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The effect of leaf area and crop level on the concentration of amino acids and total nitrogen in 'Thompson Seedless' grapes

by

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Introduction

The effects of crop load and leaf area on fruit development and vegetative growth of grapevines, and on total acidity, coloration of fruits, and concentration of sugar have been extensively investigated (4, 5, 7, 15, 16, 17, 18, 19, 20, 21). Overcropped vines are generally characterized by delayed fruit maturation, small berries, reduced vine growth, higher Balling/acid ratio at a given fruit maturity, poor fruit coloration, softness of berry texture, and reduced bud fruitfulness and crop yields the year following overcropping. Winkler (20) showed that fruits from vines with high leaf area/crop weight ratios were of higher quality than fruits from vines with lowest area/crop weight ratios. The sugar/acid ratio has generally been used as the criterion of fruit quality of grapes in California. The concentrations and ratios of other constituents in grapes, as they effect quality, have not been adequately investigated.

In none of the above investigations was the effect of crop size or leaf area on nitrogenous constituents of grapes studied. The purpose of this investigation was to determine the effect of leaf area and amount of crop on the concentrations of arginine, proline, total free amino acids, and total nitrogen in the juice of 'Thompson Seedless' grapes during the ripening period. Kliewer (3) has shown that arginine and proline are the two predominant amino acids in this variety.

Materials and Methods

Five-year-old, own-rooted vines of *Vitis vinifera* L., 'Thompson Seedless' (syn. 'Sultanina') growing in an irrigated vineyard at the University of California at Davis were used in the investigation. The vines were pruned to three canes with 14—20 buds per cane. The canes were tied to two horizontal wires about 30 inches apart and 54 inches from the ground.

In experiment I there were eight treatments. These included four levels of defoliation (50%, 33%, 25%, 20%) with 48 clusters per vine, and four crop levels (48, 36, 24, and 12 clusters per vine) with no defoliation (Table 1). Vines were defoliated by removing every second leaf (50% defoliation), or every third (33%), fourth (25%), or fifth (20%) leaf on each shoot and lateral per vine. The vines were defoliated June 6, about 15 days after anthesis. Newly arising leaves were subsequently removed in the same proportions as originally, on June 24 and July 29. There were six vines in each treatment, each vine serving as a replicate in a randomized complete block design.

Experiment II had seven treatments: two defoliation levels (25 and 50%) which were effected at three different times — June 2, June 25, and July 18. Vines not defoliated served as controls. The number of clusters per vine was not adjusted, and ranged from 59 to 85 in the various treatments (Table 2). The six vines in each ex-

Table 1

Effect of leaf area and size of crop on total soluble solids of 'Thompson Seedless' grapes at various times during the ripening period[1])

Amount of defoliation (percent)	No. of clusters per vine	Total leaf area per vine m²	Crop wt per vine at harvest kg	Leaf area per gram of fruit cm²/g	Total soluble solids (°B) July 31	August 14	August 28	September 11
50	48	12.63	14.40	8.89	13.3	17.8	20.8	23.4
33	48	12.59	16.07	7.86	13.9	18.0	20.5	22.6
25	48	13.43	17.51	7.59	13.9	17.8	20.4	22.8
20	48	14.45	17.72	8.22	14.0	17.9	20.3	22.6
0	48	17.57	24.14	7.24	13.6	16.9	19.1	21.2
0	36	17.48	20.92	8.73	14.3	17.8	19.6	22.2
0	24	16.99	15.00	11.58	14.9	19.0	21.3	23.2
0	12	20.57	8.04	25.94	16.3	20.2	22.2	23.9
L.S.D. ($P < 0.05$)					0.5	0.8	0.9	1.0

[1]) Data represent means of 6 replicates.

perimental treatment served as replicates in a randomized complete block design. The control was replicated 18 times. Leaves emerging after the first defoliation (June 2) were removed in the same proportions as originally, on June 26 and July 19. Leaves emerging after the second defoliation (June 25) were also readjusted on July 19. No further defoliations were made on vines defoliated July 18, as shoot growth had nearly ceased.

Fruits were sampled and extracted as described by Kliewer (5). Juice was analyzed for total soluble solids, arginine, proline, total free amino acids, and total nitrogen (3).

The crops from vines in experiments I and II were harvested September 12 and September 19, respectively. They were weighed and the number of clusters per vine counted. Beginning October 2, the fresh and dry weights of all leaf blades per vine were determined. The dry weight of leaf laminae per unit leaf area was determined from large numbers of samples taken from all parts of the treated and control vines 2 days prior to complete defoliation and used for calculating total leaf area per vine.

Results

Removal of 20 to 50% of the leaves on vines within 12 to 16 days after anthesis resulted in 27 to 40% reductions in crop yields, the decrease being proportional to the loss in leaf area (Tables 1 and 2). Removal of 25 or 50% of leaves from vines at the two later dates (June 25 and July 18) did not significantly reduce yields (Table 2). Vines with 36 clusters and no defoliation had significantly greater yields of fruit than did vines with 48 clusters and 25% of the leaves removed. Yields from vines with 24 clusters and no defoliation were about the same as from vines with 48 clusters and 50% defoliation (Table 1).

Neither defoliation nor reduction in number of clusters greatly affected the total soluble solids of fruits until either half the leaves were removed (cm² of leaf

Table 2

Effect of amount and time of defoliation of 'Thompson Seedless' vines on the concentrations of soluble solids, arginine, proline, total free amino acids, and total nitrogen in the juice of grapes at harvest[1])

Amount of defoliation (percent)	Date of defoliation	Number of clusters per vine	Total leaf area per vine	Crop wt per vine at harvest	Leaf area per gram fruit	Total soluble solids	Arginine	Proline	Total free amino acids (leucine equiv.)	Total N
		m^2	m^2	kg	cm^2/g	^0B	µg/ml	µg/ml	µg/ml	µg/ml
Control	None	75	19.43	30.35	6.57	20.7	350.5	293.7	2711	685.5
25	June 2	59	16.78	20.60	8.38	22.3	308.6	417.3	2865	710.0
50	June 2	65	15.13	19.00	8.29	22.6	280.2	407.0	2732	711.6
25	June 25	73	15.02	28.49	5.40	20.5	308.2	264.4	2461	632.3
50	June 25	79	12.12	28.70	4.29	18.2	334.4	201.5	2607	662.5
25	July 18	77	15.28	27.45	5.64	20.3	299.7	258.1	2551	645.8
50	July 18	85	12.24	27.70	4.47	19.0	264.4	200.3	2427	641.3
L.S.D. ($P < 0.05$) — Amount of defoliation				3.94		0.6	15.2	N.S.	N.S.	N.S.
L.S.D. ($P < 0.05$) — Time of defoliation				3.94		0.6	15.2	32.8	118.7	32.8

[1]) Data represent means of 6 replicates.

Table 3

Effect of leaf area and size of crop on concentration of arginine (μg/ml juice) in the juice of 'Thompson Seedless' grapes at various times during the ripening period[1])

Amount of defoliation (percent)	No. of clusters per vine	July 31	August 14	August 28	September 11
50	48	229.0 (12.1)	440.6 (21.9)	475.7 (23.5)	574 (27.7)
33	48	287.9 (15.5)	458.5 (23.6)	489.6 (24.8)	589 (32.7)
25	48	275.3 (15.2)	400.8 (19.4)	477.5 (24.15)	568 (27.0)
20	48	273.6 (15.3)	523.6 (25.9)	513.9 (25.8)	635 (29.4)
0	48	324.4 (17.8)	562.9 (27.5)	583.4 (29.2)	655 (30.7)
0	36	357.6 (19.1)	597.2 (29.1)	627.8 (30.3)	745 (34.6)
0	24	374.1 (19.2)	756.8 (33.2)	672.4 (29.9)	808 (33.6)
0	12	469.6 (20.6)	852.6 (33.8)	742.2 (30.6)	911 (37.3)
L.S.D. ($P < 0.05$)		54.2	73.7	97.1	91

[1]) Data represent means of 6 replicates. Values in parentheses are percent of total nitrogen.

area per gram of fruit less than 5, Table 2) or the number of clusters per vine reduced in half (cm^2 leaf area per gram of fruit greater than 10, Table 1).

The concentration of arginine in the fruits at each sampling date was considerably reduced by defoliation, but was greatly increased by reductions in the number of clusters per vine (Tables 2 and 3). Regression analysis revealed that the concentration of arginine in the berry juice was proportional to the total leaf area per vine (Fig. 1). A regression line, following the equation $Y = 28.2X + 242$, with a correlation coefficient of 0.72 (significant at the 0.1% level) was obtained, where Y = the concentration of arginine (μg/ml juice) and X = total leaf area per vine (m^2). The concentration of arginine greatly increased with fruit maturation. At the beginning of fruit ripening (July 31), arginine accounted for 12 to 20% of the total N in the juice. At harvest, arginine comprised 27 to 37% of total N.

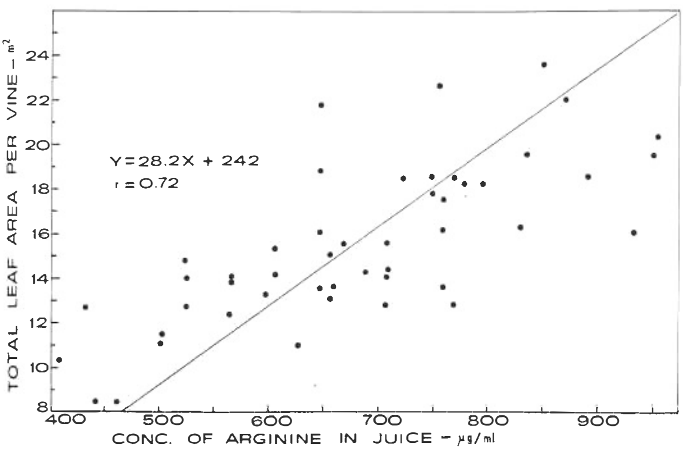

Figure 1: Regression of total leaf area per 'Thompson Seedless' vine (m^2) on concentration of arginine (μg/ml) in bery juice at harvest.

Table 4

Effect of leaf area and size of crop on concentration of proline (μg/ml juice) in the juice of 'Thompson Seedless' grapes at various times during the ripening period[1])

Amount of defoliation (percent)	No. of clusters per vine	July 31	August 14	August 28	September 11
50	48	98.3 (2.0)	201.1 (3.8)	265.9 (5.0)	380.2 (6.9)
33	48	100.9 (2.1)	192.4 (3.7)	256.0 (4.9)	319.4 (6.3)
25	48	107.7 (2.2)	182.8 (3.4)	242.9 (4.6)	331.2 (6.0)
20	48	105.6 (2.2)	205.1 (3.8)	257.3 (4.9)	352.4 (6.2)
0	48	88.3 (1.8)	160.0 (3.0)	226.2 (4.3)	266.9 (4.7)
0	36	101.3 (2.0)	184.9 (3.4)	237.0 (4.3)	288.1 (5.1)
0	24	123.8 (2.4)	221.2 (3.7)	298.4 (5.0)	389.1 (6.1)
0	12	180.2 (3.0)	291.6 (4.4)	358.8 (5.6)	455.2 (7.0)
L.S.D. ($P < 0.05$)		18.5	31.0	37.5	65.7

[1]) Data represent means of 6 replicates. Values in parentheses are percent of total nitrogen.

The data in Tables 2 and 4 indicate that the concentration of proline in the berry juice is directly related to fruit maturity (°B) and leaf area per unit weight of fruit. As with arginine, the concentration of proline greatly increased with fruit maturity. In the juices at harvest, the percent total N accounted for by proline ranged from 4.7 to 7.0%. A regression line was obtained for the relationship between concentration of proline in the berry juice and total soluble solids at harvest, following the equation $Y = 43.5X - 618$, in which Y = concentration of proline (μg/ml juice) and X = degree Brix. A correlation coefficient of 0.85 (significant at the 0.1% level) was obtained. The relationship between concentration of proline in fruits at harvest and cm^2 of leaf tissue per gram of fruit is shown in Fig. 3. A highly

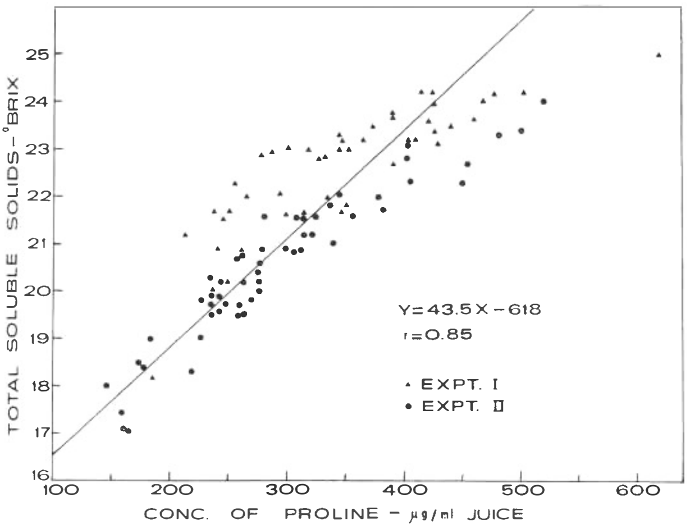

Figure 2: Regression of total soluble solids (°B) of 'Thompson Seedless' berry juice at harvest on concentration of proline (μg/ml juice).

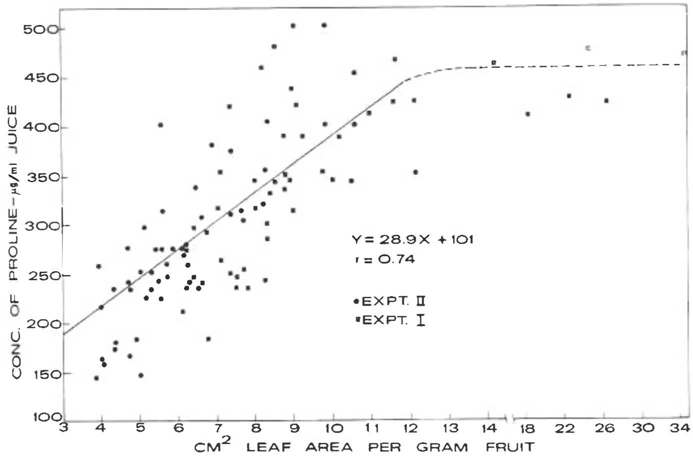

Figure 3: Regression of concentration of proline (μg/ml juice) in 'Thompson Seedless' fruits at harvest on square centimeters of leaf area per gram of fruit.

significant ($P < 0.001$) regression line following the equation $Y = 28.9X + 101$, in which Y = concentration of proline (μg/ml juice) and X = cm^2 leaf area per gram of fruit, was fitted to the values of all vines in both experiments, except the six vines in which the number of clusters was reduced to 12. The data indicate that the concentration of proline reaches a plateau at about 12 to 14 cm^2 leaf area per gram of fruit.

The ratio of arginine to proline decreased with fruit maturity (Table 5), indicating that the concentration of proline increased at a faster rate than that of arginine during the latter stages of fruit ripening. Also as crop weight decreased, as a result of either defoliation or cluster removal, the arginine/proline ratio decreased. These data indicate that the larger the crop, the greater will be the concentration of arginine in relation to that of proline.

With vines not defoliated, the concentrations of total free amino acids and total N in the berry juices generally increased with a decrease in crop weight per vine (Tables 6 and 7). These concentrations were usually lower in fruits from de-

Table 5

Effect of leaf area and size of crop on ratio of arginine to proline in the juice of 'Thompson Seedless' grapes at various times during the ripening period

Amount of defoliation (percent)	No. of clusters per vine	July 31	August 14	August 28	September 11
50	48	2.33	2.19	1.86	1.51
33	48	2.85	2.38	1.91	1.65
25	48	2.55	2.19	1.83	1.74
20	48	2.59	2.55	1.99	1.92
0	48	3.68	3.52	2.57	2.47
0	36	3.53	3.23	2.64	2.40
0	24	3.02	3.42	2.25	2.09
0	12	2.60	2.92	2.06	2.02

Table 6

Effect of leaf area and size of crop on concentration of total free amino acids (μg leucine equivalents/ml juice) in the juice of 'Thompson Seedless' grapes at various times during the ripening period[1])

Amount of defoliation (percent)	No. of clusters per vine	July 31	August 14	September 11
50	48	2860 (66.6)	2870 (69.2)	2828 (70.1)
33	48	2902 (70.7)	2709 (71.0)	2722 (75.7)
25	48	2985 (73.8)	2776 (64.2)	2876 (69.7)
20	48	2995 (74.7)	2665 (67.2)	2813 (68.7)
0	48	2811 (71.1)	2891 (71.8)	2791 (69.6)
0	36	2858 (71.2)	2852 (74.0)	2936 (76.5)
0	24	3010 (72.1)	3024 (72.1)	3006 (69.1)
0	12	3420 (71.3)	3330 (72.1)	3283 (75.1)
L.S.D. ($P < 0.05$)		219	213	167

[1]) Data represent means of 6 replicates. Values in parentheses are percent of total nitrogen.

Table 7

Effect of leaf area and size of crop on concentration of total nitrogen (μg/ml juice) in the juice of 'Thompson Seedless' grapes at various times during the ripening period[1])

Amount of defoliation (percent)	No. of clusters per vine	July 31	August 14	August 28	September 11
50	48	607.0	646.3	649.8	665.6
33	48	597.1	624.3	635.3	620.6
25	48	582.0	664.8	635.8	677.1
20	48	577.0	650.1	640.6	694.8
0	48	586.5	658.8	642.5	687.0
0	36	602.5	658.8	666.7	691.1
0	24	625.8	732.8	724.5	774.0
0	12	731.8	811.0	780.0	786.1
L.S.D. ($P < 0.05$)		57.2	52.6	51.3	79.3

[1]) Data represent means of 6 replicates.

foliated vines than in fruits from intact vines, when comparisons were made with vines of approximately the same crop weight (Table 2). However, the concentrations of free amino acids and N in fruits from vines defoliated 20 to 50% (Experiment I) did not differ greatly at harvest from the concentrations in fruits from nondefoliated vines (48 clusters); but total free amino acid and amount of N in all fruits per vine were greatly reduced due to the large reductions in crop yield (Tables 6 and 7). Total free amino acids, including arginine and proline, was estimated to account for 64 to 75% of the total N in the juice of grapes during the period of fruit ripening (Table 6).

The relationship between total N in the juice at harvest and cm^2 leaf area per gram of fruit is shown in Fig. 4. A linear regression line following the equation $Y = 7.0X + 625$, in which Y = concentration of N (μg/ml juice) and $X = cm^2$ leaf area per gram of fruit, was fitted to the values of all vines in both experiments, disregarding treatment. A correlation coefficient of 0.47 (significant at the 0.1% level) was obtained.

Discussion

The concentrations of arginine, proline, total free amino acids, total nitrogen, and total soluble solids in the juice of grapes from vines with reduced number of clusters and crop weights were significantly higher than in fruits from vines with larger crop weights (Tables 1, 3, 4, 6, 7). These data may be explained by source-sink relationships. The greater the source of nutrients, i. e., leaf area for carbohydrate synthesis and root area and volume for nitrogen uptake and amino acid storage in relation to the size of the sink (weight or number of fruits), the higher the concentration and total amount of these substances that should be in the fruits. As the crop size decreases relatively, there is less competition for photosynthate and nitrogenous compounds, and therefore a greater supply of these substances available for the remaining fruits. This explanation is supported by the correlations between total leaf area and concentration of arginine in the berry juices (Fig. 1) and leaf area per gram of fruit and concentration of nitrogen in the juice (Fig. 4). Kliewer (1)

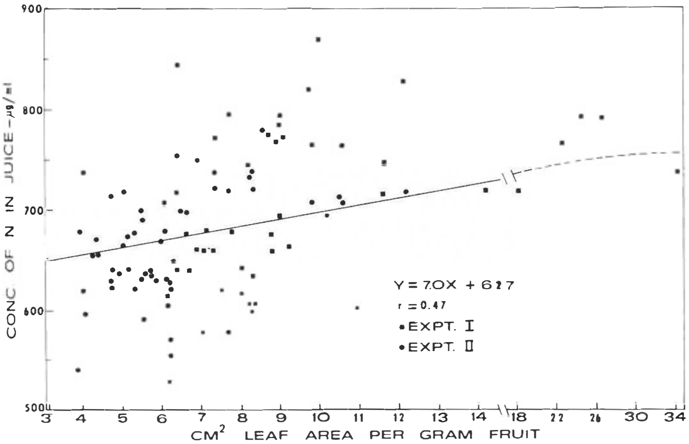

Figure 4: Regression of concentration of nitrogen (μg/ml juice) in 'Thompson Seedless' fruits at harvest on square centimeters of leaf area per gram of fruit.

found that arginine is the main form of storage nitrogen in the roots and other storage parts of 'Thompson Seedless' grapevines. Ough, Lider, and Cook (11) reported a close correlation between total nitrogen in berry juices from 10 grape varieties and the logarithm of brush weight per unit crop weight. Since brush weights are closely correlated with total leaf area per vine (Winkler, 19) Ough's data support the findings in this investigation.

Lafon-Lafourcade and Guimberteau (6), Kliewer (2, 3), and Ough (9) have shown that the concentration of proline greatly increases during fruit maturation. The data in Fig. 2 indicate that the concentration of proline in the berry juices of fruits sampled on the same day is closely correlated with total soluble solids and with leaf area per gram of fruit. Unpublished data of KLIEWER, KASIMATIS, and LIDER reveal a highly significant correlation between total soluble solids in berry juices and leaf area per unit weight of fruits from vines used in the present investigation. Proline is not found in large amounts in the leaves, roots, or other storage parts of the vine (NASSAR and KLIEWER, 8), and there is considerable indirect evidence indicating that proline is synthesized in the fruits (KLIEWER 2, 3). The direct relationship between total soluble solids and concentration of proline in the berry juice may indicate that the enzymes necessary for proline synthesis are related in some manner to the ripening processes in grapes.

The concentration of arginine in berry juice correlated erratically with total soluble solids and leaf area per unit weight of fruits. The level or arginine, like proline, greatly increases during the ripening period. Arginine often accumulates in seeds, fruits, and other storage organs of plants (REUTER, 14). The accumulation of arginine in fruits may provide a mechanism for utilization of excess ammonia, which generally decreases with fruit maturation (6, 9).

The results in this investigation emphasize the importance of crop size and leaf area, and their ratio, in comparing the concentrations of various nitrogenous compounds and soluble solids in juices of fruits from different vines. Too often, crop size is not a controlled variable, and validity of the results may be open to question. When studying the effects of such things as growth regulators, root-stocks, and fertilizers, for example, vines of the same age and nearly equal leaf area, and with equal numbers of clusters or crop weight, should be used in comparing the concentration of various constituents in fruits.

Total nitrogen accounted for by total free amino acids (assuming a nitrogen content of 12.6% for all amino acids other than arginine and proline) ranged from 64 to 75% during the period of berry ripening (Table 6). These data are in close agreement with the findings of OUGH and AMERINE (10), OUGH *et al.* (11, 12), and KLIEWER (3). The nitrogen not accounted for by the free amino acids would include that in proteins, peptides, nucleotides, nucleosides, ammonia, and nitrates. OUGH (9) reported that ammonia nitrogen accounted for 10 to 18% of the total nitrogen in the must of 'White Riesling' and 'Cabernet-Sauvignon' grapes.

WINKLER (21) has stressed the importance of maintaining enough leaf area per unit weight of fruits to produce grapes of high quality for table, raisin, and wine production. With 'Thompson Seedless', KLIEWER and ANTCLIFF (4) and KLIEWER (5) found that about 8 to 10 cm^2 leaf area per gram of fruits were required to ripen the crop fully without decreasing the total soluble solids. The data in Fig. 3 and 4 indicate that 10 to 14 cm^2 leaf area per gram of fruits are required for maximum concentrations of proline and total nitrogen in berry juices. The concentration of arginine in grapes also reached a maximum level when cm^2 of leaf area per gram reached about 12. Relatively little is known regarding the effect of concentration of various amino acids on quality of grapes, either as table fruits or for wine production. Generally wines made from must of extremely high total nitrogen or must with very low nitrogen are of lower quality. OUGH and KUNKEE (13) reported that the concentrations of total N and ammonia in must affects the rate of fermentation and thus may affect winery efficiency.

Summary

20 to 50% of the leaves and 25 to 75% of the clusters on 'Thompson Seedless' vines were removed 12 to 16 days after anthesis. In addition, 25 and 50% of the

leaves on other vines were removed 35 and 58 days after anthesis, with no cluster thinning.

Total soluble solids in fruits from vines with less than 5 cm^2 of leaf surface per gram of fruits was markedly reduced, while concentration in fruits from vines with a ratio above 10 was considerably higher, compared to the concentration in fruits from vines with ratios intermediate between these two values. The concentrations of arginine, proline, total free amino acids, and total N in berry juice were greatly increased by reducing the crop load. Also, the concentration of each of these substances increased during fruit ripening.

A significant correlation between leaf area per vine and level of arginine in the juice was obtained. The concentration of proline in the juice was highly correlated with fruit maturity (°B) and with leaf area per unit weight of fruits. Total nitrogen was also correlated with leaf area per unit weight of fruits. Between 4 and 12 cm^2 leaf area per gram of fruits there was a linear increase in the concentration of proline and total nitrogen in berry juice, while above 12 cm^2 there was generally little further increase in the level of these substances. The ratio of arginine to proline decreased with fruit maturity and with smaller crop weights per vine. Total free amino acids accounted for 64 to 75% of the total nitrogen in the juice of grapes during the fruit-ripening period. Defoliation within 16 days after anthesis reduced crop yields, while later defoliations did not significantly reduce yields.

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