

DOCTORAL DISSERTATION SERIES

TITLE LEAF ANALYSIS AND GROWTH OF
MONTMORENCY CHERRY TREES (Prunus cerasus
L.) AS INFLUENCED BY SOLAR RADIATION AND
INTENSITY OF NUTRITION
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UNIVERSITY MICH. STATE COLL. DATE 1951

DEGREE Ph. D. PUBLICATION NO. 4709



UNIVERSITY MICROFILMS
ANN ARBOR - MICHIGAN

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Edward Louis Proebsting, Jr.

A THESIS

Submitted to the School of Graduate Studies of Michigan
State College of Agriculture and Applied Science
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

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R. L. Kenworthy

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ABSTRACT

One-year-old Montmorency cherry trees were grown in sand culture with five balanced nutrient solutions ranging in concentration from zero to 8,000 ppm. Varying conditions of solar radiation were provided by moving the trees at various intervals between full sun and shade houses which were constructed with camouflage netting. Leaf analyses and growth records were obtained, and their relationships to each other and to the treatments were discussed.

Leaf analysis values for the individual elements did not increase proportionately with the concentration of the nutrient solution. Nitrogen and manganese values increased in proportion to the nutrient solution concentration, but the magnesium content decreased as the nutrient solution concentration was increased. Leaf phosphorus, potassium, calcium, and iron showed an irregular relationship with nutrient solution concentration, indicating that the absorption of phosphorus, potassium, calcium, magnesium, and iron was more dependent upon the physiological relationships among the nutrients than upon the absolute concentration of the element in the external solution.

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Marked differences in leaf analysis were induced by differences in solar radiation. These differences were of a complex nature and were influenced by other factors, such as temperature, so that the responses of one year could not be repeated in a succeeding year. On the basis of our present knowledge, prediction of the effect of solar radiation upon leaf composition probably would not be successful.

Leaf nitrogen showed a close relationship with growth responses. Very marked depression of growth was associated with leaf nitrogen greater than 3.5%, in the full sun in 1949. At 30% S.R. and 50% S.R. depressions in growth occurred with leaf nitrogen contents higher than 2.9%. There was no apparent relationship between the absorption of the other nutrient-elements and growth, as affected by solar radiation and nutrient solution intensity.

The relationship between leaf analysis and the nutrient solution and solar radiation treatments was different in 1949 from 1950. This difference appears to be associated with temperature more than solar radiation.

The conditions most favorable for the growth of Montmorency cherry trees vary in regard to the measurement of growth as follows:

- a. Terminal growth is favored by moderate temperatures and low light conditions.

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- b. Increase in dry weight is the greatest with warm temperatures and full intensity of solar radiation.
- c. Reduced solar radiation failed to stimulate terminal growth when storage reserves had been used in shoot growth prior to reducing solar radiation.
- d. Higher concentrations of nutrient solutions were more toxic at higher temperatures and reduced solar radiation. With normal solar radiation and warm temperatures (conditions favoring dry weight increase) a total salt concentration of 2,000 ppm resulted in maximum dry weight increase. Reduction of the solar radiation to 50% resulted in maximum dry weight increase at a total salt concentration of 1,000 ppm, and at 30% S.R. the best growth was observed when no nutrients were added.

Trees growing in high solar radiation are more capable of utilizing higher intensities of nutrient elements than are trees growing in reduced solar radiation. However, in order to produce a given amount of dry matter it is more important that the trees have optimum conditions of nutrition where solar radiation is relatively low than where solar radiation is high.



Experimental layout at the Horticultural Farm, Michigan State College

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Acknowledgments

Acknowledgment is given to Dr. A. L. Kenworthy, Dr. S. H. Wittwer, Dr. G. P. Steinbauer, and to Dr. C. R. Magee, Guidance Committee members, for helpful suggestions and assistance during the course of these investigations.

Also, thanks are expressed to Dr. H. E. Tukey and Dr. W. W. Aldrich of Michigan State College, and to Dr. E. L. Proebsting, of the University of California, who devoted their time in consultation and in the editing of the manuscript. An expression of appreciation is also given to Mr. R. K. Simons for assistance in conducting the experiments.

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Introduction

In recent years the use of leaf analysis as a diagnostic tool has attained considerable prominence in the field of fruit tree nutrition. Many horticulturists have studied the inter-relationships of nutrient-elements in fruit tree leaves. These investigations have been carried on at different locations in widely differing soils and climates. If the effect of climate on nutrient-element composition of fruit tree leaves could be evaluated, some of the current difficulties in the interpretation of leaf analyses might be eliminated. For this reason an experiment was designed to study the effect of some environmental factors on leaf composition. Solar radiation, one of the most important climatic characteristics affecting living plants, and the intensity of nutrition, expressed as concentration of the nutrient solution, were used as the two variables in the experiment.

Any discussion of leaf analysis would be of little value without an expression of the growth responses associated with those particular values. Therefore, experiments were designed so that questions related to the effect of

solar radiation on the growth of cherry trees could be approached simultaneously with its effect on leaf composition. For instance, pronounced differences in solar radiation exist among different areas, both in total accumulation of solar energy and in seasonal pattern. The experiments permitted a study of the influence of such differences in solar radiation upon growth in relation to the intensity of nutrition and an investigation of nutrition as a means of partial compensation for insufficient solar radiation.

Review of Literature

The use of leaf analysis as an aid in determining the nutrient-element requirements of fruit trees has been handicapped by an inability to obtain reproducible results. Several investigators have mentioned the importance of climate in causing variation in leaf analysis. This would result in a considerable range in nutrient-element composition of leaves associated with growth which appeared to be normal, that is, exhibiting no deficiency or toxicity symptoms. Boynton, Cain, and Compton (1944), working with leaf analysis of McIntosh apple trees in New York, concluded that with leaves of the same age, differences in season may produce significant differences in the percentage content of potassium and magnesium in the leaves. Boynton and

Compton (1945), in discussing the important factors influencing the interpretation of leaf analysis data, mention root, trunk, and leaf injuries, age of leaf, inter-ionic relationships and factors related to season and climate.

Lundegardh (1947) pointed out that the importance of such climatic influences lies in the fact that for practical use, in the field of fruit tree nutrition, leaf analysis must serve as a fertilizer guide for the coming year. Consequently, he says, the applicability of the results to the conditions likely to prevail is of fundamental importance. In a review of the literature on tissue analysis, Goodall and Gregory (1947) similarly cited the importance of climate in influencing leaf composition and referred to an Australian investigator, Wark (1939), who felt that solar radiation influenced the concentration of nutrient elements in the leaves of grain crops so readily that his leaf samples were taken only on bright days.

Leaf analysis apparently has been used quite successfully in the nutrition of pineapple plants in Hawaii, where large climatic differences occur within a few miles. Nightingale (1942), in reporting work done with Hawaiian pineapple made the following comments:

"Chemical analyses of leaves as applied to agriculture has often led to increased efficiency in the use of fertilizers. However, could values correlated with best yields one year be considered as standard in successive years or at different locations? Perhaps if water is not limiting and sunshine and temperature do not vary greatly from year to year such an assumption may be adequate for practical purposes."

He showed that the starch reserves were the limiting factor in determining the nitrate status of the pineapple plant, and that, in turn, if phosphate was to be used efficiently, its level in the plant must be adjusted on the basis of nitrate concentration. Similarly, nitrate was not absorbed readily if the potassium level was low. Thus he pointed out that there is a chain of inter-dependent relationships directly or indirectly associated with opportunity for carbon dioxide assimilation that necessarily varies with weather conditions.

The relationship between solar energy and leaf composition has also been shown by Chapman and Gray (1949). They reasoned that the expenditure of energy from respiration was necessary for accumulation of nutrients in roots, and that factors which influence the general health of the plant, such as light intensity, also influence the amounts and ratios of elements absorbed by the roots and finally found in the leaves.

The effect of shading on the nutrient content of plants has been investigated periodically by a number of persons but usually without a critical examination of the relationships between solar radiation and nutrient uptake and utilization. Early papers by Pagnoul (1879, 1881) showed a decrease in the total mineral content in sugar beets when heavily shaded, but an increase in mineral composition

if expressed on a percentage basis. Thatcher (1909) obtained similar percentage-wise results with potatoes, peas, and cereals. In 1930 Tyson showed an increase in the per cent of ash in sugar beets that had been shaded. Shading with cotton cloth increased the percentage of nitrogen in apple and peach shoots and was believed by Kraybill (1923) to be responsible for decreased flowering. Porter (1937) found that nitrogen absorption was not decreased in greenhouse tomatoes until the light intensity fell below 50 per cent of daylight. In testing the efficiency of the Neubauer test under different conditions, Thornton (1931) found that light conditions did not affect the total nutrient absorption by rye seedlings.

More detailed examination of the question is provided in the work of Mitchell (1934, 1936), Gast (1939), and Blackman and Rutter (1946, 1947, 1948, 1949) all of whom studied the effects of solar radiation and mineral nutrition simultaneously.

Mitchell (1934, 1936) worked with pine seedlings and measured their growth as influenced by nitrogen level and solar radiation. Increased growth was observed as the nitrogen supply increased to an optimum level above which further increments of nitrogen exerted a depressing effect on dry weight increase. At the low levels of nitrogen nutrition, growth in 50 per cent of full daylight was equal to that of unshaded plants. However, at the higher levels of

nitrogen nutrition, the full daylight plants were capable of better growth than were the shaded plants. At extremely high levels of nitrogen, where toxic effects were predominant, there was again no difference between full sunlight and fifty per cent shading.

Gast (1939) worked along similar lines and obtained similar results. He showed, with pine seedlings, that at low levels of solar radiation (below 20 per cent of full daylight) factors of nutrition had a minor influence on dry weight increase. Above 30 per cent of full daylight the factors of nutrition became more important. He showed that with moderately high intensities of radiation, an increase in nitrogen availability could offset a deficiency in radiation. In general, high intensities of radiation were of no value if the nitrogen was low, and, conversely, if the light intensity was low, the seedlings were unable to respond to more nitrogen.

In a series of papers, Blackman and Rutter showed the importance of light intensity and mineral nutrient supply and the interaction of these factors upon the ecological relations of the bluebell (Scilla non-scripta, Hoff. and Link.). They associated the distribution of bluebell with the degree of shading and showed a precise correlation between these two factors (1946). The growth of bluebell was only affected slightly by mineral nutrition, but was especially sensitive to a reduction in light intensity (1947).

This sensitivity to light intensity was established as being due to an effect on the net assimilation rate, which was directly proportional to the logarithm of the light intensity (1948). Shading increased the percentage content of nitrogen, phosphorus and potassium, the increase being largest for potassium and least for phosphorus. The percentage content was the result of two factors: absorption of nutrients and growth or dry weight production (1949).

Methods

Equipment and Procedure

One-year-old Montmorency cherry trees (Prunus cerasus, L.) nursery budded on P. mahaleb rootstock and certified virus free were used. The trees were planted in fifty-pound, lacquered metal berry cans which had been coated on the inside with an asphalt emulsion. Drainage was provided by a 5/8" hole punched in the side of the can just above the bottom seam. This opening was screened with cheese cloth or glass wool to prevent the loss of sand. The sand was obtained from a bare area of soil classified as Oshtemo sand.

The cans were arranged so that the trees were two feet apart. Then the groups of cans were enclosed in wire pens which held straw used for packing around the cans to prevent high soil temperatures. The effectiveness of the

straw mulch as a protective measure was shown by temperature records taken on a bright day with the air temperature at 87 degrees Fahrenheit. The temperature in the soil in the mulched cans was 81 degrees Fahrenheit, and in the non-mulched cans, 95 degrees Fahrenheit.

Shading was provided by two houses which were constructed by spreading camouflage netting over 48' x 12' x 8' pipe frames. One shade allowed 30 per cent of the solar radiation to pass through, while the other had holes cut in it to permit 50 per cent of the solar radiation to come through. The use of camouflage netting permitted sufficient ventilation to equalize the air temperatures inside the shade houses with the temperature in the full sun. There was no difference between maximum and minimum readings taken in standard Weather Bureau instrument shelters inside and outside the shade houses.

Nutrient-elements were provided by means of solutions. Table 1 shows the salts used, concentrations of the individual nutrient-elements at the five different intensities, and the approximate total salt concentration of the solutions.

The zero level consisted of de-ionized water which was obtained by passing tap water through two towers containing the synthetic ion exchange resins IR-4B and IR-120*. De-ionized water was used for preparing stock solutions, using

* Produced by Rohm and Haas Company, Resinous Products Division, Philadelphia, Pennsylvania.

C. P. chemicals of the individual salts, which were about 20 times as concentrated as the nutrient solutions applied to the trees. The nutrient solutions of various intensities were made from the stock solutions as shown in Table 1 and stored in five-gallon bottles until distributed to the individual trees by means of quart fruit jars. One quart of the nutrient solution was applied every other day. The cans were not covered, and periodic rainfall was sufficient to flush any accumulated salts out of the sand. As further insurance against salt accumulation, and in order to provide relatively uniform moisture conditions, the sand was maintained near field capacity by use of de-ionized water, as necessary, so that each time a quart of nutrient solution was added some solution drained from the can.

The first measurement was the initial fresh weight of the individual trees when planted. Twenty additional trees were reserved at planting time for dry weight determinations. These were cut at the bud union, and then the roots and shoots were dried separately at 65 degrees Centigrade in a forced air dehydrator. The per cent moisture of the sample trees was used to calculate the initial dry weight for each tree. The results of the 1949 experiment were extremely variable within treatments, and in an attempt to reduce this variability in 1950, all trees were pruned to an initial fresh weight of 95 grams, with a maximum variation of 5 grams. In 1949, the trees were pruned to

Table 1. Nutrient-Element Composition (ppm) in Nutrient Solutions of Varying Concentration

Approx. total salt conc.		Concentration of Nutrient Sol. (ppm)				
Chem. comp'd	Nutr. elem.	0	1,000	2,000	4,000	8,000
NH_4NO_3	(N)	0	112	224	448	896
H_3PO_4	(P)	0	34	68	136	272
KCl	(K)	0	43	86	172	344
CaCl_2	(Ca)	0	88	176	352	704
MgSO_4	(Mg)	0	29	58	116	232
H_3BO_3	(B)	0	1.5	3	6	12
MnSO_4	(Mn)	0	2.5	5	10	20
CuSO_4	(Cu)	0	1	2	4	8
FeSO_4	(Fe)	0	1	2	4	8
ZnSO_4	(Zn)	0	1	2	4	8

three buds and a length of top of 12-18 inches. The adjustment of fresh weight in 1950 was accomplished by pruning the roots after the initial pruning, which was done in the same manner as in 1949.

Trunk diameter measurements were made periodically through 1949 with a Vernier caliper, but because of highly variable results they were discontinued in 1950. Terminal growth, in centimeters, was measured at certain intervals with considerably more emphasis being placed on this measurement in 1950 than in 1949.

During the second week of September all the leaves on each tree were counted and stripped from the trees for dry weight measurement. After being washed free from the sand, the roots were separated from trunk and shoots. Dry weights were obtained for each tree part after dehydration at 65 degrees Centigrade as mentioned above.

After drying and weighing, the leaves, which were collected from all trees of each treatment, were ground with a Micro-Wiley mill to pass through a forty mesh screen, mixed thoroughly, and divided into two portions. Nitrogen determinations were made on one portion by the Agricultural Chemistry Department of Michigan State College, using the standard Kjeldahl method. The other portion was sent to the National Spectrographic Laboratory of Cleveland, Ohio, where analyses for potassium, phosphorus, calcium, magnesium, iron, and manganese were made spectrographically.

Daily solar radiation and temperature records were obtained from Mr. George Crabb, Supervisor of the Michigan Hydrologic Research Project, USDA Soil Conservation Service, in cooperation with the Michigan Agricultural Experiment Station.

Experimental Design

The experiments were conducted during two summers-- 1949 and 1950.

The trees in the 1949 experiment were planted on May 30 and were grown in full sun* without nutrient solutions until June 20. This arrangement provided a three weeks period which could be used later to evaluate the performance of the trees under identical conditions. Differential shading was begun on June 20, using three different light conditions: full sun, 50 per cent solar radiation, and 30 per cent solar radiation. The first applications of nutrient solutions were on the same date (June 20), using five different concentrations of the same formulation. The trees in each of the three light groups were then further subdivided into three lots on August 10, one lot remaining in its original light intensity, and the other two lots being moved into the other two light conditions for the rest of the summer. The trees were removed during the second week of September for dry weight determinations. Each treatment contained five single tree replicates.

* In this paper "full sun" or "100% solar radiation" refers to the solar radiation received at the surface of the earth at East Lansing, Michigan.

This arrangement gave nine different light treatments, as diagrammed in Figure 1, each of which had five nutrient levels, giving a total of 45 treatments and 225 trees.

The results obtained from this experiment showed that a change in the light condition during the latter part of the growing season had no great effect upon the accumulation of dry weight, and that the highest nutrient level was sufficiently toxic to cause death of the trees. Therefore, the 1950 design was modified to include only the four lowest nutrient concentrations, and all the variations in solar radiation were induced during the fore part of the summer with the final transfer occurring shortly after cessation of terminal growth.

The trees for the 1950 experiment were planted May 20 and divided equally into twelve sets. One set of trees consisted of five replications of four nutrient intensities. At the time of planting, half of the trees were placed in full sun and half in 40 per cent light. At predetermined periods after planting a set of trees was moved from each light condition into the other. This moving was done on the following dates: June 7, June 12, June 18, July 1, and July 22.

This design gave twelve light sequences as shown diagrammatically in Figure 2, and the use of four intensities of nutrition resulted in 48 treatments and a total of 240 trees.

Figure 1. An Outline Showing the Dates of Initiating
Solar Radiation Treatments, 1949

Percentage Solar Radiation

<u>May 30</u>	<u>June 20</u>	<u>Aug. 10</u>
	100 (75 trees)	100 (25 trees) 50 (25 trees) 30 (25 trees)
100 (225 trees)	50 (75 trees)	100 (25 trees) 50 (25 trees) 30 (25 trees)
	30 (75 trees)	100 (25 trees) 50 (25 trees) 30 (25 trees)

Figure 2. An Outline Showing the Dates of Initiating
Solar Radiation Treatments, 1950

XXXXXX Trees growing in shade						-----Trees growing in sun									
Weeks*		May		June			July			August			Sept.		
Sun	Shade	20	30	10	20	30	10	20	30	10	20	30	10	20	
Trees Started in Sun															
1/2	15 1/2	-----:XX													
1	15	-----:--XX													
2	14	-----:---XX													
4	12	-----:-----XX													
8	8	-----:-----XX													
16	0	-----:-----													
Trees Started in Shade															
1/2	15 1/2	XXXXXXXXX:X-----													
1	15	XXXXXXXXX:XX-----													
2	14	XXXXXXXXX:XXXX-----													
4	12	XXXXXXXXX:XXXXXXXX-----													
8	8	XXXXXXXXX:XXXXXXXXXXXXXXXX-----													
16	0	XXXXXXXXX:XX													

: --Approximate start of shoot growth

* --Weeks after initiation of growth

Results

Leaf Analysis--1949

The Effect of Nutrient-Element Concentration.

The concentration of the nutrient solution produced direct responses in leaf composition for some elements while for others there was no direct relation to the external concentration. Since leaf analyses were made on single composite samples for each treatment, interactions between nutrient solution concentration and solar radiation could not be demonstrated statistically. For this reason the effect of nutrient-element concentration was obtained by averaging the values from all light conditions for each of the five nutrient levels. A similar procedure was used to determine the effect of the various light conditions. These averages appear in Table 2.

Per cent nitrogen in the leaf increased as the total concentration of the nutrient solution was raised to 4,000 ppm, but when a concentration of 8,000 ppm was reached there was a slightly lower nitrogen content than at 4,000 ppm. Phosphorus was lowest when no nutrient-elements were supplied. The addition of 1,000 ppm produced a maximum phosphorus level which was maintained for the higher concentrations of nutrient-elements. Potassium, also, was lowest when the trees were grown in the zero level of

Table 2. Leaf Analysis (% dry wt.) as Affected by Concentration of
Nutrient Solution, 1949

Concentration of nutrient solution ppm	Nutrient-Element							Index of	
	N	P	K	Ca	Mg	Fe	Mn	intensity*	balance*
0	1.78	.16	1.18	1.30	.88	.020	.007	-11	95
1000	2.73	.20	1.50	1.23	.80	.020	.009	0	45
2000	2.98	.19	1.31	1.23	.74	.019	.009	- 4	34
4000	3.37	.20	1.47	1.39	.65	.020	.011	+ 5	45
8000	3.31	.19	1.63	1.63	.54	.019	.013	+ 8	104

* See Appendix Table 1.

nutrient-elements. The use of 1,000 ppm caused a sharp increase in potassium, but the use of 2,000 ppm resulted in lower potassium than 1,000 ppm. The use of 4,000 ppm caused potassium to be higher than when 2,000 ppm was used and the highest potassium value was associated with a nutrient solution concentration of 8,000 ppm. Higher calcium values were found for 4,000 and 8,000 ppm concentrations of nutrient solutions than when only de-ionized water was used, but lower calcium values were found in the 1,000 and 2,000 ppm treatments than in the de-ionized water treatment. Magnesium analysis was highest when only de-ionized water was used and decreased with each successive increase in concentration of the nutrient solutions. Iron analysis showed little or no variation in relation to concentration of the nutrient solution. The lowest iron analysis was found when the nutrient solution contained 2,000 ppm, and highest value was associated with the use of 8,000 ppm. Manganese increased with concentration except when the concentration was increased from 1,000 to 2,000 ppm, when no increase or decrease was noted.

The index of nutritional intensity (see Appendix Table 1 for method of calculation) in the leaf analyses did not increase in proportion to the increasing concentration of the nutrient solution, as recorded in Table 2. There was a very pronounced increase in the index of nutritional intensity from zero ppm to 1,000 ppm, but at 2,000 ppm the index was less than that at 1,000 ppm. The intensity

factor then increased from 2,000 ppm to 4,000 ppm, and from 4,000 ppm to 8,000 ppm. The zero level produced a high index of balance deviations (see Appendix Table 1 for method of computation of index of balance deviations) which was lowered markedly at the 1,000 ppm level. At 2,000 and 4,000 ppm the index of balance deviations remained low, but at 8,000 ppm the index was much higher.

The Effect of Solar Radiation (S. R.).

Full Season. The effect of solar radiation on the nutrient-element composition of the leaves is shown in Table 3. The values in Table 3 are the average of all nutrient levels for each solar radiation treatment.

Solar radiation produced a very definite effect on the nitrogen content of the leaves, with the 100% S.R. treatment showing a higher percentage of nitrogen than those in reduced solar radiation. Phosphorus composition of the leaves apparently was not affected by solar radiation, but the three major cations were affected. Magnesium was most markedly affected and potassium was affected relatively little. The highest concentration of no two of the major cations occurred at the same solar radiation treatment. Calcium was highest in 100% S.R., potassium highest at 50% S.R., and magnesium showed a large increase at 30% S.R. Iron content was increased when solar radiation was reduced. Differences in the indices of nutritional intensity and balance deviation were not closely associated with solar radiation treatment.

Table 3. Leaf Analysis (% dry wt.) as Affected by Varying Solar Radiation During the Growing Season, 1949.

Solar radiation		Nutrient-Element							Index of	
Initial	Final	N	P	K	Ca	Mg	Fe	Mn	intensity*	balance*
100%	100%	3.20	.17	1.33	1.58	.78	.018	.009	+ 1	75
100%	50%	2.96	.18	1.36	1.58	.59	.018	.008	- 5	68
100%	30%	2.84	.21	1.62	1.52	.46	.018	.009	- 3	96
50%	50%	2.65	.18	1.40	1.37	.44	.021	.011	- 5	72
50%	30%	2.75	.18	1.83	1.36	.42	.018	.011	- 3	95
50%	100%	2.68	.18	1.37	1.24	.63	.018	.010	- 6	25
30%	30%	2.74	.18	1.29	1.21	.95	.020	.008	- 2	70
30%	100%	2.89	.19	1.26	1.27	1.12	.020	.010	+ 6	98
30%	50%	2.81	.20	1.29	1.08	1.10	.026	.011	+10	125

* See Appendix Table 1.

Midseason Transfer. The effect of reducing solar radiation to 50 per cent and to 30 per cent is shown in Table 3. Nitrogen was decreased markedly with reduced solar radiation and was roughly proportional to the quantity of solar radiation received. Phosphorus increased with reduced solar radiation, but may reflect the influence of decreasing nitrogen rather than the effect of reducing solar radiation. Transferring the trees from 100% S.R. into 30% S.R. resulted in a very high potassium analysis, reduced magnesium, and had little effect on calcium. In this series the interrelations among the three major cations seem to be primarily between potassium and magnesium, with calcium relatively independent.

Transferring the trees into lower light intensities decreased the index of nutritional intensity, and had little effect upon the index of balance deviations.

Nitrogen increased slightly when the trees were moved from 50% S.R. into 30% S.R., but was not affected when the trees were moved into 100% S.R. Phosphorus was unaffected by increased or decreased solar radiation after being in 50% S.R. Again, potassium was highest when the trees were moved to lower solar radiation, magnesium was highest when the trees were moved into 100% S.R. and calcium was slightly less when the trees were moved into 100% S.R.

Intensity of nutrition was decreased when the solar radiation was increased or decreased from 50% S.R. The

index of balance deviations was lowest when the trees were moved to 100% S.R. and became higher as the total solar radiation was decreased.

Leaf analyses associated with trees initially in 30% S.R. and later moved into the higher solar radiation conditions are represented in Table 3. In general, there was very little effect of these changes upon the leaf analysis. Nitrogen increased when solar radiation was increased, but phosphorus was not appreciably affected. Potassium was highest at 30% S.R. , and magnesium was highest when shifted to 100% S.R., as noted for the other two groups. There was no recognizable pattern for manganese and iron in this group of treatments. The index of nutritional intensity was raised by moving the trees into higher solar radiation conditions. Balance deviations were affected primarily by the high magnesium values which prevailed throughout the 30% S.R. group.

Growth--1949

Terminal Growth.

All terminal growth had developed by August 1, 1949, hence the midseason shifting, which occurred after this date had no effect upon shoot growth. Therefore, the data, as analyzed, consisted of 15 treatments with 15 replicates each. Due to differences in tree size and rate of terminal growth during the period before any nutrient solution or

solar radiation treatments were initiated, an analysis of co-variance was employed to adjust the final terminal growth on the basis of terminal growth produced before the treatments were applied. The results obtained by using the analysis of covariance to adjust terminal growth data are shown in Table 4.

Terminal growth varied directly with the intensity of solar radiation. Maximum terminal growth was produced in 100% S.R. by the 4,000 ppm treatment, whereas, the trees in 30% S.R. and 50% S.R. grew best with 2,000 ppm added. In all three solar radiation conditions the application of nutrients increased terminal growth up to a maximum above which additional increases in the nutrient solution concentration resulted in a definite depression in terminal growth. The interaction between nutrient level and solar radiation did not have a significant effect on terminal growth. Highly significant differences in terminal growth were produced by nutrient level and by intensity of solar radiation.

Dry Weight Increase.

Because of the variability in the initial weight of the trees at planting time, dry weight increase was used as a measure of growth and was adjusted on the basis of the July 4 terminal growth by the use of covariance, Table 4. The midseason shifting had no effect upon trees which had been in 30% S.R. or 50% S.R. but shifting the trees from

Table 4. Total Terminal Growth* (cm) and Dry Weight Increase* (gms) as Affected by Concentration of Nutrient Solution and by Varying Solar Radiation During the Growing Season, 1949

Solar Radiation		Concentration of Nutrient Solution (ppm)										Average	
		0		1,000		2,000		4,000		8,000			
		Term.Dry wt.	Term.Dry wt.	Term.Dry wt.	Term.Dry wt.	Term.Dry wt.	Term.Dry wt.	Term.Dry wt.	Term.Dry wt.				
Initial	Final	gr.	inc.	gr.	inc.	gr.	inc.	gr.	inc.	gr.	inc.	gr.	inc.
100%	100%	68.4	38.8	77.0	56.7	85.0	64.5	93.8	46.3	67.4	18.0		
100%	50%	**	43.0	**	48.2	**	49.4	**	42.8	**	17.2		
100%	30%	**	31.9	**	41.7	**	49.6	**	46.7	**	17.9		
Average		68.4	37.9	77.0	48.9	85.0	54.5	93.8	45.3	67.4	17.7	78.3	40.9
50%	50%	65.0	32.9	70.0	30.9	72.6	15.4	67.8	16.4	66.6	11.8		
50%	30%	**	24.9	**	30.3	**	18.4	**	15.8	**	- 0.4		
50%	100%	**	29.0	**	28.0	**	17.0	**	14.7	**	2.7		
Average		65.0	28.9	70.0	29.7	72.6	16.9	67.8	15.6	66.6	4.7	68.4	19.2
30%	30%	62.0	24.2	67.2	22.6	70.1	15.5	64.6	16.9	63.0	8.6		
30%	100%	**	22.8	**	20.3	**	23.1	**	16.4	**	11.7		
30%	50%	**	20.5	**	20.1	**	14.1	**	16.0	**	3.2		
Average		62.0	22.5	67.2	21.0	70.1	17.6	64.6	16.4	63.0	7.8	65.4	17.1

* Adjusted by covariance on the basis of terminal growth on July 4, 1949.

**Since terminal growth stopped before solar radiation was changed, a single value is given for trees having same initial treatment.

Least Significant Difference	5%	1%
Terminal growth	9.8cm	13.0 cm
Dry weight increase	14.1gm	19.5 gm

Figure 3. Effect of Nutrient Solution Concentration and Midseason Changes in Solar Radiation on Dry Weight Increase of Montmorency Cherry Trees, 1949.

(upper) Trees started in 100% solar radiation.

(middle) Trees started in 50% solar radiation.

(lower) Trees started in 30% solar radiation.

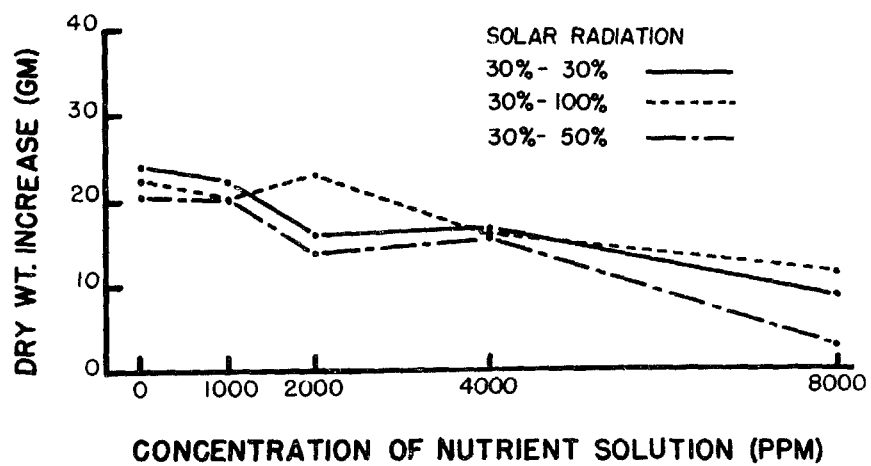
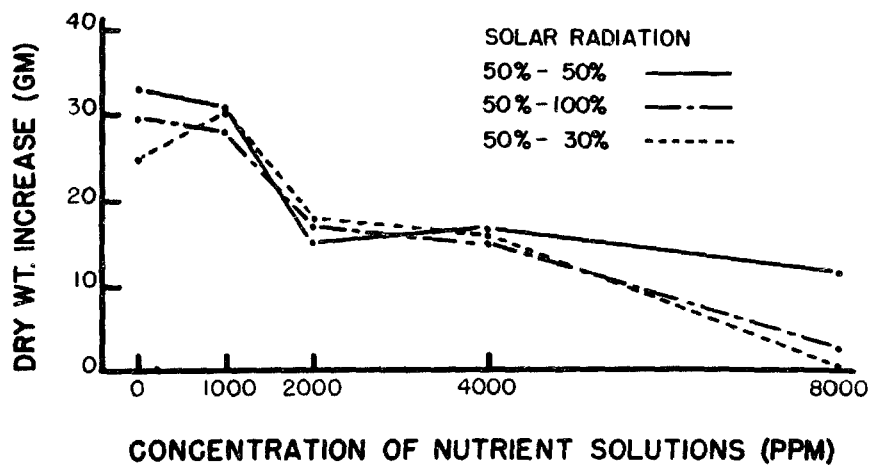
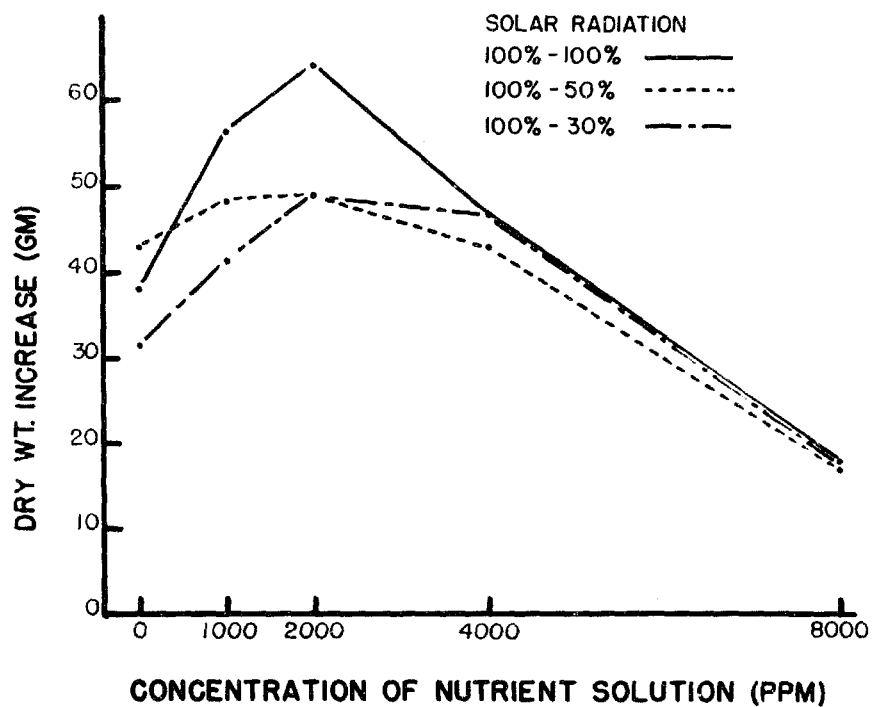


Figure 3

Figure 4. Effect of Nutrient Solution Concentration
and Solar Radiation on the Growth of
Montmorency Cherry Trees, 1949.

(upper) Terminal growth.

(lower) Dry weight increase.

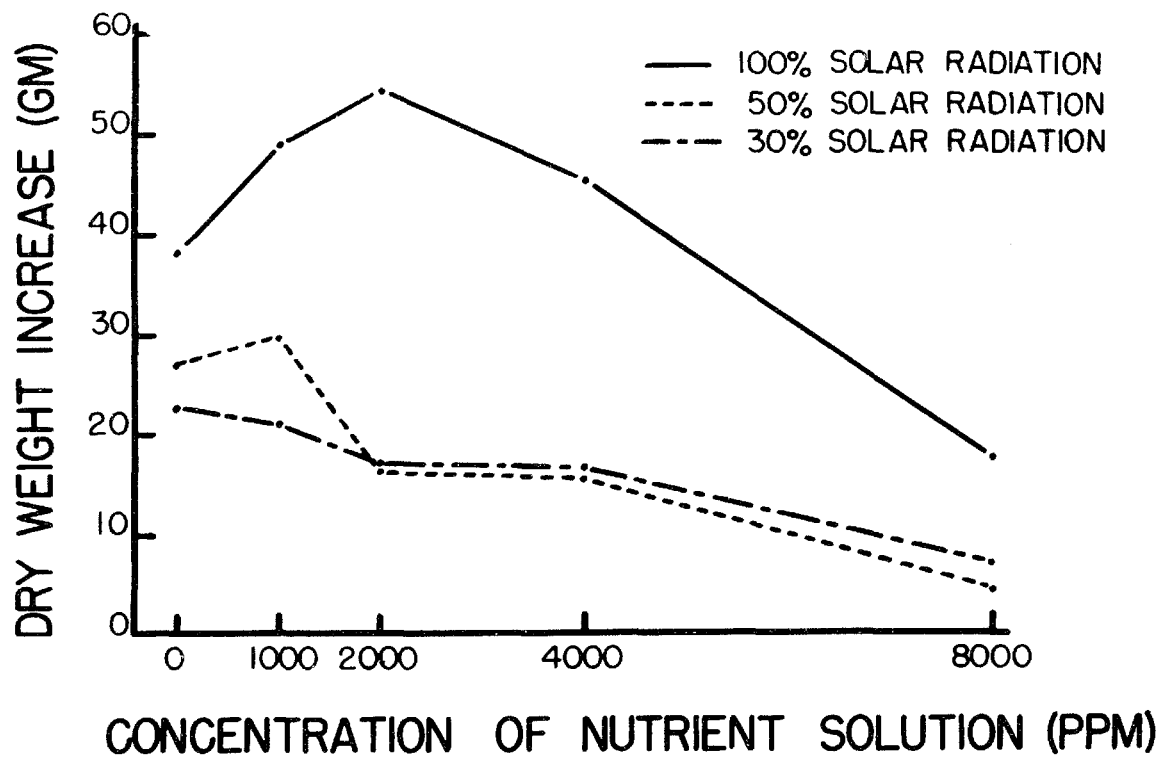
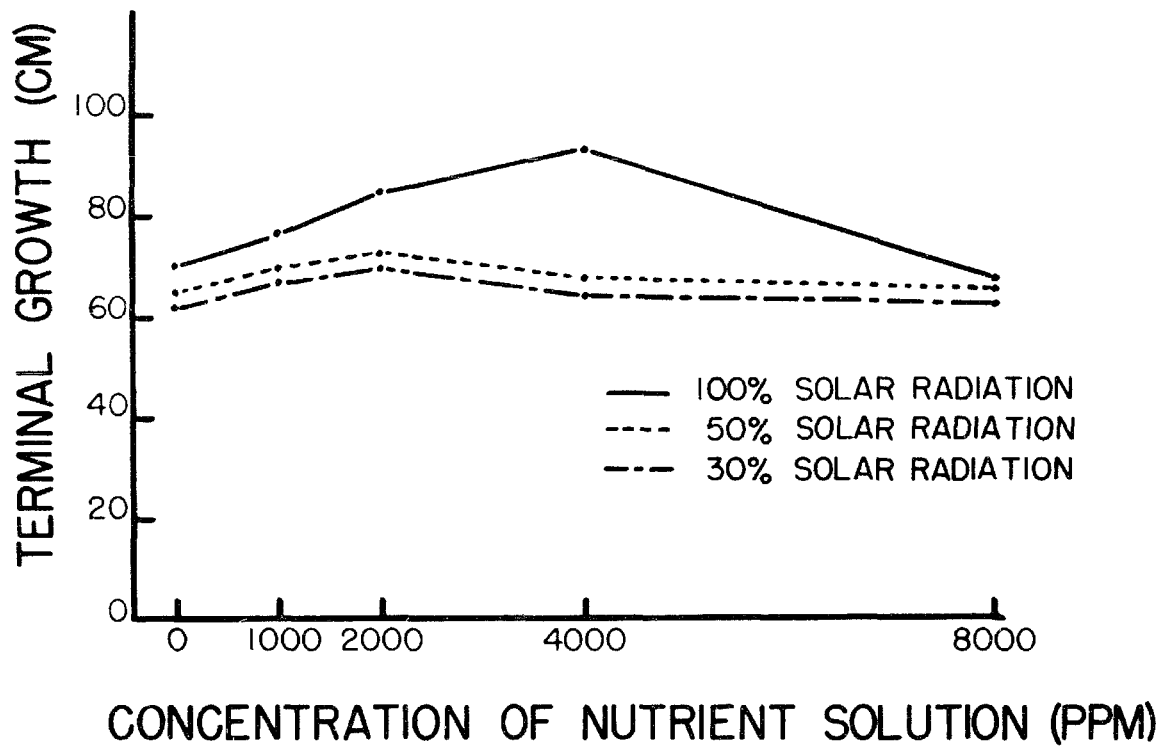


Figure 4

100% S.R. to conditions of lower intensity of solar radiation resulted in less dry weight accumulation. Highly significant differences occurred between the solar radiation treatments and between the nutrient levels; also the interaction between the solar radiation and nutrient level treatments was highly significant. The best growth in 100% S.R. was obtained with 2,000 ppm, in 50% S.R. with 1000 ppm, and in 30% S.R. the application of all concentrations depressed dry weight increase. The root and shoot weights varied similarly in all cases, but there was a tendency for the weight of the roots to decrease relative to the weight of the shoots as the concentration of the nutrient solution was increased. (Appendix Table 2)

Leaf Analysis--1950

The Effect of Nutrient-Element Concentration.

Averages for the leaf analyses of all trees given each of the four nutrient levels are presented in Table 5.

By increasing the concentration of the nutrient solution from zero to 4,000 ppm the nitrogen in the leaf was increased from 1.74% to 3.31%. Phosphorus showed no significant changes over the same range of concentration--zero to 4,000 ppm--of nutrient solutions. The lowest value of potash occurred where no nutrients were added and the highest value occurred where the 1,000 ppm nutrient solution was applied. At 2,000 ppm the potassium percentage was less

Table 5. Leaf Analysis (% dry wt.) as Affected by Concentration of Nutrient Solution, 1950

Concentration of nutrient solution ppm	Nutrient-Element							Index of	
	N	P	K	Ca	Mg	Fe	Mn	intensity*	balance*
0	1.74	.14	1.08	.89	.45	.012	.007	-33	37
1,000	2.54	.15	1.37	1.13	.55	.012	.014	-10	116
2,000	2.79	.15	1.29	1.15	.54	.012	.015	- 8	133
4,000	3.31	.14	1.35	.99	.49	.012	.014	-10	167

*See Appendix Table 1.

than when 1,000 ppm was used, and 4,000 ppm produced approximately the same value as 2,000 ppm. Calcium, also was lowest when no nutrients were added; 1,000 and 2,000 ppm produced the highest levels, and the 4,000 ppm treatment decreased the amount of calcium in the leaves somewhat. Magnesium behaved in the same manner as calcium; lowest when no nutrients were added, highest at the 1,000 and 2,000 ppm nutrient-solution concentration, and then lower at the 4,000 ppm level. Iron analysis was constant for all nutrient concentrations. The manganese content of the leaves was low when no nutrients were added, was doubled by the application of the 1,000 ppm nutrient solution, and remained at that level for the other treatments.

Computations of the indices of nutritional intensity and balance deviations were made using the overall average of the 1949 experiment as a standard (see Appendix Table 1 for method of calculation). These computations show that the index of nutritional intensity of the trees receiving no nutrient-elements was lower than where nutrient-elements were added. The 1,000 ppm treatments increased the index of nutritional intensity, but no further increases were caused by 2,000 and 4,000 ppm. Where no nutrient-elements were applied the leaf analysis values for the various elements were uniformly low, giving a favorably low index of balance deviations, zero being considered as a condition of perfect balance. As the nutrient solution

concentration was increased, the index of balance deviations was increased.

Effect of Solar Radiation.

A comparison of leaf analyses for trees which were in 100% S.R. with those in 40% S.R. for the full season (Table 6) shows little variation for nitrogen, magnesium, and manganese. Phosphorus, potassium, calcium, and iron were all higher in the leaves from trees in 40% S.R. than in those in 100% S.R., and magnesium was lower. The trends brought out by varying periods of exposure to the full intensity of solar radiation or to shaded conditions were not uniform, but some generalizations may be attempted.

Varying periods of shading had little or no effect on the absorption of either nitrogen or manganese. The absorption of phosphorus, potassium, calcium, and iron was increased in the shaded treatments as compared with the non-shaded treatments. The most outstanding trend, which applied to some extent to all four nutrient-elements just mentioned, but was best exemplified by iron, was the tendency for leaf analysis to remain constant with increasing periods of initial shade until the length of the shade periods reached 8 to 16 weeks. On the other hand, initial periods of full sun had an immediate effect in decreasing the concentration of these nutrient elements.

Table 6. Leaf Analysis (% dry weight) as Affected by Varying Solar Radiation During the Growing Season, 1950

Weeks		Nutrient-Element							Index of	
Sun	Shade	N	P	K	Ca	Mg	Fe	Mn	intensity*	balance*
Trees Started in Sun										
0	16	2.78	.200	1.58	1.24	.45	.018	.013	- 1	104
1/2	15 1/2	2.56	.145	1.52	1.05	.39	.014	.011	-16	99
1	15	2.56	.175	1.12	1.15	.52	.014	.014	-10	109
2	14	2.65	.160	1.24	1.02	.56	.014	.012	-13	78
4	12	2.57	.115	1.32	1.10	.59	.012	.013	-14	114
8	8	2.68	.135	1.27	1.05	.64	.011	.013	-13	110
16	0	2.81	.130	1.25	.90	.57	.009	.013	-17	139
Trees Started in Shade										
Shade	Sun									
0	16	2.81	.130	1.25	.90	.57	.009	.013	-17	139
1/2	15 1/2	2.52	.155	1.24	.95	.46	.009	.011	-22	112
1	15	2.48	.125	1.10	.95	.48	.009	.013	-22	125
2	14	2.35	.135	1.30	.90	.54	.009	.014	-18	138
4	12	2.74	.145	1.33	1.14	.47	.009	.014	-14	145
8	8	2.45	.130	1.04	1.00	.42	.011	.011	-23	87
16	0	2.78	.200	1.58	1.24	.45	.018	.013	- 1	104

* See Appendix Table 1.

Perhaps the most significant figure presented in Table 6 is the index of nutritional intensity, which is an expression of the whole complex of nutrient-elements in the leaf. Here, the shaded trees showed a much higher index than those receiving the full intensity of solar radiation. Also, as described for the individual elements above, there tended to be very little change in the index of nutritional intensity as the period of shade increased up to eight weeks, but progressive decreases in the index occurred as the period of full solar radiation was extended.

Growth--1950

Terminal Growth.

Terminal growth was measured at frequent intervals in order to determine the effect of the six changes in solar radiation brought about by moving the trees into or out of the shaded area. These data showed that when the trees were moved from shade to sun the rate of terminal elongation was decreased, and when moved from sun to shade, the rate of terminal elongation was increased (Table 7). An analysis of variance showed most of these differences to be highly significant. Likewise, differences in rate of terminal elongation associated with intensity of nutrition were highly significant (Table 8). The interaction between solar radiation and concentration of nutrient solution was not significant. The terminal growth differences caused

Table 7. Total Terminal Growth (cm) as Affected by
Varying Solar Radiation During the Growing
Season, 1950

Weeks		Date of Measurement						
Sun	Shade	6/6	6/8	6/12	6/17	6/23	7/6	8/14
Trees Started in Sun								
1/2	15 1/2	6.1	9.1*	16.3*	26.8*	40.5*	65.5*	72.4*
1	15	5.4	7.8	14.3	24.0*	36.6*	57.3*	63.5*
2	14	4.5	6.9	12.4	20.4	31.7*	57.7*	69.6*
4	12	3.6	5.7	11.1	19.4	29.6	56.4*	69.6*
8	8	6.6	10.0	16.9	27.4	39.8	57.1	61.6*
16	0	4.9	7.3	13.4	22.9	34.0	52.8	57.0
Trees Started in Shade								
<u>Shade</u>	<u>Sun</u>							
1/2	15 1/2	5.4*	8.5	14.0	23.8	34.2	52.5	56.6
1	15	4.6*	7.3*	14.5*	25.0	37.5	56.5	61.8
2	14	4.4*	7.4*	15.5*	26.7*	38.4	57.8	64.1
4	12	4.2*	6.9*	14.5*	26.6*	42.0*	67.6	75.4
8	8	3.7*	6.4*	13.5*	25.5*	40.9*	70.6*	81.2
16	0	4.7*	7.2	15.1*	26.0*	39.7*	67.3*	78.0*

* Trees were in the shade at this date
Least significant difference on Aug. 14

1% = 4.4 cm
5% = 3.4 cm

Table 8. Total Terminal Growth (cm) as Affected
by Nutrient Element Concentration, 1950

Nutrient-Element concentration ppm	Date of Measurement						
	6/6	6/8	6/12	6/17	6/23	7/6	8/14
0	4.2	6.8	12.9	22.4	33.7	53.3	58.3
1,000	4.6	7.3	14.2	24.4	36.9	61.7	71.1
2,000	5.1	7.9	14.8	25.3	38.4	62.2	71.0
4,000	5.4	8.2	15.7	25.9	39.4	62.6	69.7

[illegible]

Figure 5. Terminal Growth of Montmorency Cherry Trees on Successive Dates as Affected by Varying Periods of Full Solar Radiation and 40% Solar Radiation (on right) and by Nutrient Solution Concentration (on left). 1950.

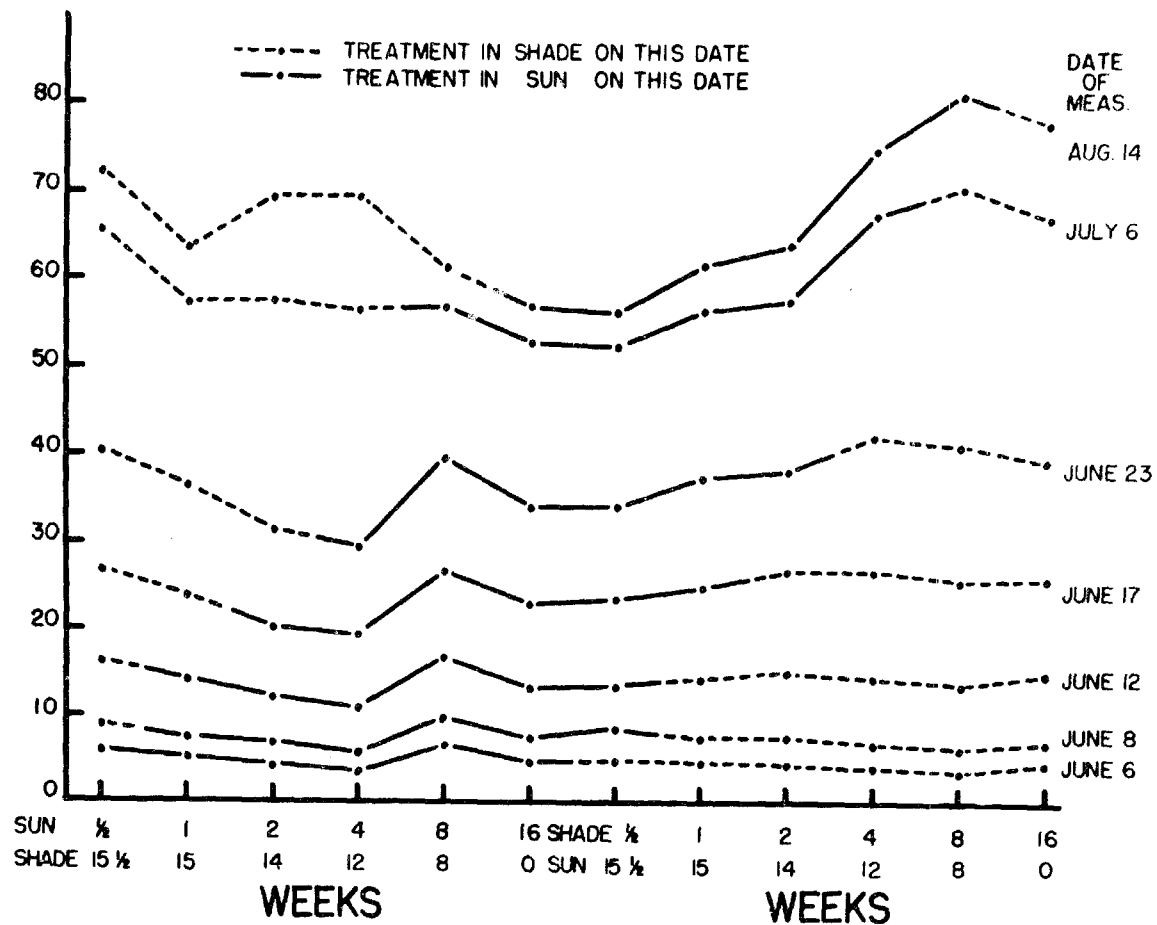
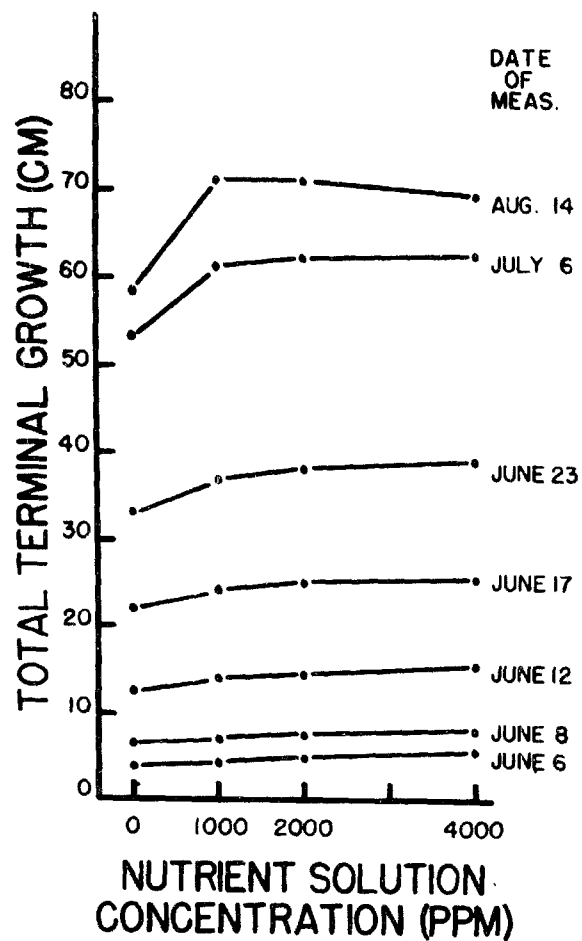


Figure 5

by nutrition indicated that the trees receiving the zero level grew poorly, but that there was an increase in terminal growth with added nutrients. This relationship prevailed until near the end of the growth period when the trees in the higher nutrient level stopped growing a few days before the 1,000 ppm level trees. This permitted the trees at the 1,000 ppm level to finish the season with slightly more terminal growth than that produced by trees at higher nutrient levels. The differences in terminal growth at the 1,000, 2,000, and 4,000 ppm levels were not significant, but the terminal growth values at these levels were all significantly greater than at the zero level.

Dry Weight

Dry weights of the trees at planting time were uniform in 1950, therefore, these figures could be used directly as the growth criteria, but for easier comparison with the 1949 data, dry weight was converted to dry weight increase by subtracting a constant value for the initial dry weight. Highly significant differences existed between nutrient levels and between solar radiation treatments (Table 9), but there was no significant interaction. The values for dry weight followed the same pattern as the values for terminal growth, and would appear to be largely determined by the amount of shoot growth because of the influence of terminal growth on leaf area. Nevertheless,

Table 9. Dry Weight Increase (gms) as Affected by Nutrient-Element Concentration and Varying Solar Radiation During the Growing Season, 1950

Trees Started in Sun											
Weeks		Concentration of Nutrient Solution									
Sun	Shade	0		1,000		2,000		4,000		Average	
		Orig.	Adj.	Orig.	Adj.	Orig.	Adj.	Orig.	Adj.	Orig.	Adj.
1/2	15 1/2	32.7	32.2	33.9	28.5	33.7	27.0	22.8	22.7	30.8	27.6
1	15	19.4	26.3	20.4	22.6	21.5	20.5	18.8	20.9	20.0	22.6
2	14	20.9	26.4	33.2	26.0	28.6	29.5	40.4	35.8	30.8	29.4
4	12	31.6	37.8	40.1	34.4	37.5	34.5	32.1	29.1	35.3	34.0
8	8	23.6	36.1	34.2	36.1	24.8	27.5	28.1	27.1	27.7	31.7
16	0	23.3	35.8	35.5	39.4	18.9	25.6	24.1	27.9	25.5	32.2
Trees Started in Shade											
Shade Sun											
1/2	15 1/2	39.2	31.2	27.7	44.8	22.9	26.1	26.6	37.1	29.6	36.8
1	15	39.2	27.8	35.8	38.6	33.6	32.4	31.4	33.8	32.1	36.0
2	14	30.7	23.8	43.4	43.4	38.8	39.2	31.5	32.9	34.4	36.6
4	12	34.5	36.2	45.1	40.6	49.2	39.5	38.5	34.8	42.2	37.4
8	8	29.6	27.3	41.6	32.1	32.3	19.2	41.6	26.9	35.7	27.0
16	0	28.8	27.8	43.0	30.4	28.3	22.5	45.9	36.6	36.2	29.6
Averages		27.1	33.0	37.0	34.7	30.8	28.6	31.8	30.5	31.7	31.7
Least significant difference						5%	1%				
Original values						17.1	22.6				
Adjusted values						14.0	18.5				

analysis of covariance between the two factors, indicated significant differences in dry weight beyond those arising from differences in terminal growth. Dry weight values adjusted by means of covariance, on the basis of terminal growth, showed a reversal of the trend shown in the unadjusted dry weights.

Discussion

Leaf Analysis--1949

In evaluating the leaf analysis data of this experiment a relationship should be established with similar data collected under field conditions.

Table 10 shows the results of a survey conducted by Kenworthy (1950) in Montmorency cherry orchards of Michigan in comparison with average results obtained in this experiment. In this survey samples were taken from apparently normal trees of bearing age which showed no visible symptoms of deficiency or toxicity. These data may be considered to represent a normal range of leaf analysis values. Variations within this range may be presumed to be produced by a number of physiological and environmental factors, solar radiation among others. Following the concepts of Shear, Crane, and Meyers (1948), there should be an optimum condition of nutrition within this range for a given set of climatic conditions. Thus solar radiation

Table 10. Comparison of Leaf Analyses from
Field Samples with Samples from
the Sand-Culture Experiments

Value	Nutrient-Element						
	N	P	K	Ca	Mg	Fe	Mn
Field Samples							
Average	2.83	.270	1.54	1.91	.74	.028	.011
Maximum	3.42	.670	2.82	3.00	1.16	.074	.028
Minimum	2.07	.090	.41	.91	.40	.002	.004
Sand-Culture Experiments							
Average	2.81	.186	1.42	1.35	.72	.020	.010
Maximum	4.16	.260	2.20	2.07	1.72	.036	.023
Minimum	1.46	.090	.83	.67	.35	.007	.005

may function not only as a determining factor in the uptake and utilization of nutrients, but also may establish conditions under which a given combination of nutrient-elements would be the most beneficial.

A comparison of leaf analyses in this experiment with the leaf analyses from field samples shows somewhat lower averages for the leaf analyses from trees in the nutrient solutions.

The extreme high and low values of individual treatments show nitrogen to be the only nutrient-element which exceeded the field samples in both extremes. Calcium and magnesium were the only other elements showing values below the range found in the field, yet no symptoms appeared during the growing season that would have suggested calcium or magnesium deficiency.

A major difference between trees in this experiment and field conditions is that the young trees of the experiment were in the vegetative condition, thus eliminating the complications of the reproductive phase. Rapid growth, characteristic of non-reproductive fruit trees, could cause a dilution in the concentration of certain nutrient-elements in the ash, while the nitrogenous constituents might remain at a relatively high level. Another factor which might have contributed to variations in leaf analysis was the fact that 20 per cent of the trees were grown under conditions of a pronounced deficiency of nutrient-elements. The latter factor alone, however, is not enough to explain

some of the differences that occur between field and nutrient-solution results because field leaf analysis averages for calcium and iron are almost equal to the maximum values observed in the controlled experiments. Also, the field average for phosphorus is higher than any found in this sand culture experiment. A third factor contributing to differences in leaf analyses may be the time of sampling. In this experiment the leaf samples were taken in September, while the field samples were collected in July and August. A seasonal curve for leaf analysis values has not been worked out for the Montmorency cherry, but as the leaves approach senescence there is a migration of certain nutrient elements from the leaf in other deciduous trees (Boynnton, Cain, and Compton, 1944; Murneek and Logan, 1932)

The results of these experiments reveal the existence of a somewhat more complex situation with respect to the effect of light upon leaf composition than has been indicated by previous workers. The absorption of nitrogen was increased, in general, by increasing the available supply of nitrogen in the nutrient medium up to 4,000 ppm nutrient-solution concentration, above which further increases in leaf nitrogen were not obtained. Nitrogen was the only element that functioned in such a manner with any consistency. This implies that nitrogen is the dominant factor in inorganic nutrition of tree fruits (Reuther, 1951; Brown, 1945), a point which is emphasized further by the close relation

between nitrogen content of the leaves and growth.

Figure 6 illustrates that growth is increased with increasing nitrogen until a limiting point is reached beyond which further increases in nitrogen content are associated with a rapid decrease in growth. Both the rate and extent of increase in growth with increasing nitrogen and the point at which depression in growth appears are dependent upon the incidence of solar energy. Since other nutrient-elements in the leaf increased along with nitrogen, it cannot be said without reservation that nitrogen was the depressing factor on growth. However, Figure 6 shows that growth decreased rapidly when leaf nitrogen exceeded 3.25 per cent in the 100% S.R. treatments and 2.9 per cent in either of the shaded treatments. No other nutrient-element showed this relationship.

The effect of solar radiation upon leaf analysis involves fundamental biochemical processes. The data may be classified into three major groups on the basis of the light intensity to which the trees were first exposed following the original initiation of treatments. The nitrogen values within these major groups behaved similarly in response to subsequent changes in the intensity of solar radiation, this behavior being a tendency toward higher leaf nitrogen when total solar radiation was increased. The exception to

Figure 6. (Upper) Relationship Between Leaf Nitrogen and Dry Weight Increase of Montmorency Cherry Trees at Different Intensities of Solar Radiation, 1949.

(Lower) Relationship Between Potassium and Magnesium in the Leaves of Montmorency Cherry Trees. Average Values for the Various Solar Radiation Treatments were used (See Table 3).

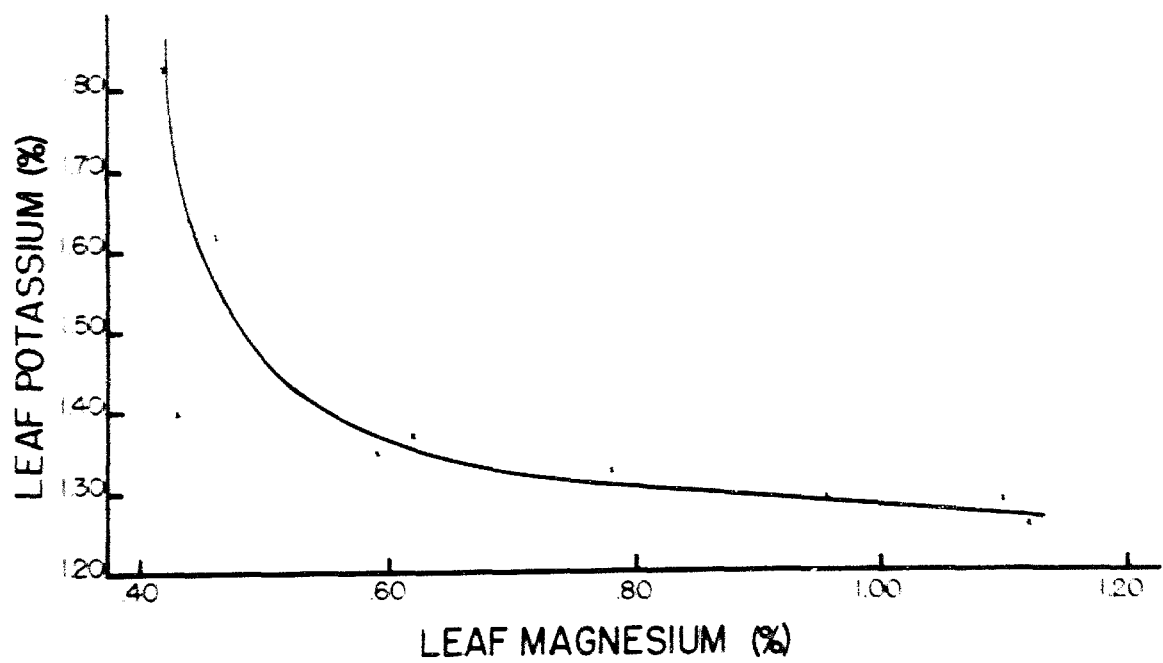
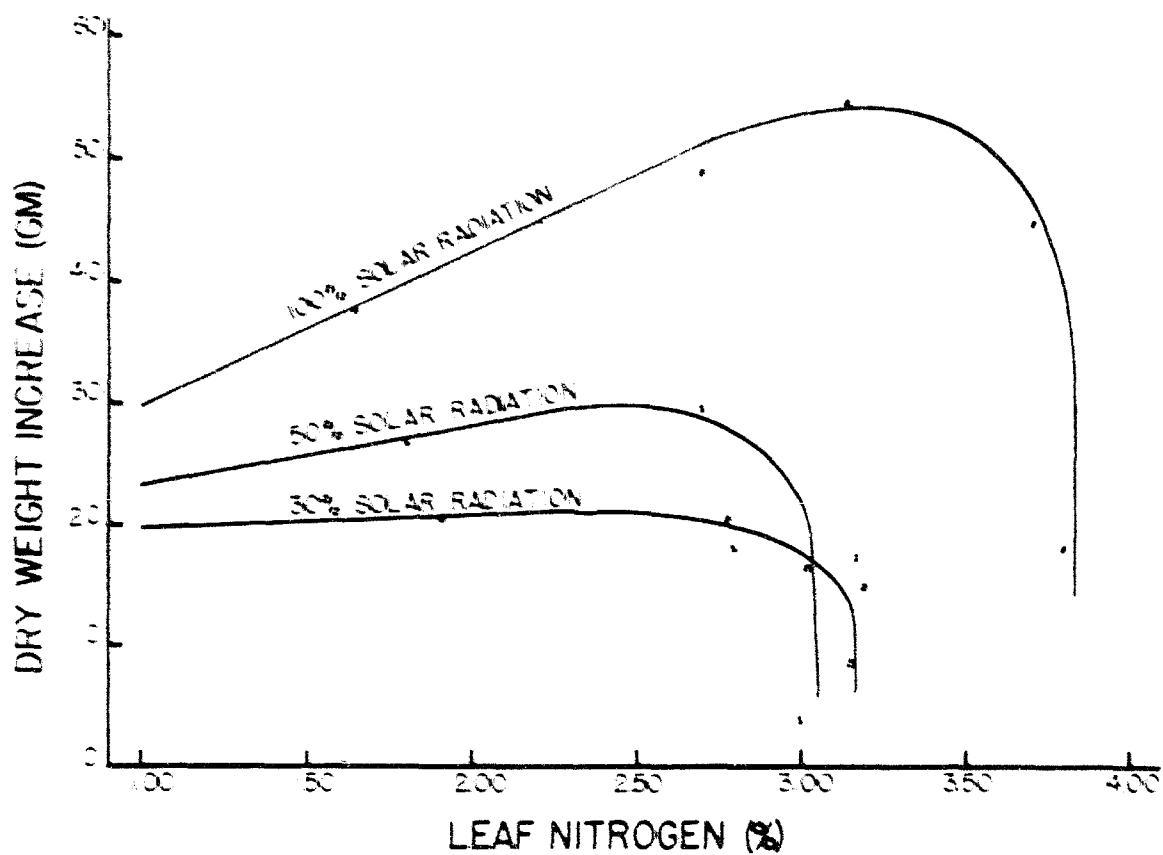


Figure 6

this is found in the 50% S.R. group where those trees shifted to 30% S.R. had a greater leaf nitrogen content than those shifted to 100% S.R. However, leaf nitrogen within the two shaded groups may not differ significantly just as the dry weight values in the same groups showed no significant differences.

There are a number of factors in nitrogen metabolism that could affect the leaf composition and from these factors some conclusions may be drawn as to the cause of differences observed in this data. An ample supply of labile carbohydrate is essential for normal functioning of protein metabolism since an active oxidative cycle, in which organic acids are formed, is necessary to provide the carbon skeleton for amination to form amino acids (Gregory and Sen, 1937; Chibnall, 1939). The condensation of amino acids to protein (assumed to be the path of protein synthesis) is an energy consuming process, and the level of carbohydrate supply has been advanced by several physiologists (Wood, 1942; Paech, 1935) as being of prime importance in regulating the protein level in plants. From this, it is possible to assume that there are different levels of energy requirement for the two processes; amino acid synthesis and condensation of amino acids to protein. Also, previous work by Gast (1937), Mitchell (1934, 1936), and Blackman and Rutter (1949) has indicated that the absolute absorption of nitrogen is independent of light supply, al-

though modifications in such a statement must be made, especially in cases where growth is increased markedly by applied nitrogen and the nitrogen is utilized extensively. This appears to be true in that group of trees which was started in 100% S.R. in which protein synthesis apparently was taking place actively and the absorbed nitrogen was thus being utilized and held in the leaf. When these trees were moved to conditions of reduced light, the energy supply was reduced and some proteolysis may have occurred, resulting in the formation of amino acids and amides that may be translocated out of the leaf and result in lower analysis for leaf nitrogen. This response may occur in the fall when the leaves approach senescence, and may be initiated by the reduced light intensity and shorter days of the fall months. Such a response would explain the loss of nitrogen from fruit tree leaves as the summer progresses, (Boynton, Cain, and Compton, 1944). Also, this effect would be prematurely induced by lowering the light intensity earlier in the season.

The trees initially at 50% S.R. were in a condition in which sufficient energy was available for amino acid synthesis, but not enough to maintain a high level of protein. Consequently, the inorganic nitrogen that was absorbed was utilized in the synthesis of amino acids and amides, the translocation forms of organic nitrogen. However, sufficient energy was not available for protein

synthesis, and as a result there was a gradient out of the leaves resulting from translocation of the amino acids and amides; the final result being reflected in lower analysis for leaf nitrogen.

The solar energy received by the trees in 30% S.R. was sufficiently low to impair amino acid and protein synthesis seriously, leading to an accumulation of inorganic nitrogen. When solar radiation was increased after a period of exposure to 30% S.R. and more energy was made available, there was an increase in leaf nitrogen which may have been due to an increase in the synthesis of organic nitrogen compounds.

Either an increase or a decrease in solar radiation from the 50% S.R. level would be expected to increase the leaf nitrogen, according to this hypothesis, and such was observed. An increase in solar radiation should increase the synthesis of protein, thus increasing leaf nitrogen, whereas, decreased solar radiation should decrease amino acid synthesis, thereby decreasing translocation of amino acids or amides out of the leaf, resulting in an increase of inorganic nitrogen.

The differences resulting from the effects of solar radiation are small compared to those due to concentration of the nutrient solution, consequently, the equilibrium between protein, amino acids and amides, and inorganic nitrogen shifts rather readily. Also it must be recognized

that this experiment did not deal with a constant source of energy, because the trees were subjected to the complete range of diurnal, as well as meteorological variations in solar radiation. Therefore, this experiment was a measurement of the resultant of many forces which gave the observed leaf analysis figure only because conditions were such that a certain portion of the overall series of reactions predominated during the period of growth.

The most striking feature of the phosphorus data was the increase in phosphorus in the 1,000 ppm level over that at the zero level, but at higher nutrient concentrations no definite effect was shown. It is probable that after the initial benefit gained from the presence of phosphorus in the nutrient medium, the effect of nitrogen (which was increased proportionately in the external solution) prevented the accumulation of phosphorus at higher concentrations. This effect, believed primarily to be anion competition (Boynton, and Compton, 1944) was strong enough to prevent the phosphorus level from approaching the average of values normally found in samples from commercial orchards.

Phosphorus was not affected markedly by solar radiation, although there seemed to be a slight tendency towards an equilibrium which is well balanced at the 50% S.R. level. Shifting trees from 50% S.R. to 100% S.R. or to 30% S.R. had no effect upon leaf phosphorus; whereas, decreasing the

solar radiation on the trees growing in 100% S.R. increased the leaf phosphorus, and increasing the solar radiation on the trees growing in 30% S.R. also increased the phosphorus level. This suggests that optimum conditions for phosphorus metabolism occurred at, or near, 50% of full solar radiation. Such an optimum would, most likely, be associated with a change in the nature of the earlier stable products of the post-photosynthetic reactions as compared with other solar radiation conditions. Any change in environment toward that condition which is associated with optimum would tend to cause an increase in phosphorus metabolized. There may have been no accumulation of inorganic phosphate at the sub-optimal environmental conditions because of the anion competition with nitrate ions.

With the exception of the magnesium present in chlorophyll and the association of calcium with pectin in cell walls, the three major cations: potassium, calcium, and magnesium, are not combined in major organic compounds. The three cations may be classified together as translocation regulators, but their specific functions are only imperfectly understood. In their functioning as translocation regulators they appear to be very closely related with each other and should therefore, be treated as a unit.

The complexities of the inter-relationships among the three elements (K, Mg, Ca) have never been fully understood. While certain relationships can be seen in an examination

of the data, strict relationships do not always hold true. In order to obtain more consistent relationships between these nutrient-elements an analysis for certain fractions of the total cation content, water soluble, for instance, would appear to be more desirable because of their physiological function.

One of the general relationships which may be pointed out as obviously being a result of cation balance was the trend towards decreasing magnesium with increasing nutrient concentration. This was not related specifically to any other trend among the cations, although potassium showed, in general, an increase with increasing concentrations of the nutrient solution. An exception to this was the consistently high potassium value observed at 1,000 ppm external concentration, which may be, in turn, a response to variations of other elements.

Within each of the three major solar radiation groups there was a strong tendency for calcium concentration to be inversely correlated with dry weight increase. Thus the minimum calcium content coincided with, or was close to, the nutrient concentration at which maximum dry weight increase was obtained, within the group of treatments that started with the same initial solar radiation treatment. This observation indicates that calcium absorption may have been relatively constant with respect to external concentration with the observed differences being due to dilution

by increased growth. Thus, although calcium was absorbed about equally in all nutrient concentrations, the nutrient level influenced calcium content in the leaf through an effect on growth.

Somewhat more orderly responses to variations in solar radiation were observed among these three cations. Calcium was not decidedly affected by shifting, but the intensity of solar radiation in the original exposure had the definite effect of decreasing calcium content with decreasing light. Crystals of calcium oxalate are commonly observed in many plant species and tissues, and are located characteristically in the palisade mesophyll of fruit tree leaves. The function of calcium in such cases is considered to be that of removal of toxic products of metabolism. Conceivably, in the 100% S.R., where metabolism would be the most active, toxic products would be most prevalent and more calcium would be required for their removal. If such a mechanism were in operation, the calcium content of the leaves measured spectrographically would be roughly proportional to the metabolic activity of the leaves and differences would be due to the formation of crystals, the remainder of the calcium being relatively constant with respect to solar radiation. Such insoluble by-products would be affected only slightly by changes in intensity of solar radiation, and would prevent an alteration of the initial intensity of solar radiation from inducing a variation in calcium content.

The changes in magnesium content in relation to decreasing light intensity may be, in a large part, associated with the behavior of chlorophyll in reduced light. In all three major groups of intensity of solar radiation shifting resulted in changes in the magnesium content which were qualitatively related directly to the light intensity. The same observations are true for the comparisons among the major light groups except that there was another factor affecting the magnesium content in the 30% S.R. group to result in the high values observed. Here, again, cation balance may be the effective factor because of the close relationship between potassium and magnesium shown in Figure 6. The relationship shown in Figure 6 applies only to variations induced by solar radiation because effects of changes in the concentration of the nutrient solution are averaged. When potassium and magnesium are increased in external concentration, this balanced relationship does not hold as closely. This is evidence in favor of a physiological balance being the causative factor in the relationship between the two elements.

The characteristic feature of the response of potassium to solar radiation changes was the relatively large increase in leaf potassium when the trees were shifted into 30% S.R. from either 100% S.R. or 50% S.R. There was no change in leaf potassium when the trees were shifted into

higher intensities of solar radiation. The balanced relationship with magnesium as conditioned by solar radiation appears to be the determining factor.

Iron in the leaf showed no consistent response to increased concentration of the nutrient solution, but did increase with decreasing intensity of solar radiation. This increase may have been due to an increasing demand for iron in the synthesis of leaf pigments. There was no question but that changes in the pigmentation occurred rapidly in the shaded trees. Within seventy-two hours the color of the leaves on the trees, shifted from sun to shade, had changed from a bright green to a definite blue-green. Increased iron mobilization may have been associated with decreased solar radiation to compensate for a reduced capacity for pigment synthesis. This could have resulted in a change in the nature of the pigments as was observed in the change in leaf color.

Manganese proved to be a dominant ion with respect to nutrient-element balance in that it showed a general trend of increasing in the leaf as the concentration of the nutrient solution was increased. Manganese may have exerted a suppressive effect on the absorption of iron comparable to that of nitrogen upon phosphorus. The effect of solar radiation upon manganese content was directly the inverse of the effect of solar radiation upon nitrogen. Recent work by Schroder, Blue and Albrecht (1948) has shown

manganese to be associated with nitrogen metabolism in some way, in that increased amino acid synthesis was associated with increased manganese. Other work has shown the action of manganese in catalyzing the reduction of nitrates (Jones, Shepardson, and Peters, 1949; Arnon, 1937). The higher manganese content in the leaf, where solar radiation is lower, may act as partial compensation for a reduction in amino acid synthesis or in nitrate reduction.

Leaf Analysis--1950

A study of the leaf composition values for the 1950 results requires a different line of reasoning than the 1949 results. Two apparent reasons for this are: the relatively short periods of exposure early in the season to sun or to shade which were used in 1950, as compared with constant full sun in the early phases of the 1949 experiment; and the extreme differences in temperature and growth between the two years. (See Appendix Table 3)

In 1950 the leaf nitrogen was nearly identical for treatments involving shade or sun for the whole season. The depressing effect on nitrogen by an early season exposure to either sun or shade followed by constant conditions for the remainder of the season was also nearly identical in either case. This suggests that a mechanism for nitrogen metabolism is established early in the growth of the shoot and is in some manner determined by the light intensity.

Any change in light intensity during the developmental period may disrupt the enzymatic system in some way, causing a reduction in the ultimate level of leaf nitrogen. During the cool summer of 1950, the rate of metabolism was relatively low, as evidenced by the low dry weight accumulation in the most productive treatment. Therefore, fundamental changes in the metabolic mechanism due to changes in light intensity would be expected to have a relatively rapid effect upon leaf composition.

The effect of increasing the concentration of the nutrient solution was very much the same, qualitatively, in 1950 as in 1949, although the 1950 averages were generally lower than the 1949 averages. Generalizations concerning the effect of solar radiation upon leaf composition for the rest of the 1950 data appear to be the same for one element as for another, with the exception of manganese which was unaffected by solar radiation.

Under the conditions of the cool summer of 1950 with normal solar radiation, it was possible to repeat the observations of the previous investigators who reported increases in percentage content of nutrient-elements due to shading; an effect which was generally agreed to be a matter of dilution, with absorption relatively unaffected. This appeared to be true where the environmental conditions were somewhat less than optimum for the plant species under investigation. Under conditions more favorable for rapid

metabolism the plant must have increased demands for certain nutrient-elements, and because of a more active metabolism the plant would be capable of increased absorption and cause the large and irregular responses noted in the 1949 data.

There was considerable uniformity of response among the several nutrient elements to changes in the solar radiation, and the indices of nutritional intensity and deviation from balance showed some clear trends. The index of nutritional intensity indicates that as short a period of exposure to full sun as half a week after the initiation of terminal growth may be sufficient to cause a reduction in the intensity of nutrition in the leaf. This reduction in nutritional intensity tended to be continuously greater as the initial light exposure became longer. Apparently very little increase in intensity of nutrition was induced by the initial shading period, because no marked differences were observed until the shade period was longer than eight weeks. Two conclusions may be drawn from this observation: one, the effect on nutritional intensity is directly due to solar radiation rather than a negative effect due to a lack of solar radiation; and the other, dilution of nutrient-elements by growth is not the complete explanation. The data suggest that solar radiation has a profound and lasting influence in the early phases of growth, upon the

enzymatic constitution of the shoot or affects some other stable factor that influences nutrient absorption over a long period of time.

The index of balance deviations showed no effect of solar radiation. The balance of nutrient-elements in the leaves of trees grown in the shade for the full season was farthest removed from the standard, while the balance of nutrient-elements closest to the standard was found in those treatments which were in shade half the season and in sun half the season. This indicates that at either extreme, a full season of either sun or shade, the index of balance deviations is increased. This disturbance of balance, which is associated with a high positive index of nutritional intensity in the shaded treatments, and with a high negative index of nutritional intensity in the treatments receiving full sun, is apparently reduced most at the mid-point between the two extremes where the opposing forces have a tendency to cancel each other.

Growth

Terminal Growth.

The first manifestation of growth in the deciduous trees is the spring flush of shoot growth. Because of the perennial nature of the plant, the initial phase of terminal growth is largely determined by the food and nutrient-element reserves of the previous year (Harley, et. al., 1949)

and the temperature of the current year. In 1949, three weeks elapsed after planting before any treatments were initiated, yet, during this period very pronounced differences, which were highly significant statistically, appeared in the terminal growth. Since growing conditions were identical for all trees, the nature of the individual trees was responsible for the initial differences. Because of the differences in initial growth, the final terminal growth values were adjusted by covariance on the basis of the initial growth. The results still showed terminal growth of the full sun treatments to be higher than that of the shaded treatments. This was in direct contrast to 1950 when treatments began at planting time and shaded trees grew more than the non-shaded trees. This comparison suggests that under the warmer conditions of 1949 (Appendix Table 3) the energy from the available stored food was the determining factor in the initial phases of growth, but that later the supply of newly elaborated food materials was the limiting factor. Interactions between temperature, especially night temperature, and light intensity have been demonstrated by Went (1945), who felt that the effects of temperature on translocation were of primary importance. The dry weight data in this paper indicates a linking of respiration with this effect of temperature. The organic compounds available for ready translocation may be considered, also, to be those which are readily available as

respiratory substrates. Wherever living cells are involved in the translocation process these compounds may be subjected to the attack of the respiratory enzymes, and if conditions conducive to a high rate of respiration exist, then the net result would be, not only a decreased net translocation, but also a decrease in total dry weight. Blackman and Wilson (1950) have reported that half to two-thirds of the material translocated toward the roots is lost in respiration. This concept may be applied in reverse to the terminal growth data. Since the 1949 season had an average mean daily temperature of six degrees higher than 1950, the respiration rate would be higher in 1949, and the ultimate limiting factor in 1949 would be food supply. Associated with the rate of respiration was the final cessation of terminal growth which was preceded by a few hot days, indicating that growth stopped when food supply became limited. The trees that received more light produced enough food to continue growing a little longer than trees that were shaded. Hormonal control appeared to be of relatively little importance because the trees were all started together under high light conditions, and were all depressed equally. The stimulation resulting from shifting into shade after growth had started was insufficient to over-balance the food deficiency. The 1950 data, where food supply was not a limiting factor and control of terminal growth appeared to be exerted by hormone inactivation, showed less effect due

to shifting trees from sun into shade than from shifting trees from shade into sun. Following this observation, the effect of shading in 1949 could not be expected to have much effect on terminal growth because of the long initial period of full sun.

In 1950 temperatures were warm enough for mobilization of stored products, yet cool enough to permit translocation to the growing regions without excessive losses due to respiration. Under these conditions a direct relationship was observed between length of shade period and amount of terminal growth without the complicating effect of a uniform initial period of full sun. The photo-oxidation of growth regulators, or an effect of light on some other factor (Galston, and Hand, 1949), may provide an adequate explanation of this relationship. An examination of Figure 5 shows that the trees which were started in the shade were remarkably uniform in growth until they were transferred to full sun conditions. The rate of growth was retarded immediately following the transfer to full sun.

The exposure of the trees to a short light period, or until the average shoot length was 2-3 centimeters, apparently caused a sufficient inactivation of the hormonal system, or perhaps of its precursors, to result in a highly significant depression of growth as compared to trees that were shaded throughout the period of shoot growth.

Applications of this concept to an explanation of known responses of trees growing in the field must be based on an assumption that different conditions are optimum at different stages of growth. Shoot growth of cherry trees takes place in the spring and early summer months when temperatures are relatively low, especially in the fruit districts of Michigan, a condition which happened to prevail during the 1950 experiment, but which did not exist in 1949. Moderate temperatures, plus reduced light seem to be optimum for shoot growth on the cherry. An examination of the average conditions with respect to these factors shows that the climate in Michigan provides a long period of cool weather and cloudy skies in the fruit belt during an average spring. The effect of Lake Michigan, which has not warmed up from the winter freeze by May, is to cool the air and simultaneously produce the cloud cover that causes the spring plateaus in the solar radiation curve for Michigan (Crabb, 1951). These conditions appear to be ideal for the production of a maximum leaf area by means of increased shoot growth. With the establishment of a large leaf area the tree would be more capable of maximum photosynthetic activity during the warmer months of midsummer.

Although the dominant factor may be that of climate, nutrition also has an effect that was expressed during both years by reduced growth when no nutrients were added. Figure 5 shows that growth started normally on stored re-

serves regardless of nutrient level, but without the addition of nutrient-elements, one or more nutrients soon became limiting, and the growth rate decreased and finally stopped earlier than did those trees supplied with nutrients. Obviously those trees in which nutrient supply became limiting early enough in the season to limit shoot growth, would continue to suffer from nutrient deficiencies and reduced leaf area throughout the summer, if climatic conditions were not limiting.

Dry Weight.

In the final analysis the net production of dry weight is probably the best expression of the efficiency of a plant, especially in young, non-bearing trees, which make fruit yield records impossible. Dry weight production represents the net result of all the factors which contribute to the growth of the plant, and, where the hazards of fruit setting are not present, is correlated with potential yield. Here, again, the fundamental difference between results of 1949 and 1950 was that production in 1949 was twice that of 1950 for the full sun treatment. In 1949 there was a large beneficial effect from the addition of 1,000 ppm and 2,000 ppm nutrient solutions in full sun but a depression by higher levels. On the other hand, at 50% S.R. trees given 1,000 ppm produced only slightly more dry weight than where no nutrients were added, and at 30% S.R.

the zero level produced the best growth, with decreased growth at all the higher levels.

Dry weight increase may be considered to measure the net result of the opposing mechanisms of photosynthesis and respiration. Unquestionably the rate of photosynthesis would be decreased by heavy shading. There may be some question, however, as to whether or not there is a maximum light intensity, within the limits of solar radiation received at the surface of the earth on a bright day, at which photosynthesis is a maximum for tree fruits. Maximum light intensities have been recorded for other plants, especially those ecologically adapted to shaded conditions under a forest cover. Heinicke and Hoffman (1933) found that maximum carbon dioxide assimilation by apple leaves could not be expected at light intensities lower than 1200 foot candles. This implies that apple trees may be expected to increase production with increasing solar radiation throughout the range of values associated with full sun since a large portion of the leaves of a mature tree do not receive direct sunlight for a full season. This point is amplified by the occurrence of higher yields in the orchards in Western United States which grow under higher light intensities than the orchards in Eastern United States.

An examination of the data for the non-fertilized treatments, where no depressing effect of high nutrient level would be involved, shows that increasing the solar

radiation increased the net accumulation of dry weight until the trees received the full intensity of solar radiation. This indicates that under Michigan conditions photosynthesis does not progress at a maximum possible rate.

In opposition to photosynthesis there is a breakdown of products of respiration which is increased markedly by the two factors: salt concentration and temperature (Steward, et. al., 1940; Woodford and Gregory, 1948). The beneficial effects of added nutrients were observed only within certain limits which depended on the solar radiation. With nutrient concentrations above that particular optimum for the given solar radiation intensity a very definite depression in growth was observed with increasing nutrient solution concentration. This may have been associated with the increase in respiration caused by the high salt concentration which consumed the elaborated food materials faster than they would be replaced by photosynthesis, and in certain cases, faster than could be tolerated by a living plant. Such a case was demonstrated in the 8,000 ppm treatments in either shade condition. Most of these dropped all their leaves and died. Trees at the 8,000 ppm level which were in 100% S.R. grew well until moved into the shade where a sharp necrosis developed and the leaves dropped.

These data suggests a relationship in which the final controlling factor in determining the dry weight would be a balance between photosynthesis and respiration, with photo-

synthesis being dominant on the ascending portion of the growth curve, and respiration being dominant on the descending portion. In the full sun, increasing nutrient supply increased photosynthesis by means of increased leaf area and more efficient utilization of the leaf area available. Simultaneously, there was a rapidly increasing effect of salt concentration in stimulating respiration. At some external concentration of the nutrient solution, above 2,000 ppm, the respiration rate was sufficiently high to prevent any further benefits from increased photosynthetic efficiency due to increased nutrient supply. When the rate of photosynthesis was reduced by shading, this compensation point, where no further benefit was realized by increasing soil fertility, was reached at a much lower concentration of nutrients. This response was demonstrated by the peak of dry weight production at 1,000 ppm in the 50% S.R. treatments and at zero ppm in the 30% S.R. treatments.

Additional evidence in favor of this hypothesis is the shoot/root ratio. The data from the full sun treatments showed, very adequately, the relationship between the root portion and shoot portion under conditions of increased salt concentration. There was a steady increase of the shoot weight as compared to the root weight. On the ascending portion of the curve, there was a gain in root weight as well as in shoot weight, but the increases were not as great for the root as for the shoots. Respiration is in-

creased by high salt concentrations (Steward et. al., 1940), and since the root must depend upon translocated food materials for dry matter the increase in respiration associated with high salt concentration would reduce root growth. Since the roots have a less direct source of new organic material than does the shoot, the effect of respiration would be relatively greater on the roots. This effect was most noticeable at the 4,000 ppm level where root growth suffered a very large decrease relative to the 2,000 ppm level, while shoot growth was affected only slightly.

The effect of shifting the trees from one light intensity to another was significantly effective only in those treatments which were first in 100% S.R. The trees in 100% S.R. that were transferred to lower light intensities showed reductions in dry weight caused by reduced photosynthesis and leaf necrosis and defoliation at the higher salt concentration which were mentioned previously. On the other hand, moving trees from reduced solar radiation to full solar radiation did not result in any increase in dry weight. This implies that the photosynthetic mechanism was the limiting factor in the leaves that had developed under conditions of reduced solar radiation. Perhaps the development of chlorophyll was limited by the lack of sufficient solar energy. At the time of shifting to higher light intensity the mechanism for the new synthesis of chlorophyll may have degenerated in the aging leaf and consequently there was no response to the benefits of additional solar radiation.

The results of the 1950 experiment were in contrast to the above. In 1950 there were responses to both light intensity and concentration of nutrient solution, but there was no interaction between light intensity and concentration of nutrient solution. The unadjusted values for dry weight followed the same pattern as the terminal growth, and were apparently heavily influenced by the terminal growth. The extent of this influence was brought out by the results of covariance which caused a reversal of order of dry weights with respect to the effect of solar radiation. The beneficial effects from increased concentration of the nutrient solution were eliminated. By this adjustment solar radiation was shown to have a slight effect in increasing the efficiency of photosynthesis. The relatively small dry weight increase in 1950 (the order of magnitude of the 30% S.R. series in 1949, and showing a similar response), indicates that a relatively low rate of photosynthesis was associated with the cooler temperatures that prevailed throughout the summer of 1950. The difference between the 30% S.R. treatments in 1949 and the 1950 treatments was that in 1949 the higher nutrient levels in combination with the higher temperatures caused a sharp reduction in the dry weight increase, while in 1950 the reductions were relatively minor at the 4,000 ppm nutrient level. The lower temperature in 1950 resulted in a decreased rate of respiration for a

given nutrient concentration, a result confirming the work of Magistad, et. al., (1943) on the relationship between salt concentration and temperature.

The whole growth picture demonstrates the highly involved nature of the multiple-factor complex which governs the growth and well-being of the plant. These experiments illustrate that not only concentration of the nutrient solution, solar radiation, and temperature affect the life processes of the plant, but that the requirements of the plant with respect to these factors is very different during different phases of growth. The question of the phase of growth being followed is so important that a set of conditions highly favorable for one phase may actually be detrimental in some subsequent phase. These points were brought out in work with strictly vegetative plants, and it is to be assumed that when the reproductive cycle is brought into the equilibrium the situation will become even more complex. Also, some of the discrepancies that seem to appear in the literature may be satisfactorily resolved if these points are considered.

Summary

One-year-old Montmorency cherry trees were grown in sand culture under varying conditions of solar radiation and nutrient solution concentrations during two seasons: 1949, and 1950. Leaf analyses and growth records were collected and their relationships to each other and to the treatments were discussed.

Leaf analysis values for the individual elements did not increase proportionately with the concentration of the nutrient solution. Nitrogen and manganese values increased in proportion to the nutrient solution concentration, but the magnesium content decreased as the nutrient solution concentration was increased. Leaf phosphorus, potassium, calcium, and iron showed an irregular relationship with nutrient solution concentration, indicating that the absorption of phosphorus, potassium, calcium, magnesium, and iron was more dependent upon the physiological relationships among the nutrients than upon the absolute concentration of the element in the external solution.

Marked differences in leaf analysis were induced by differences in solar radiation. These differences were of a complex nature and were influenced by other factors, such as temperature, so that the responses of one year could not be repeated in a succeeding year. On the basis of our present knowledge, prediction of the effect of solar radiation upon leaf composition probably would not be successful.

Leaf nitrogen showed a close relationship with growth responses. Very marked depression of growth was associated with leaf nitrogen greater than 3.5%, in the full sun in 1949. At 30% S.R. and 50% S.R. depressions in growth occurred with leaf nitrogen contents higher than 2.9%. There was no apparent relationship between the absorption of the other nutrient-elements and growth, as affected by solar radiation and nutrient solution intensity.

A close negative relationship was observed between the potassium and magnesium leaf analyses. This relationship was associated with changes in leaf composition caused by differences in solar radiation rather than with the changes caused by differences in the concentration of the nutrient solution.

The relationship between leaf analysis and the nutrient solution and solar radiation treatments was different in 1949 from 1950. This difference appears to be associated with temperature more than solar radiation.

The conditions most favorable for the growth of Montmorency cherry trees vary in regard to the measurement of growth as follows:

- a. Terminal growth is favored by moderate temperatures and low light conditions.
- b. Increase in dry weight is the greatest with warm temperatures and full intensity of solar radiation.

c. Reduced solar radiation failed to stimulate terminal growth when storage reserves had been used in shoot growth prior to reducing solar radiation.

d. Higher concentrations of nutrient solutions were more toxic at higher temperatures and reduced solar radiation. With normal solar radiation and warm temperatures (conditions favoring dry weight increase) a total salt concentration of 2,000 ppm resulted in maximum dry weight increase. Reduction of the solar radiation to 50% resulted in maximum dry weight increase at a total salt concentration of 1,000 ppm, and at 30% S.R. the best growth was observed when no nutrients were added.

Trees growing in high solar radiation are more capable of utilizing higher intensities of nutrient elements than are trees growing in reduced solar radiation. However, in order to produce a given amount of dry matter it is more important that the trees have optimum conditions of nutrition where solar radiation is relatively low than where solar radiation is high.

Bibliography

- Arnon, D. I. 1937. Ammonium and Nitrate Nitrogen Nutrition of Barley at Different Seasons in Relation to Hydrogen Ion Concentration, Manganese, Copper, and Oxygen Supply. *Soil Sci.* 44: 91-122.
- Blackman, G. E. and Rutter, A. J. 1946. Physiological and Ecological Studies in Plant Environment. I. The Light Factor and the Distribution of Bluebell (*Scilla non-scripta*) in Woodland Communities. *Ann. Bot. n.s.* 10: 361-390.
-
- _____ and _____ 1947. Physiological and Ecological Studies in Plant Environment. II. The Interaction Between Light Intensity and Mineral Nutrient Supply in the Growth and Development of the Bluebell (*Scilla non-scripta*). *Ann. Bot.* 11: 126-158.
-
- _____ and _____ 1948. Physiological and Ecological Studies in the Analysis of Plant Environment. III. The Interaction between Light Intensity and Mineral Nutrient Supply in Leaf Development and in the Net Assimilation Rate of the Bluebell (*Scilla non-scripta*). *Ann. Bot. n.s.* 12: 1-26.
-
- _____ and _____ 1949. Physiological and Ecological Studies in the Analysis of Plant Environment. IV. The Interaction between Light Intensity and Mineral Nutrient Supply on the Uptake of Nutrients by the Bluebell (*Scilla non-scripta*). *Ann. Bot. n.s.* 13: 454-489.
-
- _____ and Templeman, W. G. 1940. The interaction of Light Intensity and Nitrogen Required in the Growth and Metabolism of Grasses and Clover (*Trifolium repens*). IV. The Relation of Light Intensity and Nitrogen Supply to the Protein Metabolism of the Leaves of Grasses. *Ann. Bot. n.s.* 4: 533-587.
-
- _____ and Wilson, G. L. 1950. Physiological and Ecological Studies in the Analysis of Plant Environment. VI. The Constancy for Different Species of a Logarithmic Relationship between Net Assimilation and Light Intensity and its Ecological Significance. *Ann. Bot. n.s.* 15: 63-94.
-
- Boynton, D., Cain, J. C., and Compton, O. C. 1944. Soil and Seasonal Influences on the Chemical Composition of McIntosh Apple Leaves in New York. *Proc. Amer. Soc. Hort. Sci.* 44: 15-24.

- Boynton, D., and Compton, O. C. 1944. The Influence of Differential Fertilization with $(\text{NH}_4)_2\text{SO}_4$ on the Chemical Composition of McIntosh Apple Leaves. Proc. Amer. Soc. Hort. Sci. 45: 9-17.
-
- _____ and _____ 1945. Leaf Analysis in Estimating the Potassium, Magnesium, and Nitrogen Needs of Fruit Trees. Soil Sci. 59: 339-351.
- Brown, D. S. 1945. The Growth and Composition of Tops of Peach Trees in Sand Culture in Relation to Nutrient Element Balance. W. Va. Agr. Exp. Sta. Bul. 322.
- Chapman, G. W. and Gray, H. M. 1949. Leaf Analysis and the Nutrition of the Oil Palm (*Elaeis guineensis*, Jacq.) Ann. Bot. n.s. 13: 415-433.
- Chibnall, A. C. 1939. Protein Metabolism in the Plant. Yale University Press.
- Galston, A. W. and Hand, M. E. 1949. Studies on the Physiology of Light Action. I. Auxin and the Light Inhibition of Growth. Amer. Jour. Bot. 36: 85-94.
- Gast, P. R. 1937. Studies on the Development of Conifers in Raw Humus. III. The Growth of Scots Pine (*Pinus sylvestris*, L.) Seedlings in Pot Cultures of Different Soils under Varied Radiation Intensities. Medd. Skogsoforsokanst Stockh. 29: 587-682.
- Goodall, D. W. and Gregory, F. G. 1947. Chemical Composition of Plants as an Index of their Nutritional Status. Imp. Eur. of Hort. and Plant. Crops. Tech. Comm. 17.
- Gregory, F. G. and Sen, P. K. 1937. Physiological Studies in Plant Nutrition. II. The Relation of Respiration Rate to the Carbohydrate and Nitrogen Metabolism of the Barley Leaf as Determined by Nitrogen and Potassium Deficiency. Ann. Bot. n.s. 1: 521-561.
- Harley, C. P., Moon, H. H., and Regeimball, L. O. 1949. A Study of Correlations between Growth and Certain Nutrient Reserves in Young Apple Trees. Proc. Amer. Soc. Hort. Sci. 53: 1-15.
- Heinicke, A. J. and Hoffmann, M. B. 1933. The Rate of Photosynthesis in Apple Leaves under Natural Conditions. Cornell Univ. Agr. Exp. Sta. Bul. 577.
- Jones, L. H., Shepardson, W. B.; and Peters, C. A. 1949. The Function of Manganese in the Assimilation of Nitrates. Pl. Phys. 24: 300-306.

- Kenworthy, A. L. 1949. A Nutrient-Element Balance Chart. Mich. Agr. Exp. Sta. Quart. Bul. 32: 17-19.
-
1950. Nutrient-Element Composition of Leaves from Fruit Trees. Proc. Amer. Soc. Hort. Sci. 55: 41-46.
- Lundegardh, H. 1947. Mineral Nutrition of Plants. Ann. Rev. Biochem. 16: 503-528.
- Magistad, O. C. Ayers, A. D., Wadleigh, C. H. and Gauch, H.G. 1943. Effect of Salt, and Climate on Plant Growth in Sand Cultures. Pl. Phys. 18: 151-166.
- Mitchell, H. L. 1934. Pot Culture Tests of Soil Fertility with Observations on the Effect of Varied Solar Radiation and Nutrient Supply on the Growth and Nitrogen Content of Scots and White Pine Seedlings. Black Rock Forest Bul. 5.
-
1936. The Effect of Varied Solar Radiation upon the Growth, Development and Nutrient Content of White Pine Seedlings Grown under Nursery Conditions. Black Rock For. Pap. 1: 16-22.
- Murneek, A. E. and Logan, J. C. 1932. Autumnal Migration of Nitrogen and Carbohydrates in the Apple Tree. Mo. Agr. Exp. Sta. Res. Bul. 171.
- Nightingale, G. T. 1942. Nitrate and Carbohydrate Reserves in Relation to Nitrogen Nutrition of the Pineapple. Bot. Gaz. 103: 409-456.
- Paech, K. 1935. Uber die regulation des Eiweissumsatzes und uber der zustand der proteolytischen Fermente in den Pflanzen. Planta 24: 78-129.
- Pagnoul, M. A. 1879. Experiences diverses sur la culture de la betterave. Composition de la betterave aux diverses epoques de la vegetation. Ann. Agron. 5: 481.
-
1881. Influence de la lumiere sur les plantes particulierement au point de vie de leur richesse en nitrates. Ann. Agron. 7: 1.
- Porter, A. M. 1937. Effect of Light Intensity on the Photosynthetic Efficiency of Tomato Plants. Pl. Phys. 12: 225-233.
- Reuther, W. and Smith, P. F. 1951. Tissue Analysis as an aid in Evaluating the Nutritional Status of Citrus Trees. Proc. Rio Grande Valley Hort. Inst. 5: 34-45.

- Shear, C. B., Crane, H. L. and Meyers, A. T. 1948. Nutrient-Element Balance; Application of the Concept to the Interpretation of Foliar Analysis. Proc. Amer. Soc. Hort. Sci. 51: 319-326.
- Sheldon, V. L. Blue, W. G. and Albrecht, W. A. 1948. Diversity of Amino Acids in Legumes According to Soil Fertility. Science 108: 426-428.
- Steward, F. C., Stout, P. R. and Preston, C. 1940. The Balance Sheet of Metabolites for Potato Discs Showing the Effect of Salts and Dissolved Oxygen on Metabolism at 23° C. Pl. Phys. 15: 409-447.
- Thatcher, R. R. 1909. Influence of Shade upon Composition of Plants. J. Ind. Chem. Engin. 1: 801
- Thornton, S. F. 1931. Experiences with the Neubauer Method for Determining Mineral Nutrient Deficiency in Soils. J. Amer. Soc. Agron. 23: 195-208.
- Tyson, James. 1930. Influence of Soil Conditions, Fertilizer Treatments and Light Intensity on the Growth, Chemical Composition and Enzymic Activities of Sugar Beets. Mich. Agr. Exp. Sta. Tech. Bul. 108.
- Wark, D. C. 1939. Tests on Plant Tissue as a Guide to the Soils Available Nutrients. J. Aust. Inst. Agr. Sci. 5: 224-227.
- Went, F. W. 1945. Plant Growth under Controlled Conditions V. The Relation between Age, Light, Variety and Termop periodicity of Tomatoes. Amer. J. Bot. 32: 469-479.
- Wood, J. G. 1942. Studies on Nitrogen Metabolism of Plants. VI. Inter-relationships Among Respiration Rate, Carbohydrate, Soluble Nitrogen Compounds and Protein in Leaves. Austr. J. Expt'l. Biol. and Med. Sci. 20: 257-262.
- Woodford, E. K. and Gregory, F. G. 1948. Preliminary Results Obtained with an Apparatus for Study of Salt Uptake and Root Respiration of Whole Plants. Ann. Bot. n.s. 12: 335-370.

Appendix Table 1. Sample Calculation of Index of Nutrient Intensity and Index of Balance Deviations

Nutrient element	(1)	(2)	(3)	(4)
N	2.81	1.78	-27	16
P	.186	.16	-14	3
K	1.42	1.18	-17	6
Ca	1.35	1.30	- 4	7
Mg	.72	.88	+22	33
Fe	.020	.020	0	11
Mn	.010	.007	-30	19

Explanation of Calculations:

Column 1--Values selected for standard or optimum.

Standard for all calculations is the average of all 1949 treatments.

Column 2--Leaf analysis for individual sample or treatment.

Column 3--Values obtained by dividing figures of Column 1 into Column 2, determining algebraic deviations of the quotients from 1.00 and expressing as per cent.

Column 4--Values obtained by determining deviations of figures in Column 3 from the average value for all the figures in Column 3. Algebraic sign is not used.

Index of Nutrient Intensity--An average of the values in Column 3. Represents average deviation from standard or optimum. Values nearer zero represent conditions near optimum or standard.

Index of Nutrient-element Balance Deviation--Sum of values in Column 4. Low values represent better balance of nutrient-elements.

Appendix Table 2. Weight of Root and Top Growth as Affected by Concentration of Nutrient Solution and by Solar Radiation, 1949

Solar radiation		Concentration of Nutrient Solution									
		0		1,000		2,000		4,000		8,000	
Initial	Final	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
100%	100%	58.4	34.0	66.3	44.5	76.3	60.9	56.0	57.5	37.3	37.3
100%	50%	55.8	33.9	54.1	43.4	58.4	48.9	46.5	48.0	46.6	36.7
100%	30	58.8	35.6	59.6	49.0	61.3	59.1	52.3	47.1	38.2	32.2
50%	50%	50.5	32.8	40.1	29.7	27.7	23.9	33.6	28.8	34.8	28.0
50%	30%	38.8	26.8	38.3	33.0	32.2	24.0	30.8	24.7	29.1	16.6
50%	100%	45.6	29.0	37.7	24.9	33.1	20.9	36.4	27.9	27.1	11.3
30%	30%	39.4	25.0	35.6	26.1	33.1	26.0	34.0	27.7	27.1	16.5
30%	100%	36.2	24.0	40.9	25.0	37.6	31.1	32.5	22.5	33.1	22.0
30%	50%	32.0	22.2	36.4	29.9	31.4	25.4	25.9	31.2	27.3	16.7

Appendix Table 3. Weekly Average of Daily Mean Temperatures (Degrees Fahrenheit) and Solar Radiation (gm. cal./sq. cm./week)*

Week Ending	Temperature		Solar radiation	
	1949	1950	1949	1950
June 2	59	60		
9	61	65	568.6	573.0
16	70	67	279.1	464.5
23	72	62	457.1	423.7
30	76	67	417.9	524.6
July 7	78	62	383.9	533.4
14	69	68	415.3	572.9
21	70	67	440.0	403.4
28	75	68	417.0	503.8
Aug. 4	67	67	410.5	428.5
11	74	67	351.6	493.8
18	70	65	402.5	448.2
25	64	64	408.9	428.1
Sept. 1	65	68	251.7	249.4
8	60	59	291.1	426.7