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High Root-Zone Temperatures Inhibit Growth and Development of *Fragaria* Species[1].

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Abstract

The influence of root-zone temperature on strawberry species has not been thoroughly studied. Two experiments were conducted to determine the effect of root-zone temperature on vegetative growth, runner number, runner plant development, and water relations in *Fragaria chiloensis* Duch., *F. virginiana* Duch., and *F. viridis* Duch. In Experiment I, clones of *F. chiloensis* 'FRA 366' that originated in California, *F. chiloensis* 'FRA 606' (Alaska), *F. virginiana* 'FRA 67' (Maryland), and *F. virginiana* 'FRA 104' (Wyoming) were grown hydroponically for 21 days with root zones at 23, 29, or 35°C. All clones with roots held at 35°C had less fresh mass gain over time, fewer runners, fewer runner plants, less leaf area on mother and runner plants, and less root dry mass than plants at 23 or 29°C. Plants at 29°C had less runner plant leaf area than plants at 23°C. *F. virginiana* exhibited greater vegetative growth and produced more runners and runner plants than *F. chiloensis*, but there were no species-temperature interactions. In Experiment II, *F. chiloensis* 'FRA 366' (mother plants originating in California) and *F. viridis* 'FRA 333' (Germany) were grown hydroponically for 56 days with root zones at 23, 29, 35, 20/26 (night/day), 26/32 , or 32/38°C. *F. viridis* was more sensitive to high root-zone temperature than *F. chiloensis*, and most growth reductions were associated with reduced transpiration and leaf water potential. A low temperature (23°C) promoted maximum growth of *F. viridis*, whereas exposure to root-zone temperatures as high as 32°C fostered maximum growth of *F. chiloensis*.

Introduction

The influence of root-zone temperature on strawberry species has not been thoroughly studied. Air temperature has been shown to affect strawberry plant growth and development. In growth chamber studies air temperatures of 35 to 40°C inhibited runner development (9). Under long and short days, runner production is favored at an air temperature of 21°C whereas flower production is favored at 15.5°C (3). Root-zone temperatures ≥17°C decreased organic N concentration in leaves of *F. x ananassa.* Duch. fed NO_3±N and decreased organic N concentration in roots and leaves of *F. x ananassa* fed NH_4±N (6). The optimal root-zone temperature for growth of other plant species, such as apple, peach and maple, has been studied (1,13,14), but the influence of root-zone temperature on strawberry growth has not been thoroughly studied.

F. chiloensis and *F. virginiana* were the primary species of strawberry hybridized to produce *F. x ananassa*, the cultivated strawberry. *F. chiloensis*, *F. virginiana* and *F. viridis* differ morphologically and in response to environmental factors. For example, *F. chiloensis* is more drought tolerant than *F. virginiana* (2,8, 12). *F. chiloensis*, *F. virginiana* and *F. viridis* may differ in response to root-zone temperature as well. Their geographical distributions and ecological adaptations differ and have been described by Darrow (2) and Hancock et al. (8). *F. chiloensis* is found along the Pacific coast, from Alaska through central California, along the beaches of Chile and somewhat inland in the Andes Mountains, and at upper elevations on

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the mountains of Hawaii. *F. virginiana* is found in the meadows of eastern and central North America, from Louisiana and Georgia to Hudson Bay and the Dakotas. *F. viridis* is native to most of Europe and western and central Asia, including Siberia, and is found in grassy meadows and steppes and forest edges.

The objective of this research was to determine the effect of root-zone temperature on vegetative growth, runner number, and runner plant development of *F. chiloensis, F. virginiana,* and *F. viridis.* During the second week of July the average soil temperature in Iowa at a depth of 6 cm is approximately 30°C, the average daily soil temperature low is 27°C, and the average daily high is 32°C (4). An understanding of the effect of root-zone temperature on the growth, development, and physiology of *F. chiloensis , F. virginiana,* and *F. viridis* would benefit plant breeders, physiologists, and pomologists developing strawberry production systems.

Materials and Methods

Midwestern root-zone temperatures in summer were simulated by growing *F. chiloensis , F. virginiana* and *F. viridis* clones at constant root-zone temperatures of 23, 29, or 35°C in a hydroponic system. Daily high and low soil temperatures were simulated by growing *F. chiloensis* and *F. viridis* at cyclic temperatures of 20/26 (night/day), 26/32, or 32/38°C in a hydroponic system.

Experiment I. Growth with constant root-zone temperatures. Two clones each of *F. chiloensis* and *F. virginiana* were used in this study. *F. chiloensis* 'FRA 366' (mother plants that originated in California), *F. chiloensis* 'FRA 606' (Alaska), *F. virginiana* 'FRA 67' (Maryland), and *F. virginiana* 'FRA 104' (Wyoming) were obtained from James Luby, Univ. of Minnesota, through the National Germplasm Repository in Corvallis, OR. Runner plants were rooted for two weeks in 500 ml of quarter-strength Hoagland solution #1 with Fe as FeEDDHA and a pH of 6 (10). The solution was replaced at 7-day intervals. After 14 days, runner plants were severed from mother plants and from each other before individual placement into 500 ml of half-strength Hoagland solution #1 for 7 days.

The fresh mass of each runner plant was determined 24 h before treatments were initiated. Plants were then placed individually into 1.9-L stainless-steel pots filled with aerated, half-strength Hoagland solution #1. Each stainless-steel pot was housed within a polyvinyl chloride container through which temperature-controlled water circulated. The system to control root-zone temperature was similar to the system described by Graves and Dana (7). Four replications (blocks), each with three runner plants from all clonal selections, were included in the experiment. Within blocks, one plant from each clonal selection was randomly assigned to a root-zone temperature treatment of 23, 29, or 35°C for 21 days.

The experiment was conducted twice. Repetition one was initiated on 20 June 1995, and repetition two was initiated on 13 July 1995 (each day 0). Temperature adjacent to the leaf canopy, relative humidity, and midday photosynthetically active radiation were measured once weekly between 1200 and 1400 HR with a steady-state porometer (Li-Cor Inc., LI-1600, Lincoln, NE). Measurements for the two repetitions were averaged. The mean temperature adjacent to the leaf canopy was 22.7°C (s.d. = 0.1), mean relative humidity was 50.4% (s.d. = 5.3), and mean midday photosynthetically active radiation was 335 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (s.d. = 77.4). Natural radiation was supplemented daily for 20 h with high-pressure sodium lamps. Solution temperatures were measured twice weekly between 0800 and 1000 HR with a thermocouple thermometer. Mean root-zone temperature for each temperature treatment and repetition were calculated and averaged. Solution temperatures were maintained at 23.2 ± 0.2, 29.0 ± 0.2 , and 34.8 ± 0.2°C . The nutrient solution was replaced on days 7 and 14. Deionized

water was added to the stainless-steel containers every 3 to 4 days to replace solution lost by transpiration and evaporation.

The fresh mass of each plant was determined on days 7, 14, and 21. Percent fresh mass gain from day 0 was calculated. Plants were harvested on day 21 and the number of runners, runner plants, and crowns were counted. Mother plant and runner plant leaf areas were measured (Li-Cor Inc., Ll-3100 Area Meter, Lincoln, NE). Leaf area of all runner plants from each mother plant was taken as one measurement. Runners, plants from runners, roots, crowns, and mother plant leaves and petioles were dried for 72 h at 67 °C before determining dry mass and calculating total plant dry mass.

Data from both repetitions were combined. Data were analyzed by using an analysis of variance (ANOVA) for a randomized complete block design with four replications and a factorial arrangement of three root-zone temperatures and four clones. Data for each temperature and for each strawberry clone were pooled and analyzed by using an ANOVA. The least significant difference (LSD) between means was determined with the Statistical Analysis System at $P \leq 0.05$ (SAS Institute, Cary, NC).

Experiment II. Growth at constant and cyclic root-zone temperatures. F. chiloensis 'FRA 366' (mother plants originating in California) and *F. viridis* 'FRA 333' (Germany) were obtained from James Luby, Univ. of Minnesota, through the National Germplasm Repository in Corvallis, OR. Runner plants were rooted and placed into a hydroponics system in the same manner as in Expt. I. Four blocks, each with six runner plants from each clonal selection, were included in the experiment. Within blocks, one plant from each clonal selection was randomly assigned to a constant root-zone temperature treatment of 23, 29, or 35 °C and one plant from each clonal selection was randomly assigned to a cyclic root-zone temperature treatment of 20/26 (night/day), 26/32, or 32/38°C. Plants in the cyclic treatments were grown for 8 h at the low temperature, for 4 h at a transition period to the high temperature, and for 8 h at the high temperature followed by a 4 h transition period to the low temperature. Treatments lasted for 56 days.

The experiment was initiated on 21 March 1996 (day 0). Temperature adjacent to the leaf canopy, relative humidity, and midday photosynthetically active radiation were measured once weekly between 1200 and 1500 HR. The mean temperature adjacent to the leaf canopy was 23.9°C, mean relative humidity was 31.1%, and mean midday photosynthetically active radiation was 754 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Solutions in the temperature treatments were measured twice weekly between 0800 and 1000 (AM), and 1200 or 1500 (PM) HR as described for Expt. I. Solution temperatures (°C) were maintained in the constant temperature treatments at 23.0 ± 0.01 during AM, 23.5 ± 0.01 during PM; 28.4 ± 1.0 during AM, 29.1 ± 0.4 during PM; 33.7 ± 0.2 during AM and 35.2 ± 0.3 during PM. Solutions for plants in the cyclic temperature treatments were measured at 24.1 ± 0.1, 25.9± 0.2, and 31.6 ± 0.1 during AM at the transition phase from low to high temperatures and were measured at 25.2 ± 0.2, 32.1 ± 0.1 and 37.7 ± 0.1 during PM at the high temperature phase. The nutrient solution was replaced and replenished as in Expt. I.

The fresh mass of each plant was determined on days 0 and 56. Percent fresh mass gain from day 0 was calculated. Transpiration was measured on day 55 with a steady-state porometer (Li-Cor Inc., LI-1600, Lincoln, NE). Water potential was measured on day 56 with a Ψ pressure chamber (PMS Instruments, Corvallis, OR). Plants were harvested on day 56 and vegetative data were collected as in Expt. I.

Data were analyzed by using an ANOVA for a randomized complete block design with four replications and a factorial arrangement of six root-zone temper-

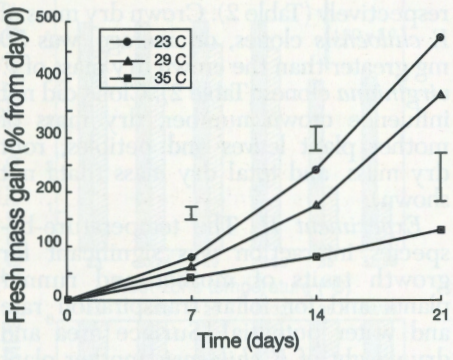

Figure 1. Effect of root-zone temperature on percent gain in fresh mass averaged over four strawberry clones over time. Means are from two repetitions, each involving four single plant replications. Vertical bars indicate LSD at $P \leq 0.05$ (day 7 = 18%, day 14 = 46%, day 21 = 102%).

atures and two species treatments. The effects of temperature, species and their interaction were assessed using ANOVA. LSD between means was determined at $P \leq 0.05$.

Results

Experiment I. Differences between repetitions were not significant and therefore averaged (data not shown). There were no interactions between main effects (data not shown). Therefore, differences related to temperatures over all strawberry clones and differences related to strawberry clones over all temperatures are reported.

Over all strawberry clones on day 14, plants with roots at 23°C had gained nearly three times more fresh mass than plants at 35°C, and plants at 29°C gained more than twice as much fresh mass as plants at 35°C (Fig. 1). On day 21, average fresh mass gains of plants at 23 and 29°C, were 3.5 times more than plants at 35°C (Fig. 1).

Plants at 23°C had 3.0 runners and 2.6 runner plants whereas plants at 35°C had 1.7 runners and 1.1 runner plants (Table 1). Root-zone temperature did not influence crown number (data not shown). Leaf area of mother plants at 23 and 29 °C was not different and was 62% more than the leaf area of mother plants at 35 °C (Table 1). The leaf area of runner plants at 35°C was one third the leaf area of runner plants at 29°C and one sixth the leaf area of runner plants at 23°C (Table 1). Runner dry mass and runner plant dry mass at 23°C was more than twice that of plants at 35°C (Table 1). The root dry mass of plants at 23 and 29°C was twice the root dry mass of plants at 35°C (Table 1). Root-zone temperature did not influence the dry mass of mother plant leaves and petioles, crown dry mass, and total dry mass (data not shown).

Over all temperatures, percent fresh mass gain on days 7, 14, and 21 varied among clones (Fig. 2). Fresh mass gain on day seven ranged from 47% for *F. chiloensis* 'FRA 366' to 80% for *F. virginiana* 'FRA 104' (Fig. 2). The range in fresh mass gain increased successively on days 14 and 21 (Fig. 2). Over all temper-

Table 1. Effect of root-zone temperature over all clones on number of runners, number of runner plants, leaf area of mother and runner plants, and dry mass of runners, runner plants, and roots of strawberry.

Root-zone temperature (°C)	No. of runners	No. of runner plants	Leaf area (cm^2)		Dry mass (mg)		
			Mother plant	Runner plants	Stolon	Runner[y] plant	Root
23	3.0[z]	2.6	114	31	280	110	260
29	2.5	1.9	126	17	220	90	250
35	1.7	1.1	74	5	120	40	120
LSD ($P \leq 0.05$)	0.6	0.7	34	9	100	60	60

[z] Means of two repetitions, each involving four single-plant replications per treatment.
[y] Runner plant dry mass includes leaves and crowns.

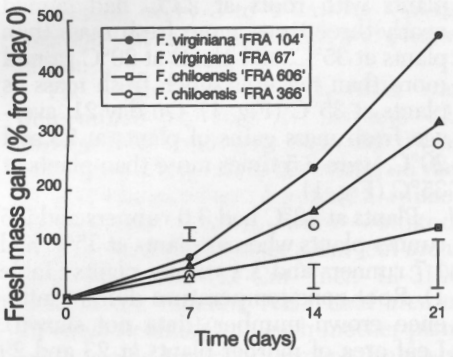

Figure 2. Effect of strawberry clone on percent gain in fresh mass over time. Means are from two repetitions, each involving four single plant replications. Vertical bars indicate LSD at P ≤ 0.05 (day 7 = 22%, day 14 = 53%, day 21 = 118%).

atures, *F. virginiana* 'FRA 104' had the most runners, runner plants, runner plant leaf area, and runner and runner plant dry mass, whereas *F. chiloensis* 'FRA 366' had the least biomass, except for crown dry mass (Table 2). *F. chiloensis* 'FRA 606' and *F. virginiana* 'FRA 67' had similar numbers of runners and runner plants, mother and runner plant leaf area, and runner plant dry mass (Table 2). Leaf area of mother plants from *F. chiloensis* 'FRA 606' were 50 cm^2 and 74 cm^2 greater than those of *F. virginiana* 'FRA 104' and *F. chiloensis* 'FRA 366', respectively (Table 2). Crown dry mass of *F. chiloensis* clones, on average, was 50 mg greater than the crown dry mass of *F. virginiana* clones (Table 2). Clone did not influence crown number, dry mass of mother plant leaves and petioles, root dry mass, and total dry mass (data not shown).

Experiment II. The temperature-by-species interaction was significant for growth traits of mother and runner plants and for foliar transpiration rate and water potential. Surface area and dry weight of *F. chiloensis* mother plant leaves were not affected by temperature. However, exposing roots of *F. viridis* to 20/26 and 32/38°C cyclically, and to 35°C continuously, reduced mean leaf area to 50, 19, and 20%, respectively, of the leaf area of plants at 23°C (Table 3). Similar effects on leaf dry weight were observed (Table 3). For *F. chiloensis*, root dry weight was reduced by continuous exposure to 35°C and by cyclic exposure to 32/38°C, whereas for *F. viridis*, any exposure to temperatures of 26°C, and higher, reduced root dry weight (Table 3). Continuous exposure to 35°C suppressed gains in plant fresh mass of both species by ≈90% compared to the gains in fresh mass at 23°C (Table 3). For *F. viridis*, a similar reduction in fresh mass gain was observed for plants exposed cyclically to

Table 2. Effect of strawberry clone over all temperatures on number of runners, number of runner plants, leaf area of mother and runner plants, and dry mass of runners, runner plants, and crowns.

Clone	No. of runners	No. of runner plants	Leaf area (cm^2)		Dry mass (mg)		
			Mother plant	Runner plants	Stolon	Runner[z] plant	Crown
F. chiloensis 'FRA 366'	1.1[y]	0.5	70	2	90	30	120
F. chiloensis 'FRA 606'	2.3	1.3	144	8	28	80	150
F. virginiana 'FRA 67'	2.3	1.4	110	17	180	80	110
F. virginiana 'FRA 104'	3.8	4.3	94	43	300	140	60
LSD (P ≤ 0.05)	0.6	0.8	39	11	120	60	30

[z] Runner plant dry mass includes leaves and crowns.
[y] Means of two repetitions, each involving four single-plant replications per treatment.

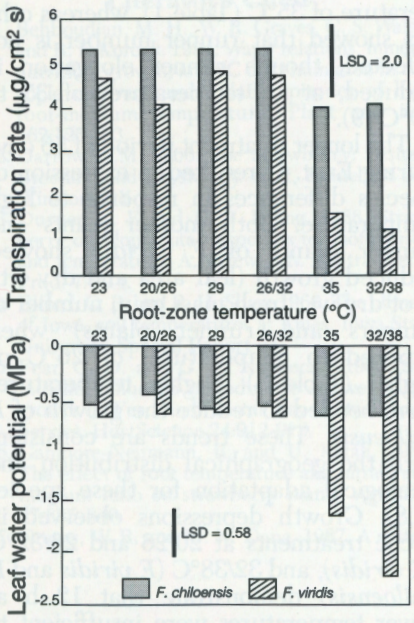

Figure 3. Effect of root-zone temperature on transpiration rate and leaf water potential of *Fragaria chiloensis* and *F. viridis*. Histograms represent means of four replications. Vertical bars indicate LSD at $P \leq 0.05$.

32/38°C, and cyclic exposure to 20/26°C reduced fresh mass gain by 44%.

Temperature did not affect the number of runners in *F. chiloensis*, but there were comparatively few runners on *F. viridis* plants exposed to 35°C continuously and to 32/38°C cyclically (Table 3). Likewise, these two temperature treatments reduced the number of *F. viridis* runner plants by ≈77% compared to the number at 23°C, while the number of *F. chiloensis* runner plants did not vary with temperature (Table 3). There were pronounced reductions in leaf area and leaf dry weight of runner plants of both species when roots were exposed to temperatures >32°C. For example, the surface area and dry weight of leaves on runner plants of *F. chiloensis* with roots at 35°C were reduced by 93% and 87%, respectively, compared to plants grown with roots at 23°C (Table 3). Cyclic exposure to 32/38°C reduced the surface area and dry weight of leaves on runner plants of *F. viridis* by 95% and 91%, respectively, compared to plants at 23°C (Table 3).

F. chiloensis and *F. viridis* plants with roots at 23 and 29°C continuously and with cyclic exposure to 20/26°C and 26/32°C had similar rates of transpiration and leaf water potentials (Fig. 3). Plants of *F. viridis* with roots continuously at 35°C or cyclically exposed to 32/38°C

Table 3. Effect of constant and cyclic temperature treatments on growth and development of *Fragaria chiloensis* and *F. viridis* species[z].

Species	Mother Plant				Runner Plants			
Temperature (°C)	Leaf Area (cm^2)	Leaf dry wt. (g)	Root dry wt.(g)	Fresh Mass Gain (%)	No. of runners	No. of runner plants	Leaf area (cm^2)	Leaf dry wt. (g)
F. chiloensis								
23	187	1.7	1.01	17.8	4	24	632	4.8
20/26	203	2.1	0.85	13.5	4	24	511	4.0
29	201	2.0	1.07	14.7	4	23	597	4.3
26/32	182	1.9	0.91	14.3	4	23	508	4.0
35	79	1.3	0.27	1.8	3	8	43	0.6
32/38	102	1.3	0.32	4.7	3	11	94	1.1
F. viridis								
23	538	3.1	1.90	35.0	11	82	1519	7.5
20/26	271	1.7	1.19	19.7	8	41	827	4.2
29	375	2.2	1.17	29.8	10	58	903	4.4
26/32	406	2.4	1.28	28.8	9	57	1045	5.4
35	104	0.9	0.20	3.0	4	19	104	0.9
32/38	105	1.0	0.20	2.8	4	18	77	0.7
LSD ($P \leq 0.05$)	173	1.1	0.51	14.4	3	18	467	2.3

[z] Means of four replications.

had reduced transpiration and leaf water potential, but those temperature regimes did not alter the water relations of leaves of *F. chiloensis* (Fig. 3).

Discussion

In Expt. I, differences in vegetative growth, runner number, and runner plant development among *F. chiloensis* 'FRA 366', *F. chiloensis* 'FRA 606', *F. virginiana* 'FRA 67' and *F. virginiana* 'FRA 104' were not due to temperature effects, but due to species and clonal effects. An elevated root-zone temperature of 35 °C inhibited vegetative growth, runner number, and runner plant development. Reduced growth at 35°C indicates that an elevated root-zone temperature inhibits optimal growth of *F. chiloensis* and *F. virginiana* (Fig. 1, Table 1). Elevated root-zone temperatures influence apple growth in similar ways. A root-zone temperature of 34°C for 24 h/day for 7 days decreases leaf and root growth of 'Royal Gala' apples (1). Root growth of peach seedlings, however, is suppressed at root-zone temperatures of 8 to 10°C and increases with increasing root-zone temperatures (13).

In our study, smaller mother plant leaf areas may have reduced photosynthesis and resulted in lower fresh mass gain. Less root growth at 35°C may have inhibited growth because of potentially limited nutrient uptake. Potassium in roots of 'Shasta' and 'Lassen' California strawberries decreased with increasing root-zone temperatures (11).

Mulches have been used to reduce soil temperatures in day-neutral strawberry production (5). Because the results of our study show that elevated root-zone temperatures reduce strawberry plant growth, mulches to reduce soil temperature should be used in areas with high soil temperatures.

Root-zone temperature and air temperature affected runner development differently. In our experiment, runner number was reduced at a root-zone temperature of 35°C (Table 1), whereas others showed that runner number is not affected, though runner elongation is reduced, at air temperatures of 35 to 40°C (9).

The longer treatment period of 56 days during Expt. II resulted in expression of species differences in response to high temperature. Both mother plants and runner plants of *F. viridis* showed reduced growth (leaf area and dry wt., root dry wt., fresh mass gain, number of runners and runner plants) when exposed to temperatures of 26°C or higher (Table 3). Higher temperatures were needed to reduce the growth of *F. chiloensis*. These trends are consistent with the geographical distribution and ecological adaptation for these species (2,8). Growth depressions observed in cyclic treatments at 20/26 and 26/32°C (*F. viridis*), and 32/38°C (*F. viridis* and *F. chiloensis*) demonstrate that 12 h at lower temperatures were insufficient to mitigate the effects of the higher temperatures during the daytime (Table 3).

Reduced growth of *F. chiloensis* at 35°C and 32/38°C was not the result of impaired water uptake because transpiration rates and leaf water potentials were not different from those at lower temperatures (Fig. 3). In contrast, the reduced transpiration rates and water potentials of *F. viridis* at 35°C and 32/38°C indicates root-zone heat limited the water uptake and/or altered stomatal function. Altered water relations, however, do not account for the reduced root growth of *F. viridis* exposed to temperatures of at least 26°C, but less than 35 or 32/38°C.

These experiments provide new information about the response of *Fragaria* genotypes to different root-zone temperatures. A low temperature (23°C) promoted maximum growth of *F. viridis*, whereas exposure to root-zone temperatures as high as 32°C fostered maximum growth of *F. chiloensis*.

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Response of Two French Hybrid Wine-Grape Cultivars to Low Light Environments

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Abstract

The response of berry set, yield, and fruit quality characteristics to low light environments were examined for 'Seyval blanc' and 'De Chaunac' grapevines in the greenhouse. Potted vines of each cultivar with either 1 or 2 clusters were subjected to high or low light conditions, created by 80% shade cloth and supplemental lighting. 'Seyval blanc' had a higher percentage of mature berries per cluster, fewer shot berries, and a larger rachis diameter compared to 'De Chaunac'. Regardless of the cultivar or cluster number, clusters subjected to low light conditions had lower set, yields, cluster weights, berry weights, berries per clusters, and rachis diameters and had higher numbers of shot berries compared to clusters grown under high light conditions. Vines with one cluster matured a higher percentage of berries, possessed larger cluster weights and rachis diameters, and had lower yields than vines with two clusters. 'Seyval blanc' and 'De Chaunac' clusters grown under low light developed their golden and blue-red color more slowly than clusters grown under high light conditions. Overall, vines subjected to low light conditions produced clusters with lower soluble solids, pH, and potassium ion concentrations compared to vines grown under high light conditions. The soluble solids and pH of 'Seyval blanc' clusters were more sensitive to light than 'DeChaunac'. Titratable acidity levels and tartaric acid concentrations of 'Seyval blanc' were less sensitive to low light compared to 'De Chaunac' clusters.

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