Effects of Day Temperature and Light Intensity on Growth and Composition of *Vitis vinifera* L. Fruits[1]

W. M. Kliewer and L. A. Lider[2,3]
University of California, Davis

Abstract. Three-year-old 'Cardinal' and 'Pinot noir' vines were grown from véraison to fruit maturity in a stationary and rotating phytotron at high (30°C) and low (20°C) day temperatures in combination with both high (>2,500 ft-c) and low (<1,200 ft-c) average light intensities. Night temperature (6 PM to 6 AM) was 15°C in all treatments. Berries were collected at weekly intervals and analyzed for various constituents.

Low temperature usually resulted in increased berry weight, total acidity, and malate, and in decreased pH, arginine, proline, and total N in the berry juices, as compared to fruits grown at high temperature. The concentrations of total soluble solids and tartrate in the fruits generally did not significantly differ with temperature. Low light intensity at both high and low temperatures generally resulted in reduced berry weight, total soluble solids, pH, and proline, and in increased levels of total acidity, malate, arginine, and total N in the berry juices compared to grapes grown at high light intensity at the same room temperature. The concentration of arginine was highly correlated with the level of total N in the fruits of both cultivars.

The effect of temperature and light intensity on total soluble solids and total acidity of grapes has been extensively studied by several investigators (1, 2, 8, 14, 15, 20). Generally, high temperatures during the ripening period are associated with grapes high in sugar and low in total acidity. Relatively little is known regarding the effect of temperature and light intensity on other constituents in *Vitis vinifera* grapes. Kobayashi et al. (14, 15) have studied temperature effects on shoot and berry growth of 'Muscat of Alexandria', as well as on total soluble solids, total acidity, and coloration in the juices of the fruits. Kliewer (8) found that fruits from 3 *V. vinifera* cultivars grown under relatively low temperatures (20°C day, 15°C night) were higher in acidity, tartaric acid, and malic acid than fruits of the same degree of maturity grown under much higher field temperatures. Kliewer (11) reported that low day temperatures (20°C) greatly increased the level of anthocyanins in the skins of 'Cardinal' and 'Pinot noir' grapes compared to fruits grown at high day temperature (30°C). He also found that low light intensity significantly reduced the coloration of 'Pinot noir' grapes at both low and high day temperatures, while low light intensity had little effect on coloration of 'Cardinal' grown at 20°C but did decrease the level of anthocyanin pigments in grapes grown at 30°C. Buttrose et al. (2) very recently showed that 'Cabernet-Sauvignon' grapes from vines grown in growth cabinets at 20°C day–15°C night were significantly higher in total acidity, malate, and anthocyanins and lower in proline and total free amino acids than grapes grown at 30°C day–15°C night. Other studies on the effect of temperature on composition of grapes have been reviewed by Amerine (1) and Kliewer (8).

This communication describes experiments in which 'Cardinal' (red table cultivar) and 'Pinot noir' (red wine cultivar) grapevines were grown in sunlit phytotrons at high (30°C) and low (20°C) daytime temperatures under both high and low light intensities during the ripening period. Berries were analyzed at weekly intervals during the ripening period for total soluble solids, total acidity, pH, total N, and for the principal organic and amino acids.

Materials and Methods

The plant material in this investigation was 3-year-old, own-rooted *Vitis vinifera* L. cvs. Cardinal and Pinot noir. The containers, growth medium, and methods of growing, handling, and maintaining the vines have been described previously (8). Treatments consisted of high (30°C) and low (20°C) day temperatures (6 AM to 6 PM) in combination with high and low light intensities. The following symbols will be used to describe these treatments: High light (HL), low light (LL), high temperature (HT), and low temperature (LT). Night temperature in all treatments was 15°C. The experiment was conducted from June 24 to August 11. One to 2 weeks before the first sign of color change in the berries, 8 vines of each cultivar were moved from the lathhouse into the stationary phytotron (7, 21) and a similar number into the rotating phytotron (18, 21). Four vines of each cultivar in both phytotrons were placed under a Saran polypropylene shade canopy that reduced the light intensity to 11 to 12% of full sunlight in the stationary room, and to 17 to 18% of full sunlight in the rotating room. Light intensity received by vines under the shade canopy will be referred to as LL and was measured with a Weston 756 light meter held horizontal and included diffused light as that admitted by the cosine filter. The remaining vines received the full solar radiation that entered the phytotron rooms through the prisms in the ceiling. In the stationary room this averaged 2,765 ft-c between 6 AM and 6 PM (Fig. 1). The corresponding intensities averaged 4,986 ft-c in the rotating room. Solar radiation received by the unshaded vines in both rooms will be referred to as HL. Each vine served as a replicate in a randomized complete block design.

Construction, operation, and light and temperature properties of the stationary (7, 21, 22, 23) and rotating phytotrons (18, 21) have been described. The methods and equipment for measuring the light intensity and the temperatures of air, soil, leaves and berries have also been described (8). Relative humidity in both rooms was usually between 50 and 60% during the daytime.

Approximately 5 berries from each cluster on a vine were harvested at weekly intervals during the ripening

[1]Received for publication May 7, 1970.
[2]Department of Viticulture and Enology.
[3]The authors are grateful to Abbas Soleimani, Jirair Carapetian, and Norman Ferrari and Po-Lung Kao for their skilled technical assistance. The authors thank F. P. Zscheile for the use and maintenance of the phytotron rooms.

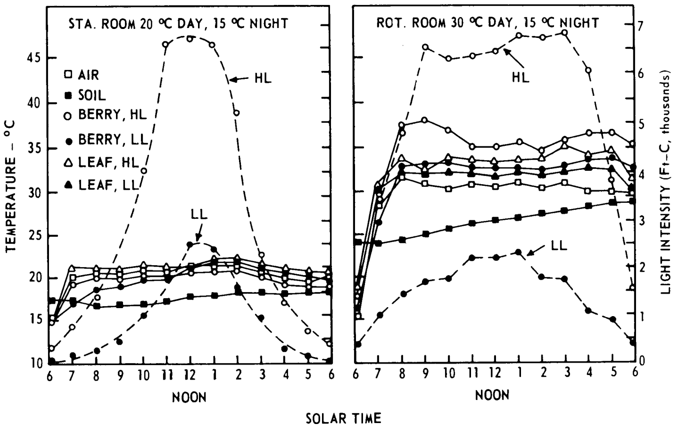

Fig. 1. Hourly fluctuations in air, soil, leaf and berry temperatures (solid lines) and light intensity (dotted lines) between 6 AM and 6 PM in the stationary (left) and rotating (right) phytotrons during the period June 24 to August 11. HL and LL designate high light and low light conditions, respectively.

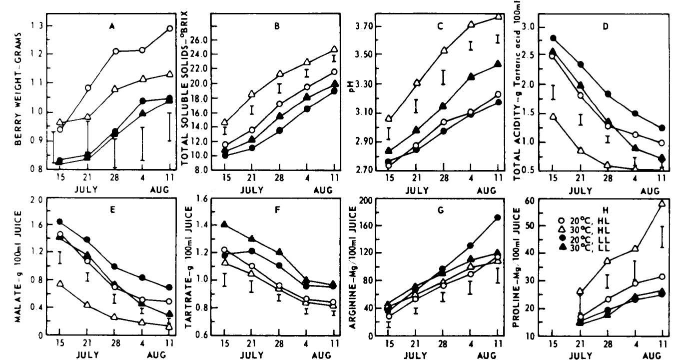

Fig. 2. Effect of day temperature and light intensity on growth and composition of 'Cardinal' grapes ripened between June 24 and August 11. Daytime air temperatures of the stationary and rotating rooms were 20 and 30°C, respectively. Night temperature was 15°C for both rooms. HL and LL designate high light and low light intensity, respectively. Vertical bars indicate difference between treatment means required for significance at the 5% level.

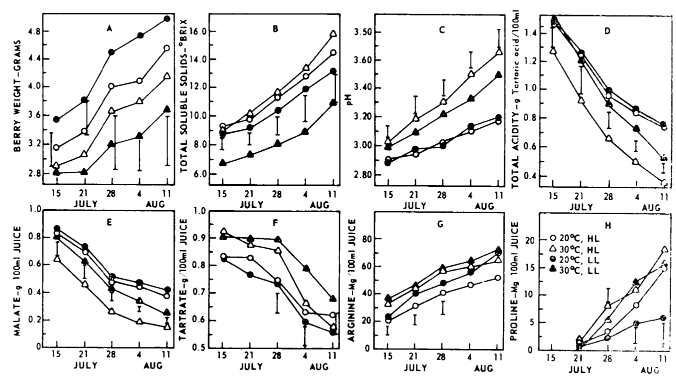

Fig. 3. Effect of day temperature and light intensity on growth and composition of 'Pinot noir' grapes ripened between June 24 and August 11. Daytime air temperatures of the stationary and rotating rooms were 20 and 30°C, respectively. HL and LL designate high light and low light intensity, respectively. Vertical bars indicate difference between treatment means required for significance at the 5% level.

period. Immediately thereafter, the juice was extracted from the fruits with a mortar and pestle, and squeezed through 2 layers of cheesecloth. Total soluble solids (degree Brix, °B), total titratable acidity, pH, and malate, and tartrate concentrations were determined as described by Kliewer (8). Arginine was determined according to the Gilboe and Williams (5) modification of the Sakaguchi reaction. Proline was determined by the acidic ninhydrin photometric method of Ough (19), and total N was determined by the macro Kjeldahl method on 5-ml portions of the juice samples.

Results

The solar radiation admitted into the rotating room averaged approximately twice that admitted into the stationary room between 6 AM and 6 PM (Fig. 1). This resulted in leaf and berry temperatures ranging from 3 to 10°C above ambient temperature in the rotating room. Leaf and berry temperatures in the stationary room, however, were always within 1 to 3 °C of air temperature (Fig 1).

Berry weight. Berries from 'Pinot noir' vines grown under LL at both high and low daytime temperatures were generally smaller in size and weight (Fig. 3A). However, for 'Cardinal', temperature appeared to be the more significant variable with berries under LT being larger than those at HT within both high and low light intensity (Fig. 2A).

Total soluble solids. Low light intensity at both high and low temperatures markedly delayed fruit maturity as evidenced by soluble solids development (Figs. 2 and 3B). In 'Cardinal' the delay under LL was considerably greater at 30°C than at 20°C (Fig. 2B). The level of soluble solids of 'Cardinal' and 'Pinot noir' fruits grown under HL did not differ significantly with temperature (Figs. 2 and 3B). The exception was 'Pinot noir' berries grown in the rotating room at 30°C, which were significantly higher in total soluble solids than fruits grown in the stationary room at 20°C (Fig. 3B).

pH. The pH of juice from grapes of both cultivars grown at HT, under either HL or LL, was always greater ($P < 0.01$) than the pH of grapes grown under LT at each of the sampling dates (Figs. 2 and 3C). The pH of the berry juice from grapes grown under LL were generally less than the pH of grapes grown under HL at the same air temperature; however, the differences were usually not significant at the 5% level.

Total titratable acidity. Low temperature, under either HL or LL, greatly increased ($P<0.01$) the total acidity of the fruits of both cultivars at each sampling date, compared to grapes grown at HT (Fig. 2 and 3D). Low light at HT or LT also resulted in fruits with higher total acidity than fruits grown under HL.

Malate. The concentration of malate was affected by temperature and light intensity in the same manner as was total acidity (Fig. 2 and 3E). Generally, the concentration of malate in fruits grown at LT, under either HL or LL, was 2 to 3 times greater than in fruits grown at HT.

Tartrate. In contrast to malate, the concentration of tartrate in fruits grown under HL was generally not significantly different at low or high growing temperatures (Fig. 2 and 3F). 'Pinot noir' fruits grown during the period June 24 to August 11 and under LL were significantly higher ($P<0.05$) in tartrate than fruits grown under HL at the same air temperature (Fig. 3F). This was also true for 'Cardinal' grown at 30°C but not at 20°C.

Arginine. The level of arginine in grapes grown under LL was markedly higher than in grapes grown under HL at the same air temperature during the entire ripening period (Fig. 2 and 3G). High temperatures were generally more favorable for higher concentrations of arginine in the berry juices than was LT under either LL or HL conditions. An exception was 'Pinot noir' fruits from vines grown at 20°C, LL, which were higher in arginine than berries grown at 30°C, LL, at the last two sampling dates.

Regression analysis showed that the concentration of arginine in the berry juice was directly proportional to the concentration of total N in the fruits of both 'Cardinal' and 'Pinot noir'. The equations of the regression lines for the 2 cultivars were $Y = -6.63 + 1.45\ X$ ('Cardinal') and $Y = -18.82 + 1.37\ X$ ('Pinot noir') where Y equals the concentration of arginine and X equals the concentration of N. Correlation coefficients of 0.84 and 0.87 were obtained for both cultivars, respectively.

Proline. 'Pinot noir' grapes grown at HT under HL had strikingly higher levels of proline than fruits grown at LT under HL, while under LL there was relatively little difference in the concentration of proline with temperature (Fig. 3H). 'Cardinal' fruits were also generally higher in proline when grown at HT rather than at LT. (Fig. 2H).

Total nitrogen. The data in Table 1 indicate that the level of total N in 'Cardinal' and 'Pinot noir' grapes was generally higher in fruits grown under LL, rather than under HL, especially during the latter stages of ripening. Fruits grown at HT were also usually higher in total N than those ripened at LT under the same light conditions (Table 1). An exception was 'Pinot noir' fruits grown at LT under LL in the stationary phytotron. Juices from these fruits were considerably higher in total N than fruits grown under the other temperature and light condition in either room.

Table 1. Effect of temperature and light intensity on the level of N in the juice of 'Cardinal' and 'Pinot noir' fruits grown in stationary and rotating phytotron rooms at various times during the ripening period.

Treatment	Time of sampling (weeks after moving vines into phytotrons)[c]	Total N (mg/100 ml juice)			
		Stationary room[a]		Rotating room[b]	
		Cardinal	Pinot noir	Cardinal	Pinot noir
30°C, HL.......	2	34.4	55.1	36.4	62.9
	3	32.8	58.0	45.0	77.6
	4	34.5	67.2	44.8	79.1
	5	43.7	70.4	44.9	85.5
	6	44.1	71.6	45.7	86.2
30°C, LL.......	2	41.4	63.2	30.4	72.1
	3	42.9	73.4	42.5	79.8
	4	50.7	76.7	42.8	86.7
	5	56.7	82.5	44.8	93.6
	6	62.5	87.6	50.2	100.5
20°C, HL.......	2	21.0	55.4	31.6	27.4
	3	31.0	61.2	31.3	36.1
	4	31.8	63.3	31.5	41.5
	5	34.5	68.8	38.1	48.2
	6	34.7	76.9	39.1	58.0
20°C, LL.......	2	23.1	74.0	27.0	47.5
	3	29.6	84.4	29.4	53.5
	4	34.0	115.8	32.9	76.7
	5	42.4	127.1	40.0	80.2
	6	47.0	131.6	38.4	83.6
LSD (5% level)..	2	7.9	14.6	4.8	NS
	3	7.2	11.0	7.0	NS
	4	7.8	13.9	7.3	24.9
	5	8.6	10.0	7.4	26.0
	6	7.8	12.6	8.6	25.8

[a]Day temperature in stationary room was 20°C from June 24 to August 11, and 30°C from August 15 to September 30.
[b]Day temperature in rotating room was 30°C from June 24 to August 11, and 20°C from August 15 to September 30.
[c]Vines were moved into phytotrons approximately 2 weeks before véraison.

Discussion

The data in Figs. 2 and 3 and Table 1 show that the temperature and light conditions in the phytotron rooms during the ripening period greatly affected berry weight, total soluble solids, pH, total acidity, and levels of malate, arginine, proline, and total N in juice of 'Cardinal' and 'Pinot noir' fruits. The concentration of tartrate was relatively little affected by the temperature and light conditions used.

The reductions in weight and total soluble solids of berries from vines grown under LL were probably due to insufficient light intensity for maximum photosynthesis, which, of course, would reduce the overall carbohydrate status of the vines. Kriedemann (6) recently reported that 'Sultana' grape leaves reach light saturation at 2,500 to 3,500 ft-c, and that the light compensation point is between 50 and 125 ft-c. If we assume a similar light requirement for 'Cardinal' and 'Pinot noir', then those vines grown under LL generally received, on an hourly average from 6 AM to 6 PM, about one-third to one-fourth the light required for saturation. The decrease in berry weight and total soluble solids under LL was generally greater, on a relative basis, for 'Pinot noir', than for 'Cardinal'. 'Cardinal' is a more vigorous cultivar than 'Pinot noir', and may have had a larger carbohydrate storage reserve available for berry growth and ripening. It is also possible that the amount of light intensity needed for saturation of 'Cardinal' is less than that required for 'Pinot noir'.

Increased rates of respiration associated with high temperatures most probably accounted for the striking decrease in total acidity and the high pH of juice from HT fruits, compared to that of LT fruits (Figs. 2 and 3, C and D). The fact that grapes ripened under LL also usually had higher acidity and lower pH than those ripened under HL at the same room temperature would be expected, since leaf and berry temperatures were often considerably less under LL than under HL conditions (Fig. 1). Reduced light intensity usually delayed fruit maturation, and this, too, would contribute to the higher acidity and lower pH of berry juice in LL fruits.

The level of malate (malic acid and salts of malic acid) remained high in the juice of fruits ripened at LT, but decreased rapidly in fruits ripened at HT. In contrast, the concentration of tartrate was scarcely effected by temperature (Figs. 2 and 3, E and F). Amerine (1), Radler (20), Kliewer (8), and Kliewer and Lider (12) have reported that elevated temperatures are associated with low acidity in grapes. Buttrose et al. (2) recently found that 'Cabernet-Sauvignon' fruits from vines grown in a growth chamber at 20°C had significantly higher levels of malate than fruits grown at 30°C, but the concentration of tartrate was not significantly different at the 2 temperatures. Several enzymes in grapes (6), including malic enzyme and malate-dehydrogenase, are capable of breaking down malate. Their activity may account for the rapid loss of this acid in fruits grown at high temperatures. Although C^{14} labeling experiments have indicated that tartaric acid can be used in respiration, especially at high temperatures (3), there is no specific information regarding tartrate degrading enzymes in grapes.

The concentrations of arginine and total N in grapes ripened under LL were usually greater than in grapes grown at HL at the same room temperature (Figs. 2 and

3G; Table 1). Berries from vines grown under LL were generally smaller than HL berries. This probably accounts, at least in part, for the higher concentrations of arginine and total N. Arginine and total N content per berry of fruits ripened at HL and LL were not greatly different. The amount of proline, both on a concentration and on a per berry basis in 'Pinot noir' fruits ripened under LL, however, was markedly less than in fruits ripened under HL at both high and low temperatures. This was also true of 'Cardinal' grown at 20°C. Kliewer (9, 10) and Lafon-Lafourcade et al. (17) found that the level of proline in grapes increases with fruit maturation, especially during the latter stages of ripening. In addition, Kliewer and Ough (13) found that the concentration of proline in 'Thompson Seedless' berries was positively correlated with the level of total soluble solids on a given harvest date. The lower level of proline in grapes ripened at LL was probably related to the slower rate of fruit maturation under reduced light intensity.

Arginine and proline are the 2 predominant amino acids in most *V. vinifera* cultivars (9, 10), but the effect of these amino acids on quality of grapes and grape products is not known. The concentrations of proline and, to a lesser extent, of arginine, were usually higher in fruits ripened at 30°C than in those ripened at 20°C. An increase in the amount of available N in the growth medium at HT may have resulted from an increase in the rate of nitrification; and this may account for, at least in part, the higher levels of arginine and proline in HT grapes. The HT growing conditions may also have resulted in the formation of greater amounts of α-ketoglutarate through increased rates of respiration. The reductive amination of this keto acid forms glutamic acid, a common intermediate in synthesis of both arginine and proline. Flanzy and Poux (4) reported that the concentration of proline was nearly 4 times greater in musts of 1962, a warm year, than in musts of 1963, a cool year. Buttrose et al. (2) also found significantly higher levels of proline in 'Cabernet-Sauvignon' fruits grown in growth chambers at 30°C, as compared to fruits grown at 20°C. However, the concentration of arginine was not significantly different in fruits grown at the 2 temperatures.

The difference in composition of grapes grown at the same air temperature in the stationary and rotating phytotrons was probably largely due to the difference in amount of solar radiation entering the 2 rooms. Total daily sunlight in the rotating room averaged 92 to 99% of that outdoors, with an overall average intensity during the daylight hours (6 AM to 6 PM) generally between 5,000 and 5,600 ft-c. The rotating room received 90 to 117% more solar radiation than the stationary room under HL, and 48 to 54% more radiation under LL. Leaf and berry temperatures during the daylight hours were considerably higher than air temperature in the rotating room; but in the stationary room, leaf and berry temperatures were usually within ± 3°C of air temperature (Fig. 1). In the rotating room, leaves and fruits on vines were always oriented to face the sun at the same angle. In the stationary room, the angle of leaves and fruits with respect to the sun changed throughout the day, as the sun moved overhead. This may also have been a factor in the difference in fruit composition between the 2 rooms at the same ambient temperature.

Literature Cited

1. Amerine, M. A. 1956. The maturation of wine grapes. *Wines and Vines* 37:27–32 and 37:53–55.
2. Buttrose, M. S., C. R. Hale, and W. M. Kliewer. 1970. Effect of temperature on the composition of Cabernet Sauvignon berries. *Amer. J. Enol. Vitic.* (In Press).
3. Drawert, F. and H. Steffan. 1965. Biochemisch-physiologische Untersuchungen an Thaubenbeeren II. Verteilung und Veratmung von zugeführten ^{14}C-Verbindungen. *Vitis* 5:27–34.
4. Flanzy, C. and C. Poux. 1965. Les levures alcooliques dans les vins. Protéolysis, proteógénése III. *Ann. Tech. Agr.* 14:35–48.
5. Gilboe, D. D. and J. N. Williams. 1956. Evaluation of the Sakoguchi reaction for quantitative determination of arginine. *Proc. Soc. Expt. Biol. Med.* 19:535–536.
6. Hawker, J. S. 1969. Changes in the activities of malic enzyme, malate dehydrogenase, phosphopyruvate carboxylase, and pyruvate decarboxylase during the development of a non-climacteric fruit (the grape). *Phytochemistry* 8:19–23.
7. Henderson, S. M. and F. P. Zscheile. 1967. A simple temperature control for phytotrons. *J. Agric. Eng. Res.* 12: 233–237.
8. Kliewer, W. M. 1968. Effect of temperature on the composition of grapes grown under field and controlled conditions. *Proc. Amer. Soc. Hort. Sci.* 93:797–806.
9. ————. 1969. Free amino acids and other nitrogenous substances of table grape varieties. *J. Food Sci.* 34:274–278.
10. ————. 1970. Free amino acids and other nitrogenous fractions in wine grapes. *J. Food Sci.* 35:17–20.
11. ————. 1970. Effect of day temperature and light intensity during the ripening period on coloration of *Vitis vinifera* grapes. *J. Amer. Soc. Hort. Sci.* 95:693–697.
12. ————, and L. A. Lider. 1968. Influence of cluster exposure to the sun on the composition of Thompson Seedless fruit. *Amer. J. Enol. Vitic.* 19:175–184.
13. ————, and C. S. Ough. 1970. Effect of leaf area and crop size on the concentration of amino acids and total nitrogen in Thompson Seedless grapes. *Vitis* 9:(In Press)
14. Kobayashi, A., H. Yukinaga, and E. Matsunsga. 1965. Studies on the thermal conditions of grapes V. Berry growth, yield, and quality of Muscat of Alexandria as affected by night temperature. *J. Jap. Soc. Hort. Sci.* 34:8–157.
15. ————, T. Fukushima, N. Nii, and K. Harada. 1967. Studies on the thermal conditions of grapes. VI. Effects of day and night temperatures on yield and quality of Delaware grapes. *J. Jap. Soc. Hort. Sci.* 36:1–7.
16. Kriedemann, P. E. 1968. Photosynthesis in vine leaves as a function of light intensity, temperature, and leaf age. *Vitis* 7:213–220.
17. Lafon-Lafourcade, S. and G. Guimberteau. 1962. Evolution des amino acides au cours de la maturation des raisins. *Vitis* 3:130–135.
18. Neubauer, L. W. and F. P. Zscheile. 1968. A phytorotor that rotates to admit maximum sunlight. *J. Agr. Eng. Res.* 13:266–279.
19. Ough, C. S. 1969. Rapid determination of proline in grapes and wines. *J. Food Sci.* 34:228–230.
20. Radler, F. 1965. The effect of temperature on the ripening of Sultana grapes. *Amer. J. Enol. Vitic.* 16:38–41.
21. Zscheile, F. P. 1969. Controlled environments for plants in research—A critique, a contribution, and future prospects. "Man and his environment—Interaction and interdependence". J. Y. Wang, ed. pp. 95–121.
22. ————, S. M. Henderson, A. S. Leonard, L. W. Neubauer, and S. V. Sluka. 1956. A sunlight phytotron unit as a practical research tool. *Hilgardia* 36:493–565.
23. ————, and L. W. Neubauer. 1967. Light transmission through plastic panels in a sunlit phytotron unit. *J. Agr. Eng. Res.* 12:94–109.