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Original paper

Relative leaf expansion rate as an indicator of compensatory growth of defoliated vines of Prokupac (*Vitis vinifera* L.)

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Abstract Reaction of the grapevine to the early defoliation is to mitigate its effects through compensatory growth by producing more lateral shoots with a greater number of leaves. In this study, we evaluated the usage of non-destructive and continuous measurements of mean and lateral leaf area on the same shoots for the purpose of monitoring the leaf area development and calculating relative leaf expansion rate - RLER during vegetation. This study has shown that the grapevine's ability to recover its leaf area after defoliation depends mainly on the time when the defoliation occurs. Early defoliated vines had time to compensate removed leaves by producing more lateral shoots with a greater number of leaves, which resulted in a larger leaf area. With the decrease in the intensity of shoot growth during vegetation, the recovery ability decreases, therefore, compensatory growth is not enough to restore the reduced leaf area. Based on the value of RLER, if defoliation is performed in the period of intensive growth of shoots, it affects the stagnation of the emergence of new shoots and leaves over several days, followed by a period of re-growth. Very slow or no growth of shoots and leaves occurred after the veraison stage.

Keywords defoliation, leaf area, compensation, relative leaf expansion rate

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Introduction

Leaf removal from the shoots in the fruiting zone is becoming common practice in vineyards with high quality wine cultivars in Serbia. The main aim of defoliation is to improve vine microclimate conditions, especially light conditions, as well as temperature and humidity inside the canopy (SMART [1]; Poni & al. [2]). Improved microclimate conditions prompt accumulation of dry matter in grapes, anthocyanins and polyphenol compounds in berry skins (KLIEWER [3]; HUNTER & al. [4]; SABBATINI & al. [5]; BAIANO & al. [6]). Better aeration of canopy and greater penetration of fungicide reduce the degree of damage caused by disease, especially of grey rot (GUBLER & al. [7]; MOLITOR & al. [8]; GAMBETTA & al. [9]). The effect of defoliation mainly depends on its intensity and the time of application. Early defoliation, carried out within the intensive shoot growing phase, causes the photosynthetic shock due to the removal of the photosynthetically active area and decreases the whole-vine photosynthesis (PETRIE & al. [10]; PALLIOTTI & al. [11]). Total shoot photosynthesis level can be reduced by up to 70%, which causes a halt in the sink organs' development (PONI & al. [12]). These modifications of the source-sink balance can affect the grape and berry structure (COOMBE, [13]; INTRIERI & al. [14]; SABBATINI & al. [5]). The most pronounced changes in the structure of grapes and berries occur when defoliation is performed in the phenological stages of flowering and fruit set, when intensive divisions of berry cells of young berries take place (PONI & al. [15]). During the fruit set, the number of pericarp cell layers is determined and each halt in assimilator inflow results in a decreased cell number. In most studies with defoliation, it is necessary to assess the consequent effect of leaf removal on leaf area change. Leaf area is an important element in the study of plant physiology, particularly when exploring the photosynthetic activity, canopy light conditions and water balance of the plant and when assessing the impact of cultural practices (BESLIC & al. [16]). Furthermore, unfavorable weather conditions, especially hail, diseases and pests can affect the loss of the leaves and reduction of the leaf area. The natural reaction of the grapevine on defoliation is to mitigate its effects through compensatory growth. Compensatory growth is defined as the restoration of morphological and physiological changes that occur in plants following defoliation (COLLIN & al. [17]). Grapevine has a strong capacity of compensation by producing more lateral shoots with a greater number of leaves (CANDOLFI-VASCONCELOS & KOBLET [18]; PETRIE & al. [19]; KURTURAL & al. [20]), which is a response to the disturbed source: sink relation and balancing act of the grapevine canopy upon manipulation (Hunter [21]). The most common method of quantification of the compensation is comparing the performance of defoliated and untouched plants (HILBERT & al. [22]; ANTEN & al. [23]). In this study, compensatory growth is defined as an increase in relative leaf expansion rate – RLER of defoliated vines relative to untouched vines. Non-destructive and continuous measurements of mean and lateral leaf area based on the same shoots enabled the monitoring of the leaf area development and the calculation of the relative leaf expansion rate - RLER during vegetation.

The main aim of this study was to evaluate the changes in RLER caused by different defoliation times and to quantify its role as an indicator of compensation.

Material and methodes

The study was conducted from 2014 to 2016 at a commercial vineyard planted with Prokupac (*Vitis vinifera* L.) variety grafted on Kober 5bb (V. berlandieri × V. riparia) rootstock. Study plots were located at the Toplicki Vinogradi Winery near Prokuplje, Serbia. The location of the trial (lat. 43.12057" N; long. 21.25031" E; alt. 359 m) belongs to the vine-growing region of Toplica, wine district of Prokuplje. It has a temperate continental climate with an annual mean air temperature of 11.4°C and a seasonal mean temperature of 17,0°C. Total annual rainfall averages 556.7 mm, with 347.4 mm of rainfall during the growing season. The vineyard soil type is a lessive cambisol that has favorable physical characteristics. The vineyard was planted in 2009 with a planting space of 2.5 × 0.8 m (5000 plants per ha). The training system is a double Cordon de Royat with a trunk height of 60 cm. At pruning, six 2-node spurs were kept on the permanent cordon corresponding to a bud-load of 12 nodes per vine. The standard vineyard management practices, except main and lateral shoot tipping, were carried out in the study plots. The trials were set in a random complete block design with three blocks and four treatments per block. Defoliation was carried out by hand removal of six basal leaves. The vines were tagged and randomly assigned to the following treatments: (K) non-defoliated (control); (v1) removal of the first six basal leaves at the phenological stage 65 (full flowering: 50% of flowerhoods fallen according to BBCH scale, LORENZ & al. [24]); (v2) removal of the first six basal leaves at the phenological stage 73 (berries groat sized, ovary diameter varying from 3-5 mm); (v3) removal of the first six basal leaves at the stage 81 (ripening begining – veraison, berries begin to color).

The single leaf area, main shoot leaf area and lateral shoot leaf area were estimated according to BESLIC & al. [25]. During the period of 15-31 May of each year, 50 leaves were randomly collected from various vines in all experimental treatments. The leaves were immediately placed in plastic bags and kept and transported in a field refrigerator. Leaf area (LA) and the length of two inferior leaf veins (l) were measured using a computer scanner and Adobe Photoshop 7.0 in laboratory conditions. These data were used to calculate the regression between l and LA. The obtained formula (LA= −111.3242 + 14.4764 × l; $r^2 = 0,98$) was used for non-destructive calculation of leaf surface on the basis of leaf vein length data collected in the vineyard. Also, during the period of 15-31 May, 30 shoots were labeled randomly from each treatment and used for calculating the leaf area during vegetation. The main shoot leaf area (MLA) was calculated for all labeled shoots individually. Leaf number (NL), the largest (Lmax) and the smallest leaf area (Lmin) was then determined for each main shoot. Multiple regression analysis was used to obtain the relationship between the dependent variable MLA1 and three independent variables (NL, Lmax and Smin). The obtained formula (MLA= −1688.43 + 128.36 × NL + 4.83 × Lmax + 14.02 × Lmin; $r^2 = 0.892$) was used for non-destructive calculation of leaf surface area for main shoots. For the lateral shoots leaf area (LLA), the analogous formula was used: LLA= −520.212 + 50.462 × NL1 + 4.806 × Lmax + 3.739 × Lmin; $r^2 = 0.974$). According to the obtained formula, MLA, LLA and total leaf area (TLA = MLA + LLA) were calculated during tree vegetation in the next periods: first measurement was between 70 to 75 days after bud break (DAB); the second was between 85 to 90 DAB; the third was between 100 to 110 DAB and the fourth was between 125 to 130 DAB. Continuous LA measurement in these intervals was used for calculating the relative leaf expansion rate (RLER) that was calculated based on the following formula (DZAMIC & al. [26]):

$$RLER = (\ln LA_2 - \ln LA_1) / (t_2 - t_1)$$

LA_1 – leaf area at the beginning of the observation (t_1), LA_2 – leaf area at the end of the observation (t_2)

Data were processed and analyzed by standard statistical methods using software packages Statistica v.9.0 (StatSoft Inc., Tulsa, OK, USA). Differences between the treatments were tested by F test and Duncan's multiple range test.

Results and discussion

During the period of investigation, defoliation reduced the lateral leaf area in v1 vines by 40% more than the values found in other variants and control plants in the first measurements (DAB 70-75, Table 1). The first measurements of the LA were carried out about 20 days after defoliation of v1 vines. At that moment, the balance between source:sink organs was still not established after the removal of the basal leaves that are the source organs, which caused stagnation in vegetative development and delayed the lateral shoot emergence. Removal of the photosynthetic most active leaves from the fruiting zone during flowering causes a significant decrease in the whole vine photosynthesis and modifies the source:sink relationship (OLLAT & GAUDILLERE [27]; PETRIE & al. [10]; PONI & al. [12]; FRIONI & al. [28]). In a similar investigation of the defoliation effect on Prokupac (*Vitis vinifera* L.), BESLIC & al. [16] emphasized a growth stagnation of up to 30 days after basal leaf removal in stage 65 (BBCH scale). The next measurements were carried out in the second half of July (DAB 85-90), during intensive shoot growth and 20 days after v2 defoliation. This removal of leaves and lateral shoots from six basal nodes was reflected on LLA on v2 vines, in which the LLA was reduced by 50% compared to the control plants. Differences between v1 and v3, and the control plants, respectively, were statistically significant, too. A similar relationship between values of LLA were in the third measurements, which were carried out in a period of decreased growth of main and lateral shoots. Many investigations of grapevine growth in temperate climates, show that the intensity of shoot growth decreases from mid-summer (Mullis & al. [29]). The third measurements were performed before defoliation (v3), so there was no reduction in LLA of v3 vines. The fourth measurements of LLA were carried out after the defoliation at verasion (v3), when the final leaf area was mostly achieved. Defoliation of v3 vines reduced their LLA by 30% in comparison to the control plants. At the end of the observed period, significant differences in LLA were obtained between the control plants and v2, and v3, respectively. V1 vines had a significantly larger LLA with regard to v3. It is evident that the early defoliated vines (v1, v2) had time to compensate removed leaves by producing more lateral shoots with a greater number of leaves, which resulted in larger total LLA. As the intensity of shoot growth decreased during the vegetation, compensation growth was not sufficient to recover the reduction of total leaf area. The growth of new shoots and leaves was induced by lost source organs. Many studies have shown that early defoliation causes an increase in both main and lateral leaf area as a compensatory response (WEAVER [30]; CANDOLFI-VASCONCELOS & KOBLET [31]; HUNTER [21]; KURTURAL & al. [20]). In similar agroecological and experimental conditions, STEFANOVIC [32] obtained a significant increase in the lateral leaf area on the early defoliated Cabernet Sauvignon compared to both defoliated vines at veraison and nondefoliated ones. Autor emphasizes that the early defoliated vines were able to re-

Table 1. Average values of lateral leaf area (LLA) (m^2) by measurement terms (2014 – 2016).

Days after budbreak	LLA			
	V 1	V 2	V 3	Control
I (70-75)	0.100^{a}	0.177^{b}	0.194^{b}	0.193^{b}
II (85-90)	0.353^{b}	0.195^{a}	0.414^{c}	0.408^{c}
III (100-105)	0.523^{b}	0.415^{a}	0.615^{c}	0.629^{c}
IV (125-130)	$0.689^{b,c}$	$0.602^{a,b}$	0.532^{a}	0.759^{c}

a,b,c Values were grouped based on Duncan's multiple range test (α = 0.05), where different letters within the same row denote significant diferences between treatments. K - control; v1- removal of the first six basal leaves at the phenological stage 65 (BBCH scale); v2 - removal of the first six basal leaves at the phenological stage 73; v3 - removal of the first six basal leaves at the stage 81.

cover their leaf area as a compensatory response to the leaf removal.

Non-destructive and continuous measurements of MLA and LLA area based on the same shoots allowed for the monitoring of LA development and calculation of the RLER during vegetation. After the second measurements of LA, RLER-1 of the main and lateral shoots and all shoots on the vine was the highest on v1 and the lowest on v2 vines (Figure 1).

RLER-1 of lateral shoots on v1 vines was 72% higher than v2 and 41% higher than v3 and the control vines. The reason for the high value at v1 and low at v2, lies in the time of defoliation and the time of LA measurements. The second measurement of LA was performed about 40 days after v1 and 20 days after v2 defoliation. During that period, v1 vines passed through a period of slow growth of the main shoots caused by the carbon assimilation depression (OLLAT & GAUDILLERE, [27]; PETRIE & al. [10]). This was followed by a period of lateral shoot emergence and their intensive growth as compensation for the removed leaves. These results are consistent with the previous experiment on defoliation at flowering stage (CANDOLFI-VASCONCELOS & KOBLET [18]; PASTORE & al. [33]; ACIMOVIC & al. [34]). Unlike the v1 vines, v2 vines were still in the phase of slow growth which was caused by recently performed defoliation. The third measurement of LA and calculation of RLER-2 were 30 days after v2 and 10 days before v3 defoliation. On Figure 1. we can see that v2 vines have the highest RLER values compared to other variants, but the differences are not so pronounced as in the previous measurement. The values of the v2 vine are about 30% higher compared to other variants. As mentioned above, the third measurement was performed during the period of slower growth of the main and lateral shoots, so the level of compensatory growth is lower compared to shoots whose leaves were removed in the phase of intensive growth. The last measurement and RLER-3 calculations were performed about 10 days after v3 defoliation, in the veraison phase, when the growth of shoots is either very slow, or it stops. This result is in accordance with the previous studies (PASTORE & al. [33]; STEFANOVIC [32]). The authors emphasize a significant reduction in the total leaf area in defoliated vines in veraison stage because there was no leaf regrowth after veraison. For the calculated RLER based on the first and last leaf area measurements, a similar situation was obtained. The RLER of the main, lateral and all shoots on the vine were highest on v1 compared to all the variants between which there was no significant difference. This is consistent with the previous condition when the early defoliated vines had time to compensate removed leaves by producing more lateral shoots with more leaves.

Conclusions

Non-destructive and continuous measurements of leaf area based on the same shoots enabled the monitoring of the leaf area development and the calculation of the relative leaf expansion rate. The grapevine's ability to recover the leaf area after defoliation depends mainly on the time when defoliation occurs. This study has shown that early defoliated vines had time to compensate their removed leaves by producing more lateral shoots with a greater number of leaves, which resulted in a larger leaf area. Moreover, the results show that with a decrease in the intensity of shoot growth during vegetation, the recovery ability decreases, so the compensatory growth is not enough to restore the reduced leaf area. Based on the values of the relative leaf expansion rate, it can be concluded that defoliation in the period of intensive growth of shoots affects the stagnation of emergence of new shoots and leaves for several days, followed by a period of regrowth. Very slow or no growth of shoots and leaves occurs after the veraison stage.

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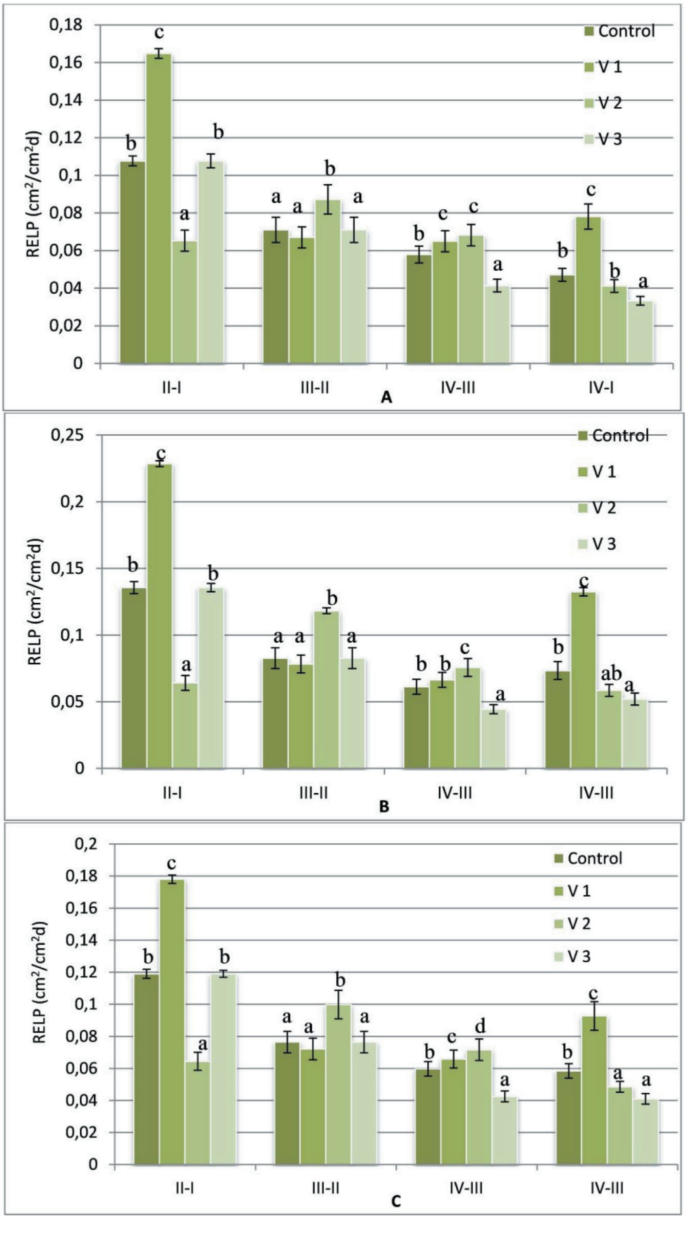

Figure 1. Relative leaf expansion rate (cm^2/cm^2d) of main (A), lateral (B) and total shoots (C). K - control; v1- removal of the first six basal leaves at the phenological stage 65 (BBCH scale); v2 - removal of the first six basal leaves at the phenological stage 73; v3 - removal of the first six basal leaves at the stage 81. (2014-2016).

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