phloem; accordingly, phloem destruction, due to girdling, must cause an interruption of transduction from the sink to the source (or vice versa). The results obtained with shoot ringing may serve as a confirmation of this.

Ringing of a strong sink like cluster must cause significant diminishing of demand for assimilates in the source leaf, owing to signal interruption from the cluster. Accordingly, the photosynthetic activity of the latter must decrease. The results obtained in our experiments with cluster ringing are in accordance with this assumption – photosynthesis abated (Table 2).

Cluster removal, like its girdling, means ceasing of signal transduction towards the source leaf. But the results obtained in this variant of experiments were unexpected – photosynthesis approached the control value. The differences between cluster-ringed and removed variants were reflected on stomatal conductivity too: the more was the photosynthesis, the higher was the conductivity. Thus, the cluster removal variant approached the control.

A study of assimilates translocation has also yielded different results in ringed and removed variants of cluster. Full isolation of cluster showed results similar to the clusterless variant in label distribution among internodes (Table 2). The picture of assimilates distribution and translocation in cluster-ringed variant was diverse: here upward translocation of labeled substances was stimulated and the total translocation index also increased, while the removal of cluster did not change the direction of translocation. So it may be assumed that there exists another way of signal transduction, by the xylem. It is known that between the phloem and xylem radial exchange of assimilates takes place, mainly via the parenchyma in apical zones (in leaf and root) [11]. When the contact of cluster – as of a sink – with the whole plant (as in the case of girdling), is retained, even partially, some signal exchange between sink and source takes place, affecting the sink-source balance of a plant. Full removal of a cluster caused ceasing of signal exchange between cluster and leaves and the plant "behaved" like a clusterless one (Table 2).

Summing up the obtained results, it may be concluded that in grapevine sink demand for assimilates is leading in source functioning and transport regulation.

მცენარეთა ფიზიოლოგია

შემორგოლვის გავლენა ფოტოსინთეზის რეგულაციაზე ვაზში

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ნაშრომში შესწავლილია ფოთლის, მუხლშორისების და მტევნის შემორგოლვის გავლენა დონორი ფოთლის ფოტოსინთეზზე ვაზში (*Vitis vinifera* L., var. Rkatsiteli). დადგენილია, რომ ფოთლის შემორგოლვა თრგუნავს მის ფოტოსინთეზს, ხოლო მუხლშორისების შემორგოლვა იწვევს ამ ზემოქმედების შემცირებას. დადგენილ იქნა კავშირი საცდელი ფოთლის ფოტოსინთეზურ აქტივობას, სახამებლის დაგროვებასა და ბაგის გამტარებლობას შორის. მტევნის შემორგოლვამ ასევე დათრგუნა დონორი ფოთლის ფოტოსინთეზი, მაგრამ მტევნის მოცილების შემთხვევაში მიღებული შედეგები კონტროლს მიუახლოვდა. დადგენილია სხვაობა ასიმილატების გადანაცვლებაში მტევანშემორგოლილ და -მოცილებულ ვარიანტებს შორის. მიღებული შედეგების ასახსნელად წარმოდგენილია მსჯელობა. დადგენილია, რომ ვაზში აქცეპტორის მოთხოვნა ასიმილატებზე წამყვანია დონორის ფუნქციონირებასა და ტრანსპორტის რეგულაციაში.

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