EFFECT OF CONTROLLED ROOT TEMPERATURE ON THE GROWTH OF EAST MALLING APPLE ROOTSTOCKS IN WATER CULTURE

By

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AN ABSTRACT

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STUART H. NELSON ABSTRACT

Clonal rootstocks have been suggested as being superior to seedling rootstocks inasmuch as they produce a known degree of vigor and precocity in the scion variety grafted upon them. The use of the most important clonal rootstocks, the East Malling or EM series, has not been too successful in many of the apple growing areas and naturally some factor of climate suggests itself for study.

In an endeavor to study the effect of root temperature on the growth of apple rootstocks, five clonal and one seedling rootstocks were grown in water culture at 44, 55, 66 and 77 degrees F. Air temperatures were the same for all treatments. The clonal rootstocks included EM I, EM II, EM VII, EM IX and EM XVI, obtained from established stoolbeds at Michigan State College, while the seedling rootstock was purchased from a commercial nursery.

The onset of new growth, both in the shoot and in the roots was enhanced by a rise in temperature from 44 to 77 degrees F.

The rootstocks exhibited definite clonal differences in the production of new roots. All rootstocks produced very slight root growth at 44 degrees F. EM VII, EM XVI and the seedling rootstocks produced an increasing amount of roots as the temperature was raised from 44 to 77 degrees F. EM I, EM II, and EM IX, however, produced the greatest amount of root at 55 degrees F. The latter two rootstocks were completely killed above 55 degrees F.

Considerable browning and sloughing of the cortical tissue was experienced at the higher temperatures, especially the plants that preferred the lower temperatures such as EM I which was particularly susceptible to injury of this nature.

At 44 degrees F the roots were thick, pearly white and non-branched, while at 77 degrees F the roots were slender, much branched, and discolored to varying degrees.

Shoot growth was closely associated with root growth. EM I, EM II and EM IX gave the greatest shoot elongation at 55 degrees F. EM XVI was almost equally tolerant to temperatures of 55, 66 and 77 degrees F but gave slightly better growth as the temperature was increased. With EM VII the greatest top growth was produced in the 66-degree treatment, while growth of the seedling rootstock was much superior at 77 degrees F.

Increases in root temperature from 44 to 77 degrees F, brought about an increase in maturation of the roots as illustrated by differentiation of primary tissues, vascular cambial activity and subsequent deposition of secondary tissues, and browning and sloughing of the cortical tissue.

The nutrient contents of the leaves from the different temperature treatments were determined. Certain trends were noted, but, for the most part, the differences were not significant.

In general, the East Malling rootstocks seem to prefer a cool soil temperature and this factor may help to explain why they have not become widely established on the North American continent, where soil temperatures are relatively high for considerable periods of time over large areas.

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INTRODUCTION

Apple trees, as grown in a commercial orchard, are composed of a rootstock and a scion variety grafted together and functioning as a unit. The graft union is usually at the ground level, with the rootstock below ground and the scion variety above ground.

Most apple rootstock material used on the North American continent is of seedling origin and is often variable in such characters as vigor, hardiness, and disease resistance.

Clonal rootstocks, that is, populations which are propagated asexually from one individual, have been suggested as superior to seedling rootstocks in uniformity of performance. Further, they have the ability to produce a known degree of vigor and precocity in the scion variety.

The most important clonal apple rootstocks are the series known as East Malling or EM rootstocks which have been classified and described by the workers at the East Malling Research Station in England. While these clonal rootstocks have been used to a considerable degree in Europe, they have not been widely employed in North America, in part, because their performance under various cultural and climatic conditions has not been understood and critically established.

At present, however, there is a considerable interest in them, due largely to demands by orchardist for a fruit tree smaller than standard size.

Since there are substantial differences in climatic conditions between the apple growing areas of Europe and those of North America, attention is naturally directed at a comparison of some features of climate. Insofar as rootstocks are concerned, soil temperatures suggest themselves as one of the first factors for evaluation.

Further, even though root temperatures have been shown to affect markedly the structure of roots, anatomical characteristics of the rootstocks have been reported as indicative of the subsequent vigor and precocity of the scion variety grown upon them and this relationship has been used as a criterion in the selection of new apple clonal rootstocks at a very young age.

It is the purpose of this paper, to present results of an experiment designed to evaluate the effect of soil temperature on the growth, development, chemical composition, and anatomical characteristics of certain East Malling rootstocks.

REVIEW OF LITERATURE

The East Malling Rootstocks

The so-called "East Malling" or "EM" rootstocks have been classified and described by Hatton (1917, 1927, 1935) and have been the object of intensive research at the East Malling Research Station in England. Maurer (1939) has published an extensive text in the German language which includes Hatton's research and further work on both the East Malling and other rootstocks.

The East Malling rootstocks, sixteen in number, have been divided into four groups based on the degree of vigor which they induce in the scion variety worked upon them. Hatton (1927, 1935), Pearl (1932), Maurer (1939), and Garner (1945) have grouped them into: (1) very dwarf, (2) semi-dwarf, (3) vigorous, and (4) very vigorous. Tukey (1944), likewise, placed them in four categories but used a terminology better suited to American conditions, namely, (1) very dwarf, (2) semi-dwarf, (3) semi-standard, and (4) standard.

Reports of tests on the more important members of this series on the North American continent have been made by Upshall (1934, 1937), Southwick and Shaw (1938), Sudds and Yerkes (1939), Tukey and Brase (1941) Sudds (1945), Gourley and Howlett (1946), Shaw (1946), Smith (1946), Tukey and Carlson (1949), Mann et al. (1953), Davis (1954), and Blair (1954). Although the selections varied in their adaptibility in the different growing regions represented, growth characteristics of the scion variety, in general, bore the same relationship to each other under the different conditions.

The five East Malling rootstocks included in the experiments reported on in this paper were EM I, EM II, EM VII, EM IX, EM XVI. EM I was named Broad-leaved English Paradise, being a chance seedling selected by T. Rivers in England about 1860. EM II had been grown in French nurseries for several centuries and was named Doucin. EM VII which is of English origin and had long been known as a mixture of Doucin, was given no special name. EM IX, almost as well known as Jaune de Metz, had its origin as a chance seedling in France about 1880. Although EM XVI was not named by Hatton, it is often referred to as Ketziner Ideal, having had its origin as Doucin seedling U.3 of Späth Nurseries, Berlin, Germany. EM IX was classified as very dwarf, EM VII as semi-dwarf, EM I and EM II as vigorous, and EM XVI as very vigorous (Hatton, 1927, 1935).

Anatomical Studies of the East Malling Rootstock

Anatomical studies at East Malling by Beakbane et al. (1939, 1941) have illustrated that the structure of the roots is correlated with the subsequent vigor of the scion variety grafted upon it. They have reported that rootstocks which induce dwarfing have a larger proportion of bark to wood in the roots than do rootstocks which supported vigorous growth.

Beakbane and Thompson (1945, 1947) have found that in the first three years of the tree's life this correlation may not be evident, and the ratio of living to non-living wood makes a better correlation with the size and precocity of the tree during the early years. They have suggested that two influences are exerted upon the size and fruitfulness of scion varieties when they are grafted upon these rootstocks. Thus EM IX, which has a wide bark and a large amount of live tissue, stimulates a dwarfing influence and early precocity in the scion variety. In contrast, EM VII, which has a wide bark but a small amount of live tissue in the root produces a vigorous scion in the early life of the tree. Later as growth lessens, fruiting begins.

Tubbs (1951) found that the regression on the logarithmic scale between girth and the percentage of bark of the root fitted well. This was also true when trunk girth was compared to the percentage of total live tissue in the root. He also found a close fit when the regression on the logarithmic scale between stem elongation and the proportion of wood other than rays was considered.

The large amount of live tissue was not confined to the roots, but extended also to the stems of dwarf rootstocks (Mosse, 1951).

Other possible correlations between anatomy of the root and the subsequent vigor and precocity of the scion have been studied. Over a period of years, Beakbane and her co-workers (1939, 1941, 1945, 1952) have noted that in some families there was a correlation between vigor and the percentage area of vessels; in others there was none. Dwarf rootstocks were observed often to have smaller vessels and squarer ray cells in cross-section. The percentage of fibres in the bark of the root was frequently low in dwarf rootstocks.

Temperature and Root Anatomy

From the accumulated data at the East Malling Research Station, Beakbane (1952) reported that the structure of the apple rootstocks under conditions prevailing there depended upon the genetic type rather than on environmental factors. The weather conditions, however, were reported to be relatively uniform over a period of years. In the United States, however, Nightingale (1935) found striking differences in the structure of young apple and peach roots when they were subjected to a wide range of root temperatures. The cortex was thicker at low temperatures, while at the extremely high temperatures the cortex was sloughed off and often completely lacking. Overall maturation of the root tissue progressed more rapidly as the root temperatures were increased from 45 to 95 degrees F.

Similar results were obtained with roses (Shanks and Laurie, 1949), with Colonial bentgrass (Stuckey, 1942) and with Kentucky Blue Grass (Darrow, 1939).

Conant (1927), studying the resistance of roots of tobacco to pathogens, found that cork formation was more rapid at 30 than at 20 degrees C.

Temperature and Root Growth

Although the literature concerning temperature and its effects on growth of tree fruits is meagre, there is an abundance of literature on other crops, some of which contain interesting observations.

Each genus and species appears to have its own root temperature requirements. Darrow (1939), Wort (1940), Stuckey (1941, 1942) and Brown (1943) have found that the greatest amount of root growth in forage crops occurred in the early spring and in the fall when the temperatures were low. There was little or no development at the high summer temperatures.

With cereal crops, Dickson (1923) and Wort (1940) observed that the greatest amount of root growth also occurred when the temperatures were low. Root growth of vegetable crops according to reports of Burkholder (1920), Richards (1921), and Bushnell (1925) was variable in response to changes of root temperature.

Goff (1898) observed that root elongation began before bud break in the spring with some twenty species of trees and fruits. With specific reference to the effect of temperature on the growth of apple trees, Harris (1926) and

Collison (1935) found that root growth occurred at temperatures almost approaching freezing. At 40 degrees F, Batjer et al. (1939) observed poor root growth with apples, while Nightingale (1935) noted that poorer root growth occurred at extremes of 45 and 95 degrees F than in the centre of this range at 65 degrees F. He also noted that the presence or absence of fibrous roots influenced the growth of new roots at low temperatures. Rogers (1939) reported that apple trees growing in the orchard in England developed increasingly more roots as the temperature was raised from 7 to 21 degrees C. These results were substantiated later by Proebsting (1943).

Some temperature effects have been reported for other horticultural crops: roses (Shanks and Laurie, 1949), strawberries (Gray, 1941 and Roberts, 1953), citrus (Girton, 1927 and Haas, 1936), pecan (Woodruff and Woodruff, 1934) and pineapple (Watanabe, 1932).

Temperature and Shoot Growth

Cannon (1917) has noted the effect of root temperature on top growth of _Opuntia versicolor_ when growing under unfavorable conditions.

Among forage crops, reports on the effect of root temperature have been published by Jones and Tisdale (1921), Darrow (1939, 1943), Stuckey (1942) and Earley and Catter (1945). Although there were differences between species, it was found in general that growth was less at excessively low and excessively high root temperatures. Dickson (1923) and Wort (1940) found for wheat and Dickson (1923) found for corn that the optimum root temperature for the growth of the shoot varied with the physiological age of the plant.

In a survey of a number of greenhouse crops, Allen (1934) observed that each genus exhibited a different shoot growth response when the soil temperature was raised. With specific reference to roses, Shanks and Laurie (1949) observed that the fresh and dry weights of the shoots increased with increase in temperature from 52 to 72 degrees F.

All citrus crops did not react alike. Halma (1935) found that lemon seedlings were more adaptable to change in root temperature than orange and grapefruit seedlings and Haas (1936) reported an increase in shoot growth from 19 to 31 degrees C.

Poor shoot growth was noted at root temperature extremes of 13 and 40 degrees C for tobacco by Johnson and Hartman (1919), of 28.4 and 82.4 degrees F for peas by Leitch (1916), of 7 and 38 degrees C for pecans by Woodruff and Woodruff (1934).

Vyvyan (1934) has reported that a relatively constant shoot-root ratio exists regardless of soil type. This has been partially substantiated by Nightingale (1935), Batjer et al. (1939), Proebsting (1943) and Rogers (1952), who observed that the top growth of apple trees is closely associated with the amount of roots produced. Apple varieties, however, do not react all alike to soil temperatures. Nightingale and Blake (1934) reported that Stayman preferred a low temperature while Baldwin did quite well at relatively high temperatures.

A direct correlation between temperature and shoot growth of strawberries was reported by Roberts (1953). The roots did not show this correlation and therefore the top-root ratio increased with increasing temperatures from 45 to 75 degrees F. Cooper (1954) working with salvia found that at 70 degrees F there was almost twice as much growth as at 50 degrees F.

Temperature and Shoot Morphology

Balls (1908) working with the so-called sore-skin disease of cotton, obtained a smooth mycelium which had almost no branches at 20 degrees F, while at 34 degrees F the mycelium had a fluffy appearance caused by a very branched feathery growth.

In a study of the effect of soil temperatures on the behavior of blueberry plants, Bailey and Jones (1941) observed that the plants grown at temperatures above 65 degrees F were tall and upright, while the plants grown at lower temperatures were short and spreading in habit.

Pfahl et al. (1949) and Kohl et al. (1949) observed a reduction in the flowering of roses at excessively low and excessively high temperatures, while Allen (1934) noted a similar variation in the production of several greenhouse crops.

A greater proportion of culm to leaf at low temperatures gave barley a more upright growth (Walster, 1920). According to Darrow (1939), Kentucky Bluegrass was tall, succulent and bushy with many leaves at 15 degrees C, while at 35 degrees C it had only a few leaves and the plants were short, non-succulent and erect.

Temperature and Nutrient Uptake

As a result of researches conducted by Hoagland and Boyer (1936) and Ashby and Oxley (1935) it was proposed that nutrient uptake by the roots was influenced by light intensity, concentration of the nutrient solution, and temperature. Wanner (1948) stated that salt absorption from solutions of high concentration was less affected by temperature than from solutions of low concentration. Apparently this was an energy phenomenon, with less energy being required to bring about absorption at the high salt concentrations. This was substantiated further by Roberts (1953) working with strawberries.

Nightingale (1933, 1935) found that nitrates were absorbed by plants of tomato, apple and peach at temperatures very close to the minimum for growth. Nitrogen uptake was greater at the high temperatures, and the translocation of nitrogenous materials was influenced by the temperature of the medium (Nightingale and Blake, 1934a). Similar results were obtained by Batjer et al. (1939, 1943), Aldrich (1931), and Smith (1935). Curtis (1929) reported that temperatures of 4 to 6 degrees C, which were low enough to stop protoplasmic streaming, severely reduced translocation. However, in 1936, Curtis and Hertz changed their opinion and reported that there was a significant amount of translocation at 0 to 2 degrees C.

Went (1944) found that phosphate uptake was greater at 26.5 degrees C than at 18 degrees C.

The uptake of water is strongly influenced by the temperature of the medium. With cotton, Arndt (1937) reported wilting at 10 to 18 degrees C and surmised that it was due to the lowered capacity of the plant to absorb and transmit water, to increased viscosity of the water, and to decreased permeability of the cell membranes.

Kramer and Currier (1950) suggested that water exchange due to osmotic pressure was more important quantitatively than absorption at the expense of energy. Increased water absorption, however, occurred with rising temperatures (Kramer 1933, 1942, and Batjer et al., 1939). Clements and Martin (1934) found a marked decrease in transpiration below 50 degrees F and Batjer et al. (1939) observed that low temperatures caused both a decrease in transpiration and an early closing of the stomata. They (Batjer et al. 1939) surmised that water shortage was at least partially responsible for the poor growth.

PROCEDURE

Equipment

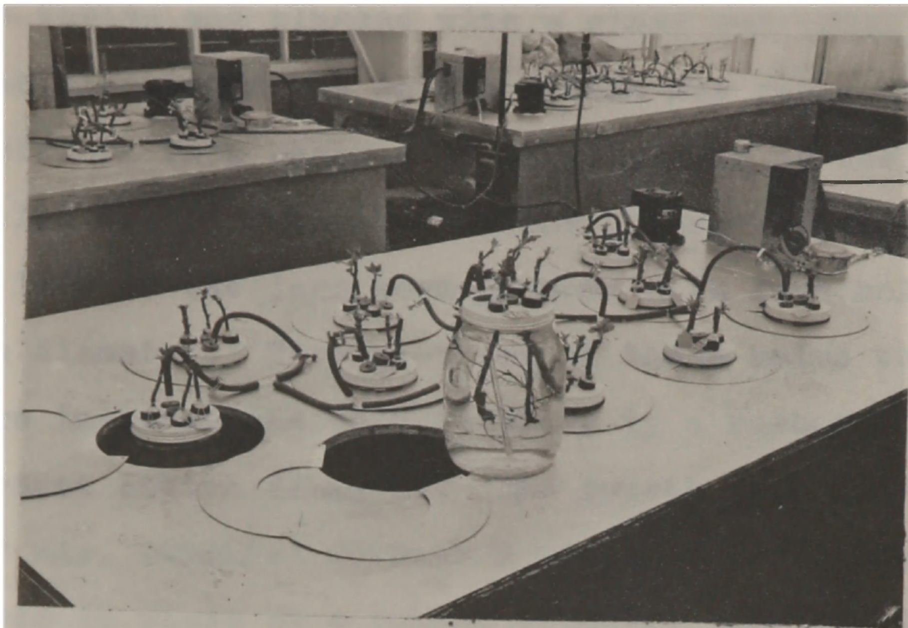
The experiments were conducted in controlled temperature tanks, constructed and described by Roberts (1953). Essentially, the tanks were reinforced round-end stock troughs that had been enclosed in well-insulated plywood boxes. The top was cut so that twelve 9-inch crocks of sand could be inserted and supported on a framework submerged in the water of the tank. The temperature of the water was controlled by heating cables and refrigeration units. Each tank was an individual unit and the water circulated by means of a standard centrifugical pump of 6-gallon-per-minute capacity.

Since it was desirable to observe the roots, the crocks of sand were replaced with 1-gallon, wide-mouthed glass jars containing nutrient solution. Owing to the slight shoulder on the jars and the necessity of removing them periodically for inspection, removable metal collars were made to exclude the light around the neck of the jar (Fig. 1).

Each jar was supplied with air pressure controlled by a needle valve on the main line. The volume of air was controlled at each jar by means of a screw clamp. A small piece of perforated plastic tubing was placed on the end of

Figure 1A - View of controlled temperature tanks, Plant Science Greenhouse, Michigan State College.

Figure 1B - Close-up view of jar with aerating tube and plants inserted.



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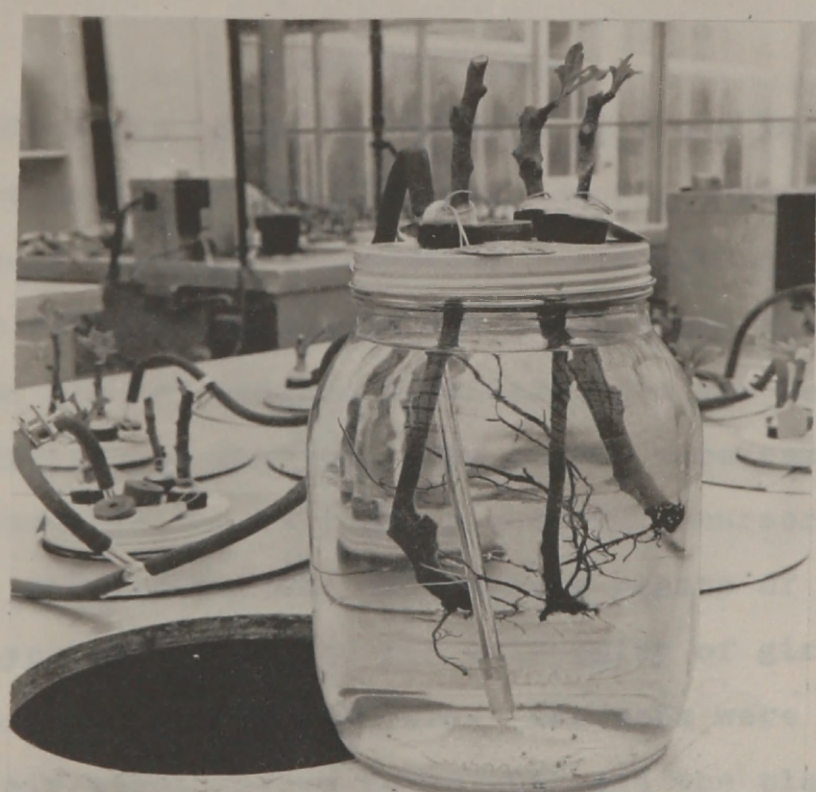


B

the glass tubing and plugged with a glass rod (Fig. 1). Later, the plastic in the entire system was replaced by a glass capillary tube because of algal growth on the plastic which filled the perforations at the higher temperatures.

The lids of the jars were punched with five holes, 1 inch in diameter. Through three of these holes the young trees were inserted and held in place by a rubber collar and non-absorbent cotton (Fig. 1). The fourth hole contained the source of air, supplied through a piece of 7-millimeter glass tubing held in place by a rubber stopper. The remaining hole was stoppered and used for the addition of nutrients and water without disturbing the plants and the air supply.

Plant Material

Rooted shoots of EM IX, EM VII, EM I and EM II, and EM XVI were used, representing very dwarf, semi-dwarf, vigorous, and very vigorous rootstocks, respectively. They were taken from established stool-beds at Michigan State College, having been secured originally direct from the East Malling Research Station in England. The plants were removed from the stool-beds in the fall and placed in a nursery cellar. During the storage period, twenty-four plants of each numbered type were selected for uniformity of girth, amount of root, and freedom from injury. The tops were pruned to approximately eight inches in height, and the plants were returned to storage until they were planted in the greenhouse.

Another rootstock of seedling origin was purchased from a commercial nursery and planted into the jars immediately upon arrival. All rootstocks were inserted into the jars on February 11, 1954.

Temperatures

Each of the four tanks was held at a different but constant temperature throughout the entire experiment, namely 44 degrees, 55 degrees, 66 degrees and 77 degrees F.

Nutrient Solutions

All treatments received the same controlled supply of nutrients. The plants were placed first in a 0.5 Hoagland nutrient solution. After three weeks, when growth was well started, the concentration was increased to a 1.0 Hoagland nutrient solution (Hoagland, 1950). When the plants were small, the solutions were renewed at 3-week intervals, but as the plants became larger, the renewals became more frequent and were 7 days apart during the last 3 weeks of the experiment. Between changes of nutrient solution, the level in the jars was adjusted daily with distilled water to keep the total nutrient salts uniform in each temperature treatment.

Growth Measurements

The plants were inspected daily and the date of first bud break for each plant was recorded. Subsequent buds were removed as soon as they were noted.

The jars were removed from the tanks daily to record the first appearance of new roots. After this, the plants were disturbed as little as possible.

Linear shoot elongation was measured at 25-day intervals from the date of planting. Side shoots were removed from the axils of the leaves as soon as they were formed in order to keep the shoot to one stem.

The diameters of the original stem were recorded 1 inch above the lids of the jars at a position previously marked by a small streak of paint. Measurements were made at the beginning and at the end of the experiment and later converted to cross-sectional areas.

Diameter measurements of the new shoot were recorded and these values were converted to cross-sectional areas. The measurements were made 1 inch above the point where they emerged from the old stem.

Both fresh- and oven-dried weights of the shoot, stem and leaves included, were recorded for the individual trees.

The fresh weights of the new roots were recorded for the individual trees. The oven-dried weights, however, were so small that they were combined and recorded per treatment.

Inorganic Analysis of the Leaves

In view of the small amount of total dry matter in the tops of the plants, the six replicates were combined to form on sample. The samples were prepared for analysis by grinding the dried plant material in a Wiley mill (20 mesh) and stored in glass bottles. Prior to the inorganic determinations, the samples were oven-dried again for 24 hours to remove the slight amount of moisture that might have been taken up by the previously oven-dried material.

Inorganic determinations were made in the laboratories of the Department of Agricultural Chemistry at Michigan State College (a). Nitrogen determinations were made by the Kjeldahl procedure, while potassium evaluations were made on the Flame Photometer. The content of boron, calcium, copper, iron, magnesium, manganese and phosphorus was determined spectrographically.

Anatomical Studies

Samples from various parts of the plants were placed in formaldehyde-acetic acid-alcohol (5 millilitres of 40 per cent formaldehyde, 5 millilitres of glacial acetic acid, and 90 millilitres of 70 per cent ethyl alcohol) killing solution immediately after the trees in the experiment were harvested. The samples were aspirated immediately and imbedded at a later date.

The new roots were dehydrated in a series of tertiary-butyl alcohol (Johansen, 1940) and imbedded in Histowax. Sections 8 microns in thickness were stained in safranin and counter-stained with aniline blue (Johansen, 1940).

(a) Kjeldahl, Flame Photometer, and Spectrographic determinations conducted by Dr. E. J. Benne, Mr. R. Bacon and staff.

Preliminary examinations were made of the first five centimetres with longitudional sections and then cross-sectional examinations were made at 5, 7½, and 10 centimetres from the root apex.

Free-hand sections were made of the new shoot approximately 1 inch from the original stem. Staining was similar to that described for the root sections.

Statistical Analysis

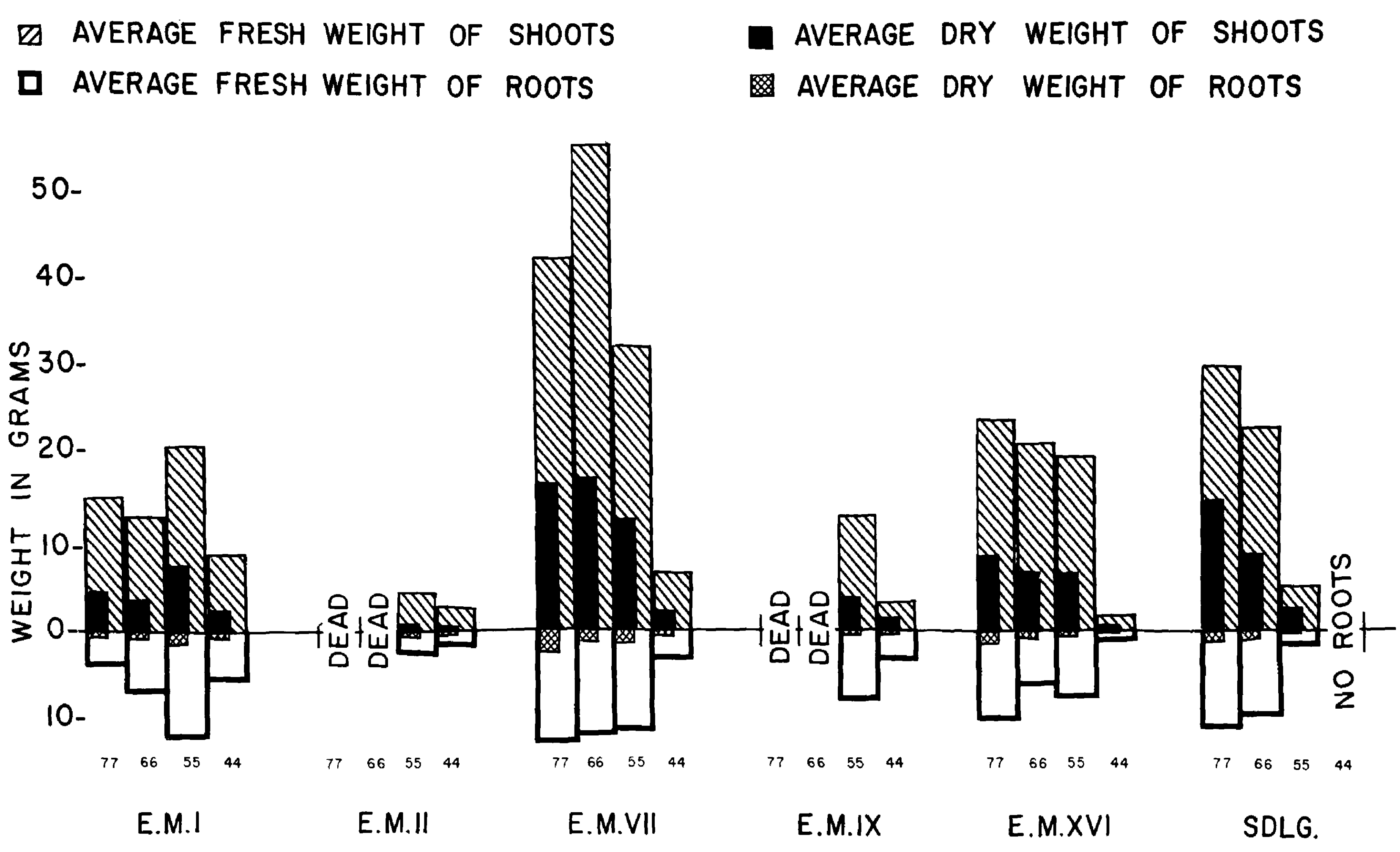
The data for bud break, new root initiation, fresh weight of shoot, oven-dried weight of shoot, fresh weight of new roots and cross-sectional area of the shoots were subjected to analysis of variance. Analysis of co-variance was used on the data for the cross-sectional increase of the original stem.

Analysis of the inorganic ash content data was subjected to statistical methods suggested by Kenworthy (1953) and plotted upon nutrient element balance charts. The treatment that produced the greatest shoot growth (Fig. 2) in each rootstock was used as a standard. Coefficients of variability values from a national survey (Kenworthy, 1954) were used for each element concerned. Nutrient element plots that did not extend to the white band of the chart were considered to be significantly lower than the standard.

Missing blocks in analysis of variance were calculated by formulae suggested by Baten (1939). In the analysis of co-variance, missing blocks were calculated in a similar manner. The values for the original cross-sectional area

Figure 2 - Graphic representation of shoot and root growth (fresh and dry weights) of apple rootstocks grown at different root temperatures.

GROWTH OF APPLE ROOTSTOCKS UNDER CONTROLLED ROOT TEMPERATURES



were discarded and new values for both the original cross-sectional area and the final cross-sectional area were estimated by methods prescribed by Baten (1939) for analysis of variance.

EXPERIMENTAL RESULTS

The temperature of the medium influenced the growth of the apple rootstocks. In general, both root growth and shoot growth were affected in a similar manner, as illustrated in Fig. 2.

It will be noted that no plants of EM II and EM IX survived in the 66- and 77-degree treatments. Similarly EM II did not grow well at 55 degrees F, with half of the plants dying in this treatment. Mortality in other plots included one plant each in the following treatments: EM I at 66 and 77 degrees F and EM VII at 77 degrees F. On all of the dead plants it was noted that the new roots were first brown and translucent at the point of emergence and that this discoloration developed toward the apex of the root. The root system was reduced to a slimy mass, followed closely by the development of a chlorotic condition in the shoot. The subsequent death of the plant occurred within ten days of the first appearance of discoloration.

Because of the large number of plants of EM II which died, it was impossible to carry out statistical analyses. With EM IX, however, statistical comparisons were made between the 55- and 44-degree F treatments. With the other rootstocks of the East Malling series, missing values were estimated and complete analyses made.

The seedling rootstocks were variable in performance. Many of the plants failed to form new root systems so that growth of individual trees was severely affected. Averages of seedling performance (Tables I to X) were records of growth from those plants which formed a new root system, including three plants at 77 degrees F, four plants at 66 degrees F, and four plants at 55 degrees F. No plants formed a new root system at 44 degrees F, and consequently no statistical analyses were made on the performance of this rootstock.

Root Growth

As shown in Table I there was a high degree of significance between treatments. In general, new roots were initiated significantly sooner as the temperatures were raised. Differences were not significant, however, for the following treatments: 66 and 77 degrees F for EM I, EM II, EM VII and EM IX; 55 and 66 degrees F for EM IX and EM XVI; and 44 and 55 degrees F for EM VII.

The average fresh weights of the new roots at the termination of the experiment are presented in Table II. Greatest root growth of EM I occurred at 55 degrees F and was significantly better than the 44- and 77-degree treatment. All treatments were significantly better than the 44-degree treatments with EM VII and EM XVI, the greatest growth occurring at 77 degrees F for both rootstocks. The 55-degree treatment was significantly superior to the 44-degree treatment for EM IX.

TABLE I

EFFECT OF ROOT TEMPERATURES ON INITIATION OF NEW ROOTS BY DORMANT APPLE ROOTSTOCKS

Root temperature (degrees F)	Average number of days from planting (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	13.67	21.18	9.67	16.50	29.18	----
55	9.18	9.18	9.33	8.18	15.83	16.00
66	4.50	4.00	5.00	4.18	12.00	16.50
77	3.67	4.33	3.33	4.18	6.50,	10.75
L.S.D.-5%	3.26	4.92	3.42	5.59	5.43	(*2)
L.S.D.-1%	4.51	6.81	4.73	7.73	7.51	

(*1) Averages of six plants per treatment unless otherwise noted.

(*2) No analyses were made on the seedling rootstocks due to missing blocks. Averages are based on those plants that formed new root systems.

TABLE II

EFFECT OF ROOT TEMPERATURE ON THE FRESH WEIGHT OF NEW ROOTS OF APPLE ROOTSTOCKS

Root temperature (degrees F)	Average weight (grams) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	4.27	0.80	2.30	2.62	0.75	----
55	10.00	2.07	9.20	6.42	6.10	1.38
66	5.72	Dead	9.82	Dead	5.07	7.73
77	3.15	Dead	10.30	Dead	8.00	9.00
L.S.D.-5%	5.21	(*2)	3.61	2.57	2.91	(*3)
L.S.D.-1%	7.21		5.00	4.03	4.02	

(*1) Averages of six plants per treatment unless otherwise noted. These averages included values calculated for missing blocks in analysis of variance computations.

(*2) Averages for three and five trees at 55 and 44 degrees F, respectively. No L.S.D. calculations.

(*3) No analyses were made on the seedling rootstocks due to missing blocks. Averages are based on those plants that formed a new root system.

The average oven-dried weights are presented in Table III for the number of living plants in each treatment.

It was quite evident at the time of harvesting that much of the root material had been lost, especially in the higher temperature treatments. At temperatures above the optimum for growth there was considerable browning and sloughing of the cortical cells of the roots (Fig. 3). Most severely affected were roots of EM I, where roots at 77 degrees F were severely browned. Considerable cortical debris had settled in the bottom of the jar. This condition was evident in the 66-degrees treatment to a slightly lesser extent and it was not until temperatures of 55 degrees F were reached that a predominance of white roots existed. The roots at 44 degrees F were white and had made surprisingly good growth as compared to the other rootstocks grown at the same temperature.

Although there were only a few plants to compare with EM II and EM IX, it was observed that there was considerable browning of lenticel callus and some browning of the roots on trees grown at 55 degrees F. Both of these rootstocks produced a large amount of lenticel callus, especially at the higher temperatures. This callus was very soft and spongy and might well have been the point of entry for the Phycomycete organism which caused the destruction of the root systems.

The rootstocks that were more tolerant of the high temperatures did not show this browning to as great a degree as did those that preferred the cooler temperatures.

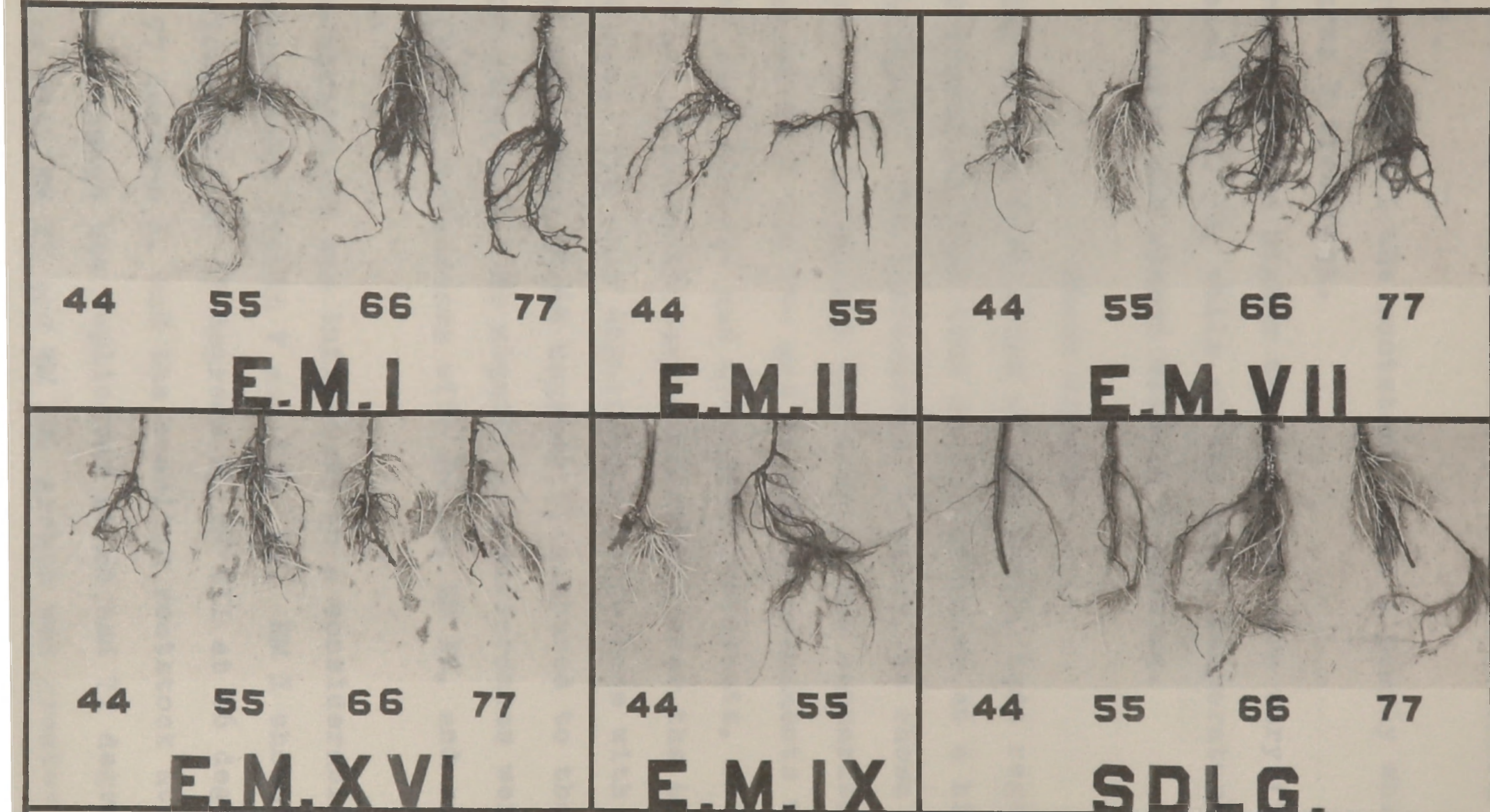
TABLE III

EFFECT OF ROOT TEMPERATURE ON THE OVEN-DRIED WEIGHT OF NEW ROOTS OF APPLE ROOTSTOCKS

Root temperature (degrees F)	Average oven-dried weight (grams) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	0.43	0.06	0.34	0.43	0.06	----
55	1.32	0.17	1.11	0.53	0.56	0.18
66	0.68	Dead	1.01	Dead	0.55	0.77
77	0.33	Dead	1.26	Dead	0.72	0.80

(*1) Roots of living plants were bulked per treatment. No attempt was made to calculate missing block or L.S.D. values.

Figure 3 - Roots of apple rootstocks grown at different root temperatures showing extent and habit of growth.



44 55 66 77
E.M.I
44 55
E.M.II
44 55 66 77
E.M.VII
44 55 66 77
E.M.XVI
44 55
E.M.IX
44 55 66 77
SDLG.

The roots were predominantly white even in the 77-degree temperature.

The roots of all the rootstocks were a pearly white in the 44-degree F treatment.

The roots at the higher temperatures were very fine and much branched (Fig. 3), while at the lower temperatures they were much thicker and almost without branching.

Shoot Growth

Similar to the initiation of new roots, buds regenerated visible growth in less time on plants grown at a higher root temperature. The differences, however, as shown in Table IV are not significant for most of the comparisons. In the case of EM I the 77- and 66-degree treatments were significant over the 55- and 44-degree treatments, while for EM VII all treatments were significant over the 44-degree treatment. The only significant difference with EM XVI was with plants grown at 66 degrees F, compared to those grown at 77 degrees F. No significant differences were encountered between treatments with EM II, EM IX, and seedling rootstocks.

Shoot elongation was influenced to a considerable degree by root temperature (Table V and Fig. 4). EM I showed the greatest elongation at 55 degrees F, EM VII at 66 degrees F, EM XVI at 77 degrees F, and the seedling rootstock at 77 degrees F. Although the replicates at 66 and 77 degrees F were missing with EM II and EM IX, growth was greater at 55 degrees F than at 44 degrees F. With the exception of EM II

TABLE IV

EFFECT OF ROOT TEMPERATURE ON BUD BREAK OF DORMANT APPLE ROOTSTOCKS

Root temperature (degrees F)	Average number of days from planting (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	13.00	13.67	13.50	16.67	14.00	6.67
55	13.17	16.00	11.18	13.50	13.67	6.50
66	9.33	8.67	9.67	11.33	14.85	6.33
77	8.00	7.00	9.18	13.18	12.33	6.18
L.S.D.-5%	2.11	N.S.	2.25	N.S.	2.48	N.S. (*2)
L.S.D.-1%	2.92		3.11		3.43	

(*1) Averages of six plants per treatment.

(*2) Dormancy of seedlings might have been broken in transit.

TABLE V

EFFECT OR ROOT TEMPERATURE ON SHOOT ELONGATION OF APPLE ROOTSTOCKS

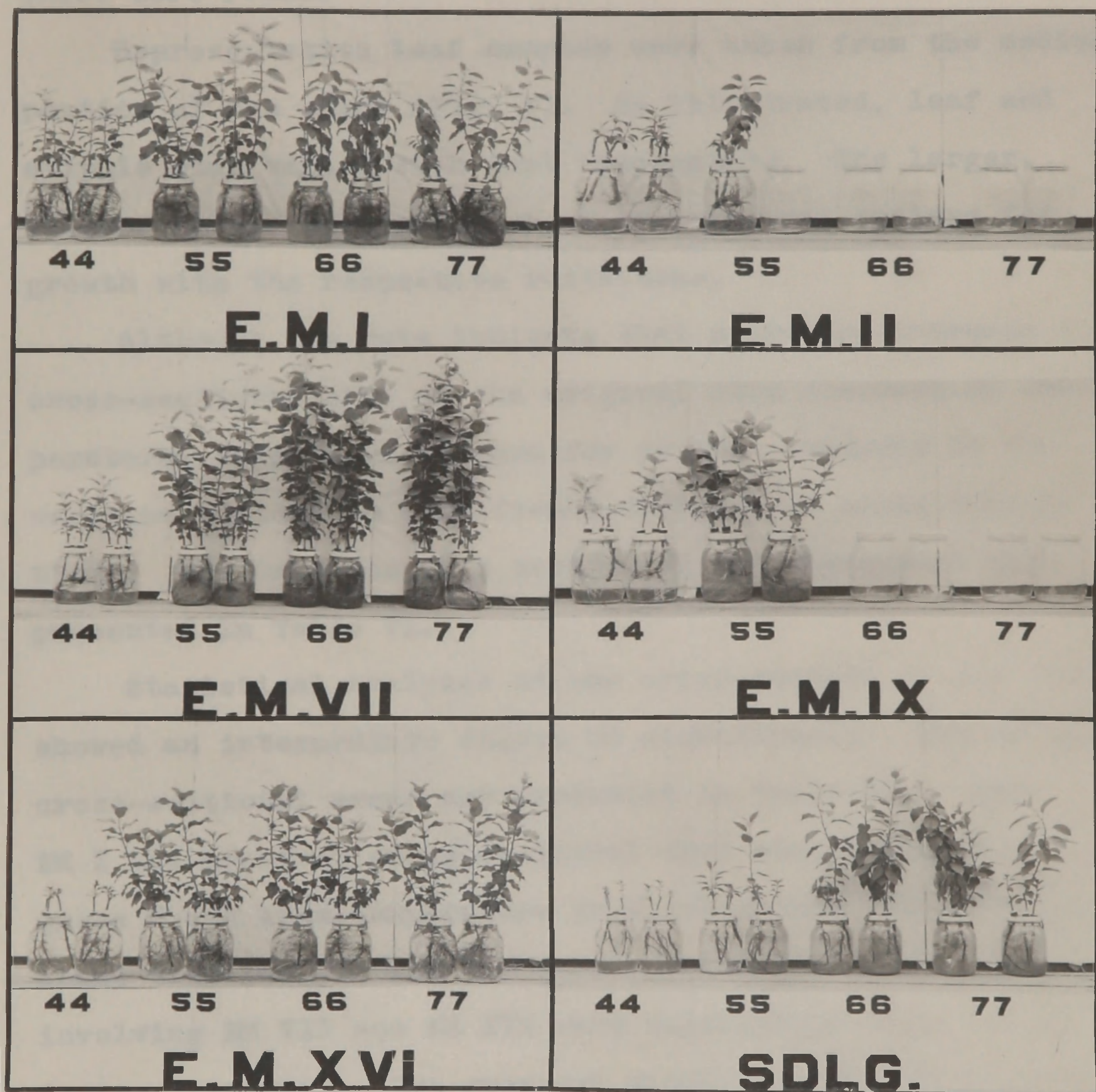
Root temperature (degrees F)	Average growth (centimeters) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	18.97	4.42	14.75	5.43	16.10	-----
55	40.05	10.97	56.05	26.12	29.10	15.68
66	32.57	Dead	67.61	Dead	32.73	21.48
77	30.97	Dead	56.45	Dead	37.53	47.07
L.S.D.-5%	9.89	(*2)	11.72	7.06	10.11	(*3)
L.S.D.-1%	13.67		16.21	11.07	13.99	

(*1) Averages of six plants per treatment unless otherwise noted. These averages included values calculated for missing blocks in analysis of variance computations.

(*2) Averages for three and five trees at 55 and 44 degrees F, respectively. No L.S.D. calculations.

(*3) No analyses were made on the seedling rootstocks due to missing blocks. Averages were based on those plants that formed a new root system.

Figure 4 - Illustration of shoot elongation and root density of apple rootstocks grown at different root temperatures.



44 55 66 77
E.M.I
44 55 66 77
E.M.II
44 55 66 77
E.M.VII
44 55 66 77
E.M.IX
44 55 66 77
E.M.XVI
44 55 66 77
SDLG.

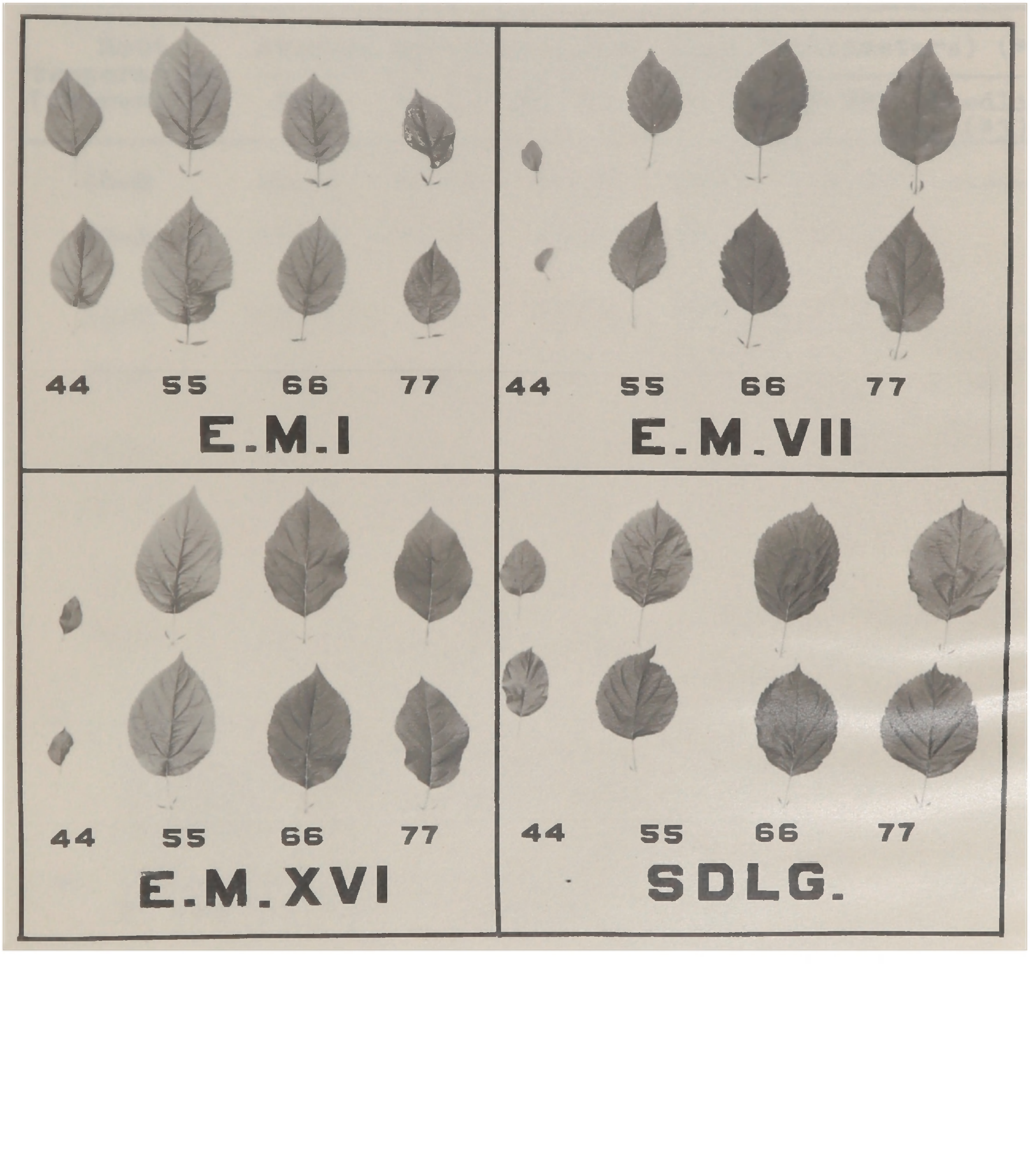
and the seedling rootstock on which no analyses were made, all temperature treatments showed a significant difference over the 44-degree treatment. No other significant differences were found.

Representative leaf samples were taken from the medium portion of the shoot (Fig. 5). As illustrated, leaf and stipule size varied with root temperature. The larger, thicker leaves were produced at temperatures optimum for growth with the respective rootstocks.

Although the data indicate that a greater increase in cross-sectional area of the original stem occurred at temperatures which were optimum for growth, analysis of covariance yielded no significant differences among populations. The data for this portion of the experiment are presented in Table VI.

Statistical analyses of the cross-section of the shoot showed an intermediate degree of significance. The average cross-sectional areas are presented in Table VII. With EM I the greatest cross-sectional area occurred at 55 degrees F and this temperature produced growth that was significant over the 77- and 44-degree treatments. All treatments involving EM VII and EM XVI were significant over the 44-degree treatment. The greatest growth for EM VII occurred at 44 degrees F and for EM XVI at 77 degrees F. Cross-sectional areas of EM IX were significantly larger at 55 degrees F than at 44 degrees F.

Figure 5 - Representative leaves from medium part of shoots of apple rootstocks grown at different root temperatures.



44
55
66
77
E.M.I
44
55
66
77
E.M.VII
44
55
66
77
E.M.XVI
44
55
66
77
SDLG.

TABLE VI

EFFECT OF ROOT TEMPERATURE ON CROSS-SECTIONAL AREA INCREASE OR ORIGINAL STEMS OF APPLE ROOTSTOCK

Root temperature (degrees F)	Average cross-sectional area (millimeters) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling (*3)
44-B	44.44	27.16	26.57	30.74	27.20	-----
44-A	46.63	24.32	28.32	32.19	27.94	
55-B	48.63	22.05	31.68	28.80	32.76	19.90
55-A	53.96	22.65	39.74	34.67	36.00	21.28
66-B	44.11	-----	30.49	-----	24.51	22.38
66-A	49.12	Dead	39.29	Dead	28.37	26.96
77-B	53.23	-----	26.62	-----	23.96	21.01
77-A	56.44	Dead	36.25	Dead	30.49	26.36

(*1) Averages of six plants per treatment unless otherwise noted. These averages included values calculated for missing blocks in analysis of co-variance computations. No treatments were significant in analysis of co-variance.

(*2) Average of three and five plants at 55 and 44 degree F, respectively. No analysis attempted.

(*3) No analysis were made on seedling rootstocks due to missing blocks. Averages were based on those plants that formed a new root system.

A - After treatment.
B - Before treatment.

TABLE VII

EFFECT OF ROOT TEMPERATURE ON THE CROSS-SECTIONAL AREA OF THE SHOOTS OF APPLE ROOTSTOCKS

Root temperature (degrees F)	Average cross-sectional area (millimeters) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	31.91	11.65	18.70	11.30	10.94	-----
55	59.06	17.28	50.85	30.23	48.90	22.67
66	45.59	Dead	73.34	Dead	46.73	46.59
77	34.80	Dead	72.34	Dead	53.31	61.64
L.S.D.-5%	17.21	(*2)	23.42	15.37	20.50	(*3)
L.S.D.-1%	23.80		32.39	24.11	28.34	

(*1) Averages of six plants per treatment unless otherwise noted. These averages included values calculated for missing blocks in analysis of variance computations.

(*2) Averages of three and five trees at 55 and 44 degrees F, respectively. No L.S.D. calculations.

(*3) No analyses were made on the seedling rootstocks due to missing blocks. Averages were based on those plants that formed a new root system.

Average fresh weight values of the shoots are presented in Table VIII. The greatest fresh weight occurred at 55 degrees F with EM I and was significantly different from the values for the 66- and 44-degree treatments. All other temperature treatments were significantly better than the 44-degree treatments for the rootstocks EM VII and EM XVI. In the case of EM VII the greatest growth occurred at 66 degrees F, while with EM XVI the greatest growth occurred at 77 degrees F. The 55-degree treatment was significantly better than the 44-degree treatment with EM IX.

As expected, the results with dry weights were very similar to those found for the fresh weights. The only difference in the behavior of the rootstocks was that with EM I the 55-degree treatment was significant over the 77-degree treatment. The data for the dried weight are presented in Table IX.

Shoot-Root Ratio

Data representing the shoot-root ratio (Table X) were based on the average dry weights of the roots and the shoots already presented in Tables III and IX, respectively. At best, these figures are only an indication, inasmuch as sloughing of cortex from the roots may have influenced the root weights considerably. As previously mentioned, with some of the rootstocks considerable cortical debris had settled in the bottom of the jars at the high temperatures. This material was lost in nutrient solution changes.

TABLE VIII

EFFECT OF ROOT TEMPERATURE ON THE FRESH WEIGHT OF THE SHOOTS OF APPLE ROOTSTOCKS

Root temperature (degrees F)	Average fresh weight (grams) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	6.90	2.09	5.10	2.47	1.05	-----
55	17.05	2.97	27.30	10.37	16.08	3.92
66	10.42	Dead	45.88	Dead	17.33	18.70
77	12.10	Dead	35.51	Dead	19.58	24.07
L.S.D.-5%	6.39	(*2)	12.78	2.85	8.09	(*3)
L.S.D.-1%	8.84		17.67	4.48	11.18	

(*1) Averages of six plants per treatment unless otherwise noted. These averages included values calculated for missing blocks in analysis of variance computations.

(*2) Averages of three and five trees at 55 and 44 degrees F, respectively. No L.S.D. calculations.

(*3) No analyses were made on the seedling rootstocks due to missing blocks. Averages were based on those plants that formed a new root system.

TABLE IX

EFFECT OF ROOT TEMPERATURE ON OVEN-DRIED WEIGHT OF THE SHOOTS OF APPLE ROOTSTOCKS

Root temperature (degrees F)	Average oven-dried weight (grams) (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	2.40	0.82	1.87	1.00	0.43	----
55	6.25	1.70	10.55	3.07	5.10	1.82
66	3.78	Dead	14.27	Dead	5.65	6.78
77	3.85	Dead	14.12	Dead	6.88	12.17
L.S.D.-5%	1.84	(*2)	3.98	1.63	2.51	(*3)
L.S.D.-1%	2.54		5.50	2.55	3.48	

(*1) Averages of six plants per treatment unless otherwise noted. These averages included values calculated for missing blocks in analysis of variance computations.

(*2) Averages of three and five trees at 55 and 44 degrees F, respectively. No L.S.D. calculations.

(*3) No analyses were made on the seedling rootstock due to missing blocks. Averages were based on those plants that formed a new root system.

TABLE X

EFFECT OF ROOT TEMPERATURE ON THE SHOOT-ROOT RATIO OF APPLE ROOTSTOCKS

Root temperature (degrees F)	Shoot-root ratio (*1)					
	EM I	EM II	EM VII	EM IX	EM XVI	Seedling
44	5.58	13.67	5.50	2.33	7.17	-----
55	4.73	10.00	9.50	5.79	9.11	10.11
66	5.56	Dead	14.12	Dead	10.27	8.81
77	11.67	Dead	11.21	Dead	9.56	15.21

(*1) Shoot-root ratios based on the average dry weight of the roots and the shoots. No statistical analyses.

As shown in Table X there was considerable variation in the shoot-root ratios under the conditions of the experiment, but no trends were established. With EM I, trees that had the greatest weight of shoots yielded the lowest shoot-root ratio, while with EM VII and the seedling rootstock trees with the greatest weight of shoots yielded the highest shoot-root ratio. Similar differences were encountered when EM II and EM IX were compared.

Anatomical Studies

Macroscopic examinations of free-hand sections of the stem showed that no differences had been induced in the stem by the various temperatures at which the plants were grown. No differences in development were observed and the conducting tissues were heavily stained indicating a large amount of lignified tissue.

Contrary to this, however, the root temperatures at which the rootstocks were grown strongly influenced the growth and development of the roots. It was observed that the temperature of the media affected the degree of maturation of the root tissues. Greatest maturation occurred at 77 degrees F and the least at 44 degrees F, with intermediate development at 55 and 66 degrees F.

The progressive increase in maturation as the temperatures were increased from 44 to 77 degrees F was exemplified throughout the development of the root.

Differences began to show first in the differentiation of the primary vascular tissues from the procambial strand.

The development of vascular cambium, the deposition of secondary xylem and phloem tissues, lignification of the xylem and phloem tissues, and the rupturing and sloughing of the cortical tissues occurred more rapidly as the temperatures were increased.

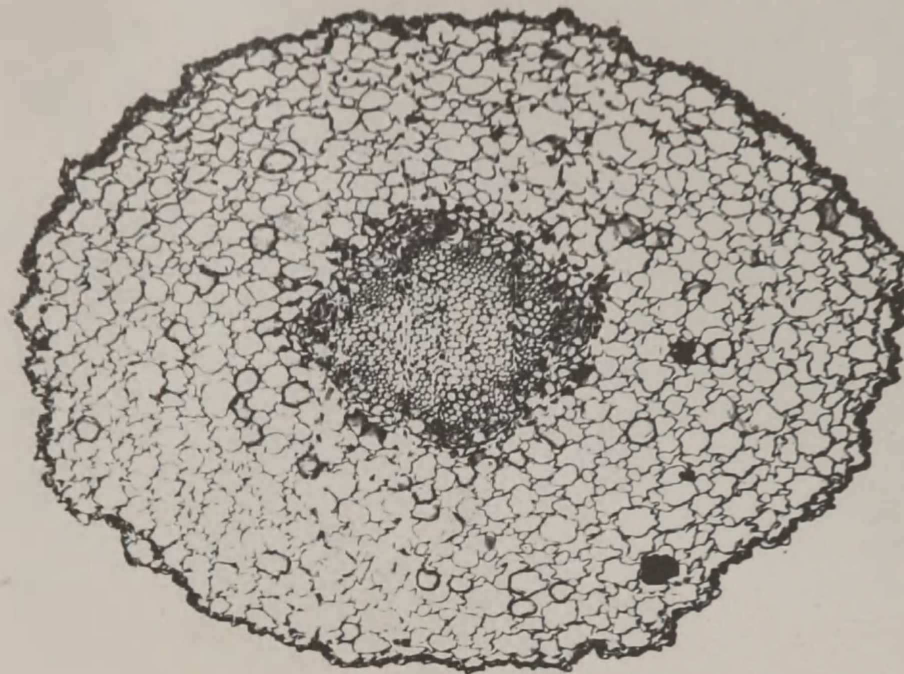
Further, it was observed that the amount of cortical tissue in proportion to stelar tissue was least at the highest temperature (77 degrees F), greatest at the lowest temperature (44 degrees F), and intermediate at temperatures of 55 and 66 degrees F.

The effect of root temperature on the development of root tissues can be more fully understood by a brief description and accompanying figures of cross-sections taken from various parts of roots grown at different temperatures.

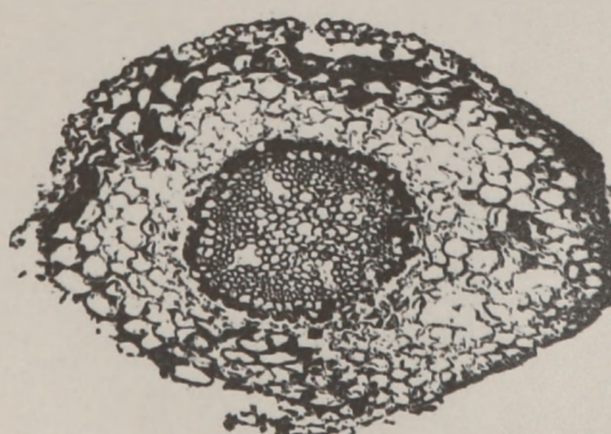
44 degrees F: A representative cross-section taken five centimeters from the tip is shown in Figure 6 for roots grown at 44 degrees F. Very little vascular development occurred at this temperature. Only a small proportion of the primary vascular tissue had differentiated and no vascular cambial activity was evident. The cortical tissue was entire and the pericycle was two-layered for the most part.

At seven and one-half centimeters from the root tip, most of the primary tissues had differentiated. There were, however, only slight indications of maturation at the protoxylem points. Cambial activity was evident to a small degree internal to the primary phloem. The cortex was entire and there was no indications of sloughing.

Figure 6 - Cross-sectional comparison of EM I roots taken five centimeters from the tip showing increased stelar development at 77 degrees F as compared with 44 degrees F.



44 degrees F.



77 degrees F.

The pericycle was still two-layered.

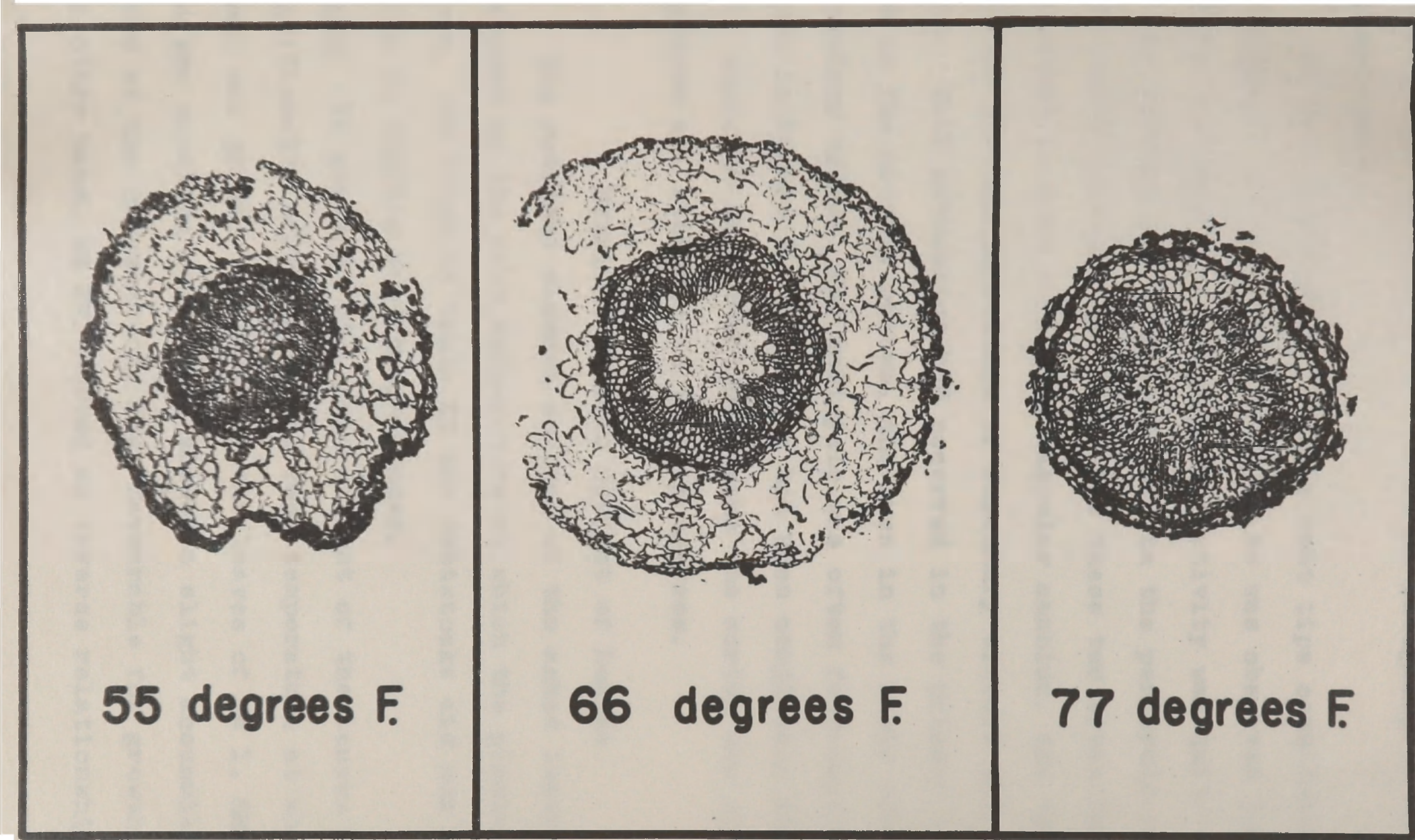
No samples were available for sectioning at ten centimeters from the tip, due to poor root growth at 44 degrees F.

55 and 66 degrees F: Roots grown at 55 and 66 degrees F were intermediate in development between those grown at 44 and 77 degrees F. Representative cross-sections taken ten centimeters from the root tip for the 55-, 66- and 77-degree treatments shown in Figure 7.

77 degrees F: At five centimeters from the root tips of trees grown at 77 degrees F most of the primary tissues had differentiated as shown in Figure 6. Cambial activity was visible. The cortex was entire and the pericycle was two-layered. Indications of maturation in the protoxylem points was present to a slight extent.

Cross-sections made at seven and one-half centimeters from the tips showed considerable difference from those made at five centimeters. At seven and one-half centimeters the primary tissues were well differentiated. Cell maturation had occurred in the protoxylem points, in some of the older cells of the metaxylem, and in the primary phloem to a slight degree. Cambial activity was quite evident and extend almost to the protoxylem points, but little radial enlargement had occurred. The pericycle was two- and three-layered and had become active above the protoxylem points. As yet, however, a complete ring of vascular cambium had not been formed. The cortex was often ruptured and in some cases partially sloughed off, especially with EM I plants which were

Figure 7 - Cross-sectional comparison of EM I roots taken ten centimeters from the tip showing an increased amount of rupturing and sloughing of the cortical tissues.


55 degrees F.
66 degrees F.
77 degrees F.

particularly susceptible to cortical sloughing at the higher temperatures.

At ten centimeters from the root tips considerable development of the secondary tissues was observed in the 77-degree treatments. Meristematic activity was quite evident in the primary phloem regions and in the pericycle at the protoxylem points. In many cases these two areas had become connected to form a ring of vascular cambium, and radial expansion through deposition of secondary tissues was noticeable. Cell maturation had occurred in the primary xylem, and in the primary phloem, and even in the newly formed secondary xylem. The pericycle was often four-layered. As shown in Figure 8, the cortex had been completely sloughed off, while in the other rootstocks the cortex was often ruptured and sloughed to varying degrees.

Nutrient Element Content of Leaves

The nutrient element content of the ashed leaves was affected by the root temperature at which the plants were grown. As shown in Table XI the rootstocks did not react alike to varying root temperatures.

Boron: In general, the boron content of the leaves was not significantly affected by the root temperature at which the plant was grown. Analyses of the leaves of EM I, EM VII, and the seedling rootstocks showed a slight accumulation of boron at the temperatures less favourable for growth. On the other hand, EM XVI showed an inverse relationship.

Figure 8 - Cross-sectional comparison of the development of root tissues at 77 degrees F for four rootstocks taken ten centimeters from the tip.

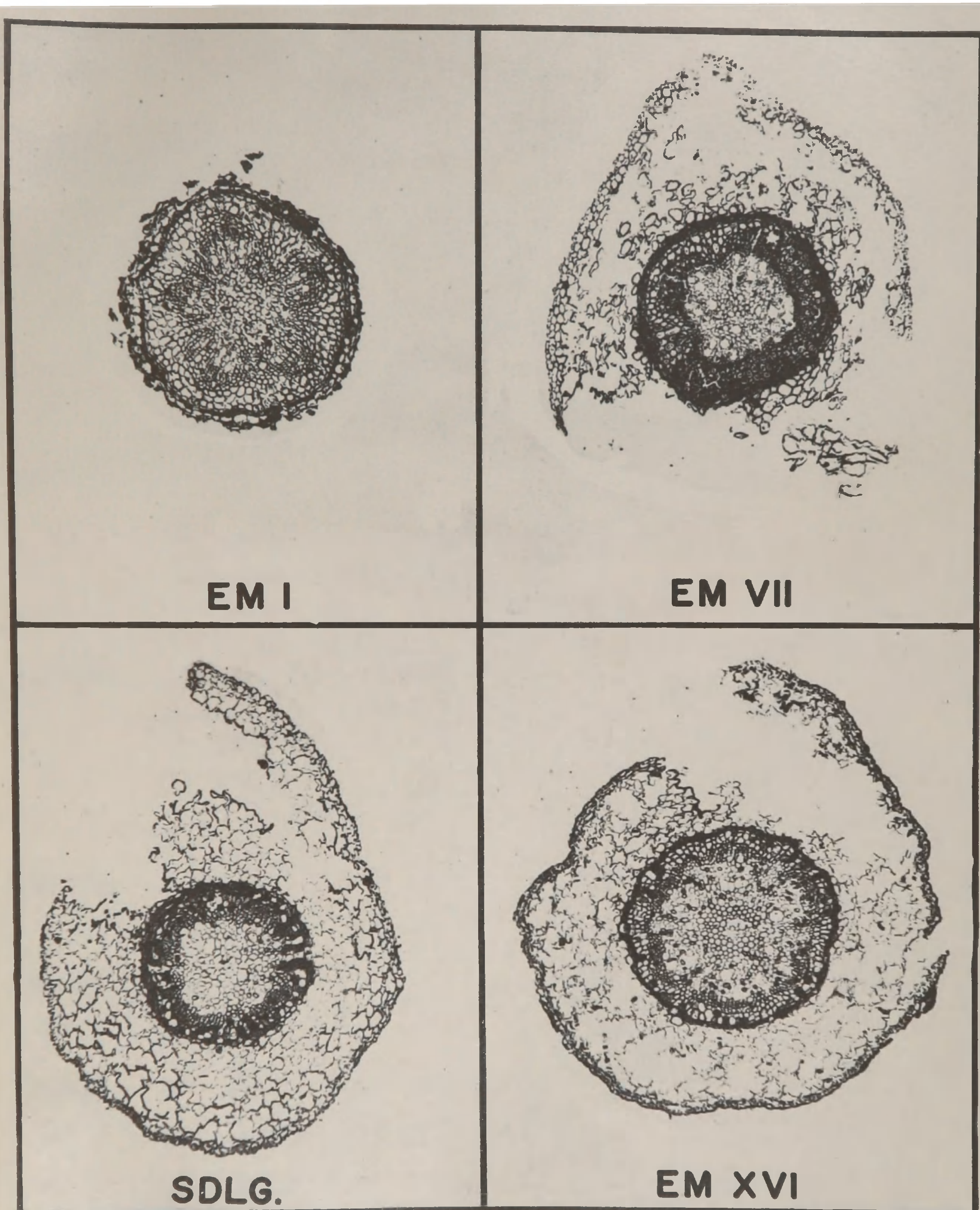

EM I
EM VII
SDLG.
EM XVI

TABLE XI

EFFECT OF ROOT TEMPERATURE ON NUTRIENT ELEMENT CONTENT OF APPLE ROOTSTOCK LEAVES

Root-stock	Temperature (°F)	Per cent composition (*1)								
		B	Ca	Cu	Fe	K	Mg	Mn	N	P
EM I	77	.0030	1.25	.0015	.0034	1.68	.43	.0090	2.46	.21
"	66	.0032	1.55	.0018	.0058	1.82	.50	.0105	2.76	.24
"	55	.0029	1.25	.0013	.0035	1.60	.45	.0088	3.00	.26
"	44	.0030	1.15	.0016	.0042	1.74	.53	.0100	3.24	.26
EM VII	77	.0030	.83	.0017	.0039	2.00	.46	.0076	3.26	.23
"	66	.0026	.81	.0017	.0053	1.87	.29	.0068	3.44	.22
"	55	.0033	1.00	.0014	.0036	1.49	.39	.0069	3.55	.27
"	44	.0029	.76	.0018	.0036	1.37	.33	.0067	3.15	.18
EM XVI	77	.0042	.53	.0015	.0036	1.88	.49	.0074	2.86	.28
"	66	.0034	.66	.0017	.0043	2.20	.47	.0082	3.15	.29
"	55	.0038	.89	.0018	.0053	1.97	.43	.0078	3.59	.38
"	44	(*2)	--	--	--	1.72	--	--	--	--
EM IX	55	.0027	1.15	.0016	.0029	1.42	.50	.0078	3.00	.34
"	44	--	--	--	--	1.30	--	--	3.43	--
EM II	55	--	--	--	--	1.93	--	--	3.06	--
"	44	--	--	--	--	1.88	--	--	--	--
Sdlg.	77	.0025	.43	.0016	.0024	1.60	.37	.0057	2.32	.18
"	66	.0028	.68	.0017	.0037	1.97	.44	.0080	2.92	.31
"	55	.0030	.79	.0016	.0039	1.68	.41	.0073	2.65	.21

(*1) Averages of results from replicate determinations expressed on the oven-dry basis. Nitrogen was evaluated by the Kjeldahl procedure, potassium flame photometrically, and the remainder spectrographically.

(*2) Insufficient sample to analyze.

Calcium: With the rootstocks EM I and EM VII the calcium content of the leaves apparently was affected more by the temperature of the medium itself than by the conditions that produced the greatest growth. Calcium percentages were low in the plants grown at 44 degrees F, high in the plants grown at the intermediate temperatures, and again low in the plants grown at 77 degrees F. For EM I the greatest accumulation of calcium was in the plants grown at 66 degrees F, while for EM VII the greatest accumulation was at 55 degrees F. Both values were significant over the other treatments in the respective rootstocks.

There was not enough dried leaf material to make analyses of the 44-degree treatment for EM IX and the seedling rootstocks. In both rootstocks the accumulation in the leaves of the plants grown at 55 degrees F was very high and decreased as the temperature was raised to 77 degrees F. Both the 55- and 66-degree treatments showed a significantly greater accumulation of calcium than the 77-degree treatments.

Manganese: No significant differences or trends were noted in the manganese content of the leaves of EM I, EM VII, and EM XVI in the various treatments. With the seedling rootstock, however, there was a significant accumulation in the leaves as the root temperatures were lowered and became less favorable for growth.

Magnesium: In general, magnesium accumulation in the leaves of EM I, EM VII and the seedling rootstock increased as the root temperatures became less favorable for growth. With EM XVI, however, an inverse relationship occurred. The differences in magnesium accumulation were not significant in the EM XVI treatments, but reached significant proportions in the following root temperature treatments: 44 degrees F over 55 degrees F with EM I, 55 and 77 degrees F over 66 degrees F with EM VII, and 55 and 66 degrees F over 77 degrees F with the seedling rootstocks.

Nitrogen: Significantly higher amounts of nitrogen were obtained in the leaves of plants grown at 55 and 66 degrees F with the seedling rootstock and significantly lower amounts in the leaves of EM I grown at a root temperature of 77 degrees F than the values obtained for the treatments that gave the optimum growth in the respective rootstocks. The other treatments, although not significant, showed a definite trend toward increased accumulation of nitrogen in the leaves as the temperature was lowered regardless of the optimum root temperature for the growth of the rootstocks.

Iron: The rootstocks showed a varied response to iron accumulation at different root temperatures. Increased iron accumulation in the leaves was very significant with EM XVI and the seedling rootstocks as the temperatures were lowered and became less favorable for growth. With EM VII, however, all treatments had a significantly lower accumulation of iron in the leaves than the 66-degree treatment which was the most favorable temperature for growth of this rootstock. The behavior of the EM I rootstock was erratic.

Increased accumulation at a root temperature of 66 degrees F was quite significant, while the 44- and 77-degree treatments were approximately the same as the 55-degree treatment which yielded the greatest growth.

Phosphorus: The data for the accumulation of phosphorus in the leaves of plants at the different root temperatures were inconsistent. Apparently the growth rates of the plants had no effect on the phosphorus content of the leaves. There was, however, some evidence that a temperature effect existed with the phosphorus accumulation being lower at the two extremes in root temperatures. Peak accumulation occurred at 66 degrees F for EM I and the seedling rootstocks and at 55 degrees F for EM VII and EM XVI rootstocks.

Copper: Copper accumulation in the leaves of EM VII and the seedling rootstocks varied very little at the different root temperatures and no trends were established. With EM I and EM XVI there was an increase in the amount of copper in the leaves in the treatments where the temperatures were less favorable for growth. The 44- and 66-degree treatments were significant over the 55-degree treatment with EM I and the 55-degree treatment was significant over the 77-degree treatment with EM XVI.

Potassium: No over-all trends were established when the potassium content of the leaves in the various treatments was considered. The content of potassium in the leaves of the EM I rootstocks grown at root temperatures less favorable for growth were higher, but none of the differences were significant. With EM VII there was an increase in potassium accumulation in the leaves as the temperature was raised from 44 to 77 degrees F. The amounts of potassium in the 44- and 55-degree treatments were significantly lower than the amount in the 66- and 77-degree treatments. In both the EM XVI and seedling rootstocks the 66-degree treatments had a significantly large potassium accumulation in the leaves than the 77-degree treatments which yielded the greatest growth in both rootstocks, while the plants grown at 55 degrees F, however, had only slightly more potassium in the leaves than those grown at 77 degrees F.

DISCUSSION

In evaluating the results of this experiment, it should be kept in mind that these rootstocks were grown in nutrient solution. Conceivably, the reactions might vary under similar temperature conditions in soil, out-of-doors, in the nursery row. Further the plants were transferred abruptly from the cool temperature of the nursery cellar to the temperatures used in this experiment and did not experience the gradual increase in temperature which would occur under outdoor conditions. From the data presented, however, it is quite evident that the external and internal effects of root temperature are expressed in many ways.

Temperature and New Shoot and Root Initiation

Apparently the requirements for breaking dormancy of the East Malling rootstocks were satisified by the storage period up to February 11, since satisfactory new growth of both roots and shoots occurred with all of the plants so handled. Initiation of vegetative growth of both shoot and root was influenced by the root temperature at which the plants were grown. As the temperatures were increased from 44 to 77 degrees F, new growth of roots and shoots occurred progressively earlier. In general, the initiation of new roots occurred somewhat before the vegetative buds of the stem had begun to open. These results are in accord with observations made by Goff as early as 1898.

The seedling rootstock was variable in the formation of new roots and there was no significant difference in bud break when the various treatments were considered. Inasmuch as the seedlings were secured from a commercial source, it was felt that the dormancy of the vegetative buds had been broken in transit and that growth had been initiated before the plants had been placed in the temperature tanks. The failure of many of the seedling plants to form new roots is unexplained.

Temperature and Root Growth

It was very definitely illustrated in this experiment that root temperatures influenced root elongation. Poor root growth was encountered with all rootstocks at 44 degrees F similar to the results obtained by Nightingale (1935) and Batjer et al. (1939) for apple roots.

Increased root growth with progressively increasing temperatures was noted by Rogers (1939) and Proebsting (1943). However, in this trial as the data indicate, certain rootstocks did not react in this manner and showed varietal differences similar to those obtained by Nightingale and Blake (1934) with the Baldwin and Stayman apple varieties. The EM VII, EM XVI and seedling rootstocks showed an increase in fresh and dry weight as the temperatures were raised from 44 to 77 degrees F, but the EM I, EM II, and EM IX rootstocks showed a decline in performance above 55 degrees F.

The complete mortality of plants of EM II, and EM IX in the 66- and 77-degree treatments, and the reduction of root growth in EM I rootstocks at temperatures above 55 degrees F were indicative of the fact that these rootstocks prefer a low soil temperature. EM VII and EM XVI rootstocks are apparently tolerant to root temperatures from 55 to 77 degrees F, while the seedling rootstock grew much better at 66 and 77 degrees F.

In general, the East Malling rootstocks preferred a cooler soil temperature. This fact may well explain why they have not been widely adopted on the North American continent. Thus, they have not been successful in the State of Kansas where Filinger (1954) has reported maximum soil temperatures of 101 degrees F and well above 90 degrees F for a considerable period of time. In the State of Michigan, the growth of the East Malling series has been more favorable as reported by Tukey and Carlson (1949). Maximum soil temperatures at Michigan State College, as reported by Bouyoucos (1916), are much below those of Kansas (93 degrees F) and the duration of the high temperatures was very much shorter than experienced in Kansas. Further, in England, where these East Malling rootstocks thrive and are of great commercial importance, the highest soil temperatures encountered by Rogers (1952) were 70 to 75 degrees F. The maximum temperatures experienced even in England would appear to be higher than those optimum for the growth of some rootstocks in this experiment. These temperatures, however, are not of long duration and as reported by Brenchley (1922), plants are better able to withstand fluctuating temperatures than a constant high temperature.

The newly formed roots at 44 degrees F were pearly white, thick, and unbranched, while at 77 degrees F, they were very slender and much branched. Although the rootstocks varied in reaction to the 77-degree F treatments, considerable browning of the cortex was observed. These results are in agreement with the findings of Nightingale (1935) for apples, Laurie and Shanks (1949) for roses, Stuckey (1942) for Colonial Bentgrass, and Darrow (1939) for Kentucky Bluegrass. Heinecke (1932) also experienced severe injury to the rootlets of apple trees which were submerged at high temperatures.

Temperature and Shoot Growth

The data obtained for shoot elongation, cross-sectional area of the new shoot, and fresh and dry weights of the new shoots indicate that there is a definite varietal difference in the reaction of the rootstocks to root temperature. Similar varietal differences were encountered by Nightingale and Blake (1934) with the Baldwin and Stayman varieties of apples.

In general, shoot growth was closely associated with the amount of roots produced, similar to the findings of

Nightingale (1935), Batjer et al. (1939), Proebsting (1943), and Rogers (1952). Poor shoot growth was observed with all rootstocks at 44 degrees F. Similar temperature relationships were experienced with shoot growth with the exception of EM VII which produced slightly more growth at 66 degrees than at 77 degrees F.

Very few lateral shoots were formed and no differences in shoot morphology were noted at the different temperature treatments.

Temperature and Shoot-Root Ratio

Vyvyan (1934) and Rogers (1952) have reported a relatively constant shoot-root ratio according to soil type. The data presented in this paper emphasizes the importance of temperature in shoot-root ratios. Although the behaviour of the different treatments varied, there was a tendency for a higher shoot-root ratio in the higher temperatures, Roberts (1953) has reported similarly for the strawberry.

The shoot-root ratios may have been affected by sloughing of the root cortex at the higher temperatures. At best, these values are only indicative of the shoot-root ratios existing at time of harvest, and are not indicative of what the shoot-root ratio might have been if all the root tissue could have been accounted for.

Temperature and Root Anatomy

Microscopic examinations of root cross-sections from various parts of the newly formed roots showed that root temperature definitely affected the development of the new roots. The results obtained in this experiment were in agreement with the work of Nightingale (1935) for apple, Shanks and Laurie (1949) for roses, Stuckey (1942) for Colonial bentgrass, and Darrow (1939) for Kentucky Blue Grass. An increase in temperature from 44 to 77 degrees F brought about progressively greater maturation in the root tissue as illustrated by primary tissue differentiation, subsequent vascular cambial activity and deposition of secondary tissue, maturation of the xylem and phloem tissues, and browning and sloughing of the cortical tissues. A reduction in the proportion of cortical to stelar tissue was also experienced similar to the results of Nightingale (1935) for apple and Shanks and Laurie (1949) for roses.

The data obtained in this experiment, raise the question as to whether the correlations between root anatomy and subsequent vigour and precocity of the scion as reported by Beakbane and her co-workers (1945, 1947, 1952) are applicable to a wide range of temperature. Before the anatomy of the root can be used as a diagnostic tool for the selection of new rootstocks at a very young age on the North American continent, it would seem that further work at particular temperatures would be necessary in order to establish the relative proportions of living to non-living tissue in the roots of these rootstocks which induce a dwarf and a vigorous habit in the scion variety.

Temperature and Nutrient-Element Content

Basically this experiment was not designed to be a nutritional study. Only one nutritional treatment was used throughout the four temperatures. For the most part, the results under the condition of this experiment have not been significant.

SUMMARY

In an endeavour to study the effect of root temperature on the growth of apple rootstocks, five clonal and one seedling rootstocks were grown in water culture at 44, 55, 66 and 77 degrees F. Air temperatures were the same for all treatments. The clonal rootstocks included EM I, EM II, EM VII, EM IX and EM XVI, obtained from established stool-beds at Michigan State College, while the seedling rootstock was purchased from a commercial nursery.

The onset of new growth, both in the shoot and in the roots was enhanced by a rise in temperature from 44 to 77 degrees F.

The rootstocks exhibited definite clonal differences in the production of new roots. All rootstocks produced very slight root growth at 44 degrees F. EM VII, EM XVI and the seedling rootstocks produced an increasing amount of roots as the temperature was raised from 44 to 77 degrees F. EM I, EM II, and EM IX, however, produced the greatest amount of root at 55 degrees F. The latter two rootstocks were completely killed above 55 degrees F.

Considerable browning and sloughing of the cortical tissue was experienced at the higher temperatures, especially the plants that preferred the lower temperatures such as EM I which was particularly susceptible to injury of this nature.

At 44 degrees F the roots were thick, pearly white and non-branched, while at 77 degrees F the roots were slender, much-branched, and discolored to varying degrees.

Shoot growth was closely associated with root growth. EM I, EM II and EM IX gave the greatest shoot elongation at 55 degrees F. EM XVI was almost equally tolerant to temperatures of 55, 66 and 77 degrees F but gave slightly better growth as the temperature was increased. With EM VII the greatest top growth was produced in the 66-degree treatment, while growth of the seedling rootstock was much superior at 77 degrees F.

Increases in root temperature from 44 to 77 degrees F, brought about an increase in maturation of the roots as illustrated by differentiation of primary tissues, vascular cambial activity and subsequent deposition of secondary tissues, and browning and sloughing of the cortical tissue.

The nutrient contents of the leaves from the different temperature treatments were determined. Certain trends were noted, but, for the most part, the differences were not significant.

In general, the East Malling rootstocks seem to prefer a cool soil temperature and this factor may help to explain why they have not become widely established on the North American continent, where soil temperatures are relatively high for considerable periods of time over large areas.

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