EFFECT OF HUMIDITY ON GROWTH OF SELECTED ORNAMENTAL PLANTS

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EFFECT OF HUMIDITY ON GROWTH OF SELECTED ORNAMENTAL PLANTS

By

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A THESIS

Submitted to the College of Agriculture of Michigan State University of Agriculture and Applied Sciences in partial fulfillment of the requirements for the degree of

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Department of Horticulture

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DEDICATION

To my parents

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The author wishes to express his gratitude and appreciation for the guidance and understanding of Dr. D. P. Watson; to Dr. F. B. Widmoyer for help in the anatomical descriptions; and to James R. Lonsway for assistance in preparation of copy.

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INTRODUCTION

An office or lobby without foliage silhouettes to soften sharp architectural lines and angles is a rare sight. The slow growth and frequent death of many of these plants during the winter months in centrally heated homes may be caused by the dry atmosphere in which they are growing. It is natural to suppose that plants which are tropical in origin would grow more luxuriantly in a saturated atmosphere. This limitation of growth assumes greater significance with the ever expanding popularity of decorative plants. With this in mind, an investigation was undertaken of the effects of high and low humidity on certain selected ornamental plants.

Small evergreens, native to temperate regions, have rarely been used as house plants. Their acceptance by the consuming public would be greatly enhanced if it could be shown that they could withstand an atmosphere of low humidity. Naturally, much depends upon the ultimate appearance and type of growth made, but an opportunity to provide another outlet for nursery products prompted the inclusion of these plants in the present experiment.

SURVEY OF PERTINENT LITERATURE

Macroscopic Effects

Nightingale and Mitchell (1934) observed that nitrogen deficient tomato plants exposed for nine days to a relative humidity of 95% elongated three to four cms. more than plants grown in 35% relative humidity. Plants grown in high humidity were also darker green with succulent expanded apical leaves whereas no change in appearance was observed in those grown in low humidity. Plants given adequate nutrition responded in like manner; those in high humidity exhibiting a 12 to 15 cm. increase in stem length compared to five to seven cms. in low humidity. They were darker and more evenly green as well as being extremely succulent. Plants in low humidity were woody, stiff, and mottled green in appearance.

They found the same relationship for two year apple seedlings. In fact, the high humidity was associated with a greater number of broad but thin, dark green leaves. Again, they reported for the apple a cessation of all terminal growth of current stems in low humidity.

Newcombe and Bowerman (1918) reported similar findings in that seedlings grew taller and produced larger, more numerous leaves in a small stagnant bell jar than in a larger chamber with circulating air. In 1917, Hanson mentioned that possibly humid air caused leaf size increases, greater root development, and that leaves grew at right angles to the stem in moist air.

Anatomical Effects

Macroscopic differences have been correlated with definite anatomical changes (Hanson, 1917; Nightingale and Mitchell, 1934). Hanson referred to observations that increases in cuticle thickness, stomata number, amount of sclerenchyma, woody tissue, and palisade cells accompanied growth in dry air. He believed that reductions in storage tissue, fibrovascular bundles, and intercellular spaces as well as increases in amount of chlorophyll and number of stomata per leaf were characteristic of plants in highly saturated atmospheres. Furthermore, these chlorophyll cells were more isodiametric along with pronounced epidermal cell wall waviness. Nightingale and Mitchell (1934) also made note of the unusually high concentration of chlorophyll present in the greater number of chloroplasts found in leaves of plants exposed to high humidity. Thinness of cuticle and cell walls in addition to loosely compacted palisade and spongy mesophyll with large intercellular spaces were also observed. On the other hand, plants from low humidity exhibited comparatively thick cuticle, relatively thick xylem, and compact small celled palisade and spongy mesophyll with greatly reduced intercellular spaces.

These differences might perhaps be best accounted for by a quotation from Pool (1923) who asserted that "of all the histological features of the leaf, the chlorenchyma is probably the most plastic, or most readily modified by environmental variations, so that some of the commonest and most striking differences between mesophytic and xerophytic leaves are to be found in the relative development of palisade

and sponge and in the relative proportion of lacunar volume in the chlorenchyma as a whole." Pool then proceeded to a comparison of mesophytic and xerophytic leaf anatomy which was in many respects similar to the above mentioned differences between plants grown in high and low humidity. Yet, xerophytic plants growing in arid habitats were more prone to foliar water deficits due to low soil moisture and absorption as well as excess transpiration (Shields, 1950). The consequent water shortage resulted in limited stretching growth, cell surface, epidermal cell enlargement, and laterally expanding spongy mesophyll. This was reflected in thicker cell walls, increased number of stomata per unit area, more prominent development of palisade, and denser network of veins. These reduced tissue proportions and structural modifications were the result of internal water deficits and were influenced solely by rate of transpiration and water supply as opposed to absolute water loss (Shields, 1950).

Physiological Effects

Transpiration rate differencials were also of great significance in the growth of adequately watered plants in low and high humidity. According to Nightingale and Mitchell (1934), the contrasting growth responses due to humidity differences were the results of greatly accelerated transpiration accompanied by internal changes. The effect that foliar anatomy exerted on rate of transpiration was evident from the work of Turrell (1936) who found a close relationship between transpiration losses and amount of internal leaf surface area. The high transpiration rate of xerophytic leaves was thus explained by their

more compact structure with numerous small air spaces and usually more palisade layers. The extensive internal evaporative surface was accounted for primarily by the greater development of palisade type of mesophyll which exposed 1.6 to 3.5 times as much surface, per unit volume, as the spongy type (Turrell, 1936). However, Pool (1923) attributed low xerophytic transpiration rate to the evaporative obstacle from the interior of the leaf presented by the compact chlorenchyma. Yet, there was no doubt that a lowering of relative humidity was accompanied by increased transpiration (Kisselbach, 1916). But there was a limit to this correlation as reported by Bialoglowski (1935). He found that transpiration and humidity presented a linear relationship provided they were within a certain range. Below 60% relative humidity or 68°F., pronounced retardation in rate of water loss was observed. This was supported by the earlier work of Henderson (1926) who maintained that the effect of changes in humidity on transpiration was not ascertainable below 60% relative humidity because changes occurred near the wilting point and that these changes affected the rate of evaporation from cell walls. Thut (1938), on the other hand, provided data to prove that transpiration losses presented an inverse linear function over the entire relative humidity range. He inferred that as relative humidity rose, transpiration declined to a point where plant leaves in high humidity were actually absorbing water from the surrounding air instead of losing it. In fact, Breazeale, McGeorge, and Breazeale (1950) found that enough water was absorbed by the leaves of tomato plants in saturated air and transported to the roots to raise the soil moisture above field capacity. The authors thereby concluded that

pressure developed by absorbing roots was not as great as that maintained in foliar absorption. Thut's (1938) explanation depended upon the validity of the absorption lag in roots as recorded by Kramer (1938). This difficulty in obtaining and transporting adequate water for transpiration created a deficit which was transmitted to the leaves accounting for absorption in humid air. The resulting increased water content of the leaf in high humidity was of no little significance. The water balance of the leaf as a whole was reflected in the turgor changes assumed to be associated with guard cell movements and the consequent size of stomatal apertures (Wilson, 1948). An increase in the moisture content of the leaf would therefore bring about wider opening of the stomatal apertures. Yet, the effect of low relative humidity on stomatal aperture size was slight except at high temperatures when the stomata became more nearly closed (Wilson, 1948). This result was observed by Nightingale and Mitchell (1934) who reported that the stomata of tomato and apple plants grown at 70°F. in high humidity (95%) were much more open than those of plants grown in low humidity. But according to Muenscher (1915) and Knight (1917), there was no observable relationship between transpiration rate and number or size of stomata per unit of leaf surface. Size of stomatal opening also had no apparent effect on the carbon fixation of leaves (Mitchell, 1936). Knight even maintained that small changes in leaf water content did not influence the opening or closing of stomatal apertures. It was concluded that the water content of the leaf was more significant than the degree of stomatal opening (Livingston and Brown, 1912; Henderson, 1926). High water content thereby tended to produce a high transpiration rate and

low transpiration accompanied low water content (Knight, 1917). Granting that leaf water content did exert a significant effect on transpiration, there was no assurance that leaves in high humidity actually absorbed water from the surrounding air under all conditions. Briggs and Shantz (1915) and Henderson (1926) indicated that leaves in a completely saturated atmosphere still transpired. Henderson (1926) found that leaves in 100% relative humidity were of a higher temperature than that of the surrounding air. This would indicate that a hypothetical relative humidity of above 100% would be needed to completely stop transpiration. However, leaf temperature was determined by the evaporative power of the air at relative humidities less than 100% (Henderson, 1926). Thus, the leaf was often cooler than surrounding air in diffuse light but with the complete spectrum supplied by sunlight to counterbalance evaporative respiratory heat loss, leaf temperatures would undoubtedly be higher than the surrounding air temperature. This would account for Curtis' (1936) conclusion that small differences of a few degrees between leaf and air temperature may exert a great influence on transpiration.

Clum (1926) reported no definite relationship between transpiration rate and differences between leaf and air temperature. It was felt by Yarwood and Hazen (1944) that this might be due to high and variable radiation on the test surfaces. This would be similar to natural light conditions during the day. Ehlers (1915) did find that even diffuse light will result in from 0.5°C. to 2.0°C. higher leaf temperatures. The same effect was found in winter when he reported that evergreen conifer leaves maintained temperatures from 2°C. to 10°C. higher than

the surrounding air. This differential was increased to a 10.31°C. difference in still air and decreased to 8.83°C. with a slight breeze.

Moreland (1937) found, moreover, that the effect of relative humidity on leaf temperature was not as evident as that exerted by air movement. His experiments showed that sugar cane leaves in sunlight were 5°C. to 7°C. warmer than surrounding still air. The difference was slight, however, (1°C. to 2°C.) in strong breezes. Conversely, the leaf was cooler than the air in shade. These small differences were not changed to any great extent by humidity differentials except that greater differences between leaf and air temperature in sunlight were noticed at higher relative humidities. This same effect in diffused light was reported by Henderson (1926). He found that raising the humidity from 70% to 80% resulted in a 0.5°C. rise in leaf temperature. He further stated that an ivy leaf reached atmospheric temperature at around 95% relative humidity with gentle air movement, diffuse light, and 68°F. air temperature.

Nutritional Effects

The contrasting growth responses due to transpiration differences caused by low and high humidity were undoubtedly accompanied by internal changes (Nightingale and Mitchell, 1934). Their findings indicated high dry matter content for plants grown in low humidity as evidenced anatomically by thick xylem and chemically by heavy starch and other carbohydrate depostions. This increase in dry matter could be caused by rapid loss of water as suggested by Nightingale and Mitchell. It was believed that carbohydrate increase and moisture loss are generally

associated with the condensation of simple amino acids to protein. This would explain the comparatively high concentration of "total elaborated nitrogen in the form of complex, relatively immobile, dehydrated protein" found by Nightingale and Mitchell in the tissues of slow growing, non-succulent plants grown in low humidity. In fact, the condensation of soluble organic nitrogen to relatively complex protein fractions accounted for the developing terminal buds of apple seedlings grown in low humidity, according to Nightingale and Mitchell. Carbohydrate accumulation in low humidity was also substantiated by the further work of Mitchell (1936) who maintained that photosynthesis was not affected to any great extent by low humidity. He based this assertion on the sustained rate of carbon fixation by squash, wax bean, cabbage, geranium, primula, and tomato leaves even in low humidity of 15 to 20 hours duration. Moreover, he cited other workers whose findings he had found to support his own (Kisselbach, 1916; Nightingale, 1933).

The influence of an external nitrogen supply on half of the plants evidently exerted a stronger beneficial effect on growth than high humidity in that fertilized plants in low humidity grew two to three cms. more than unfertilized plants in high humidity (Nightingale and Mitchell, 1934). The plants which received the complete nitrogen feeding and subsequently grew more exhibited a depletion in sugar and starch because of the synthesis of less complex, water soluble, organic proteins made necessary and possible by fertilization. This was evidently followed by proteolysis and increase in growth since hydrolysis of proteins generally comes after decreases in dry weight. Nightingale and Mitchell (1934) cited: Nightingale and Robbins, 1928;

Nightingale and Schermerhorn, 1928; Nightingale, Schermerhorn, and Robbins, 1928, 1930; Pearsall and Ewing, 1929, and Nightingale, 1933, as evidence of complete agreement with this hypothesis.

Other Effects

It has been indicated that the conversion of soluble organic nitrogen to relatively complex protein fractions with concomitant build-up of carbohydrates accounted for the developing terminal buds of apple seedlings grown in low humidity. Indeed, the presence of abundant carbohydrates has been shown to be a factor resulting in plant reproduction (Kraus and Kraybill, 1918; Nightingale, Schermerhorn, and Robbins, 1928, 1930). It has been mentioned by Nightingale and Mitchell that a hastening of flowering and fruiting is attributed to low humidity.

High humidity produced by mechanical misting systems has been utilized with great success in the propagation of difficult to root cuttings (Fisher, 1941; Gardner, 1941; Stoutemeyer, 1942), and the production of better quality Better Times roses (Kohl, 1955). Although callusing of apple cuttings was inhibited by tissue desiccation as humidity was decreased, only slight callusing resulted from 100% relative humidity unless damp peat or sphagnum was used as a storage medium (Shippy, 1930). Fully saturated atmospheres were also important in the storage of various horticultural crops such as narcissus (Hume, 1937), apricots, plums, peaches, apples, grapes (Allen and Pentzer, 1935), and potatoes (Loomis, 1927), the latter in combination with high temperatures and damp moss. High humidity was further recommended for holding cut flowers, especially carnations, which lasted from two to three times as

long in relative humidities over 80% (Hitchcock and Zimmerman, 1929). On the other hand, papaya fruits were severely injured in relative humidities greater than 60%, but were not visibly affected by lower humidities (Jones, 1939).

Pollen (Pinus strobus and P. resinosa) longevity has also been found to be influenced by 50% relative humidity, practically no germination being observed in 0% to 10% relative humidity (Duffield and Snow, 1941).

Humidity had at best only a minor effect on the critical daylength of Xanthium and other plants (Long, 1934).

PROCEDURE

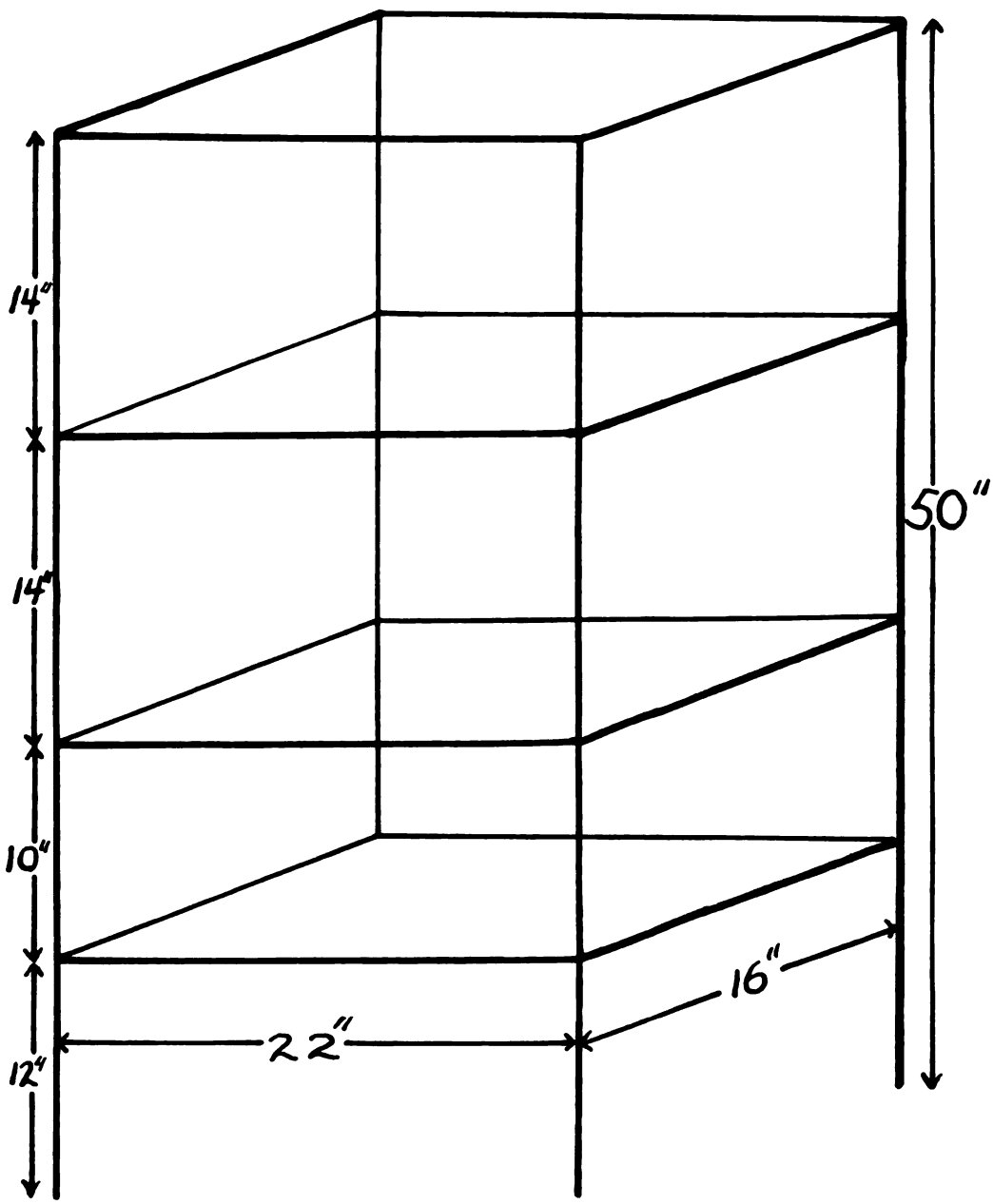
Seven or more stem cuttings of Group I: Taxus cuspidata capitata, Taxus cuspidata Andersoni, Taxus media Hicksi, Juniperus chinensis and Pinus nigra seedlings were included in the experiment; as well, mature plants of Group II: Scindapsus aureus, Cissus rhombifolia, Peperomia obtusifolia variegata and Dracena godsefianna were selected for observation. Rooted stem cuttings of the conifers (Group I) were potted in four inch pots on January 18, 1957. They were pruned uniformly to within five inches of the soil level and remained in the greenhouse for three weeks when they were inserted into the experimental chambers (Figure 1). Twenty of each species of broad leaf plants (Group II) growing in two and one-half inch pots were placed in the chambers on January 25, 1957.

The experimental chambers (Figure 1) consisted of a wooden frame supporting three shelves. The whole structure was sprayed white. Each of the four chambers had a capacity for about forty plants. Two of the chambers were enclosed with transparent "Saran-Wrap" to conserve humidity. The other two were left uncovered. The plants were numbered and placed on the shelves so that each species occupied the same relative position in each of the treatment chambers. The chambers were located on a table in a laboratory facing an east window. The temperature of the surrounding air was not altered in any manner. There was slight reduction in the amount of light received because of the condensation of moisture in the closed chambers. Constant temperature and

Figure 1

GROWTH CHAMBERS

(SCALE: 1" - approximately 8")



High Humidity - covered with transparent "Saran-Wrap"

Low Humidity - left open

humidity records were made with two "Hygro-Thermographs"[1], one for each treatment, and since there were four chambers, the same instrument was rotated weekly between the two chambers of each treatment. The amount of water supplied to every species was recorded as were length of new terminals produced by the conifers (Group I) and the production of new leaves by foliage plants (Group II).

At the termination of the experiment on June 15, 1957, fresh weight, dry weight, height of plants, leaf area, and leaf thickness were recorded and comparisons were made for the plants in each treatment. Representative samples for anatomical investigation were collected on May 1 and again on May 15.

Mid portions of newest needle leaves over 2 mm. long comprised samples from Group I plants. Group II samples consisted of 1 mm. squares from the edges of the newest mature leaves near the apex. Samples were killed and fixed in FAA (5 ml., formaldehyde; 5 ml., glacial acetic acid; 90 ml., 70% ethyl alcohol), dehydrated, embedded in paraffin and transverse sections were cut 10 micra thick. The preparations were stained in saffranin-fast green.

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[1] Friez Instrument Division, Bendix Aviation Corp., Baltimore, Md.

DISCUSSION OF RESULTS

Humidity

It was suggested in the Introduction that poor growth of plants during the winter months might be due to their growth in the dry atmosphere of centrally heated homes. The significance of the experiment thus depends upon the similarity of experimental atmospheric conditions to those of a home. Pertinent data (Table I) indicates that average temperatures around 75°F. with a relative humidity of 34% were maintained in the uncovered chambers.

According to results published by Phillips (1940), 2½ of the homes heated to 70°F., where observations were made, had indoor relative humidities between 30% and 40% when outside temperatures ranged between 20°F. and 29°F. With 10°F. increments in outside temperature, between 30°F. and over 60°F., respectively, the percentages were: 36%, 44%, 34%, and 39%. It may be argued that reduced humidity would have been more desirable in order to better duplicate atmospheric conditions of heated homes in winter. Yet, Phillips' figures and charts did show quite a percentage spread at any particular outside temperature with no one relative humidity range predominating at all outside temperature ranges.

Watering

The differences in amount of water required by plants in the two treatments is striking (Figures 2, 3). It was apparent that plants kept in drier atmospheres needed larger amounts of water more frequently.

TABLE I

Time in Weeks	Mean Temperature (in degrees Fahrenheit) Night (8pm–8am) Humidity Low	High	Day (8am–8pm) Humidity Low	High	Mean Humidity (in percent) Night (8pm–8am) Humidity Low	High	Day (8am–8pm) Humidity Low	High
Jan. 25–Feb. 1	74.5	74.5	75.5	75.0	20.5	76.5	21.5	69.0
Feb. 1–Feb. 8	73.5	73.0	73.0	74.5	20.0	98.0	19.0	98.0
Feb. 8–Feb. 15	72.0	74.0	73.5	74.5	32.0	98.0	28.0	98.0
Feb. 15–Feb. 22	66.5	67.0	70.0	70.0	21.0	83.0	25.0	92.5
Feb. 22–Mar. 1	69.0	70.0	75.0	76.5	36.5	98.0	34.0	98.0
Mar. 1–Mar. 8	69.0	70.0	71.0	70.0	23.0	98.0	25.0	98.0
Mar. 8–Mar. 15	70.0	74.0	73.5	81.0	33.0	98.0	29.0	98.0
Mar. 15–Mar. 22	68.5	72.5	73.0	74.0	31.0	98.0	26.0	98.0
Mar. 24–Apr. 1	69.5	71.0	70.5	80.5	28.0	84.0	28.0	81.0
Apr. 1–Apr. 8	69.5	71.0	70.5	71.0	38.0	98.0	37.0	98.0
Apr. 8–Apr. 15	70.0	70.0	81.0	85.0	32.0	98.0	33.0	98.0
Apr. 15–Apr. 22	77.0	77.0	78.5	85.0	38.0	98.0	41.0	98.0
Apr. 22–Apr. 29	76.0	73.0	83.0	87.5	47.0	93.0	44.0	89.5
Apr. 29–May 6	77.5	80.0	78.5	86.0	28.5	93.0	30.0	89.0
May 6–May 13	79.5	77.0	78.5	90.5	38.0	87.0	43.0	76.0
May 13–May 20	71.0	73.0	77.5	79.5	45.0	93.0	41.5	91.0
May 20–May 27	75.5	77.0	79.0	84.0	48.0	80.0	47.0	77.0
May 27–June 3	75.0	77.5	80.0	85.0	43.5	96.0	41.5	97.5
June 3–June 10	77.5	78.0	77.0	86.0	38.5	96.0	38.0	88.0
June 10–June 17	84.0	83.0	86.0	90.0	53.0	93.0	49.0	96.0
AVERAGE	73.1	74.1	76.2	80.4	34.7	92.9	34.0	90.9

DAY + NIGHT AVERAGES	Temperature	Humidity
Low Humidity	74.65° F.	34.35%
High Humidity	77.20° F.	91.90%

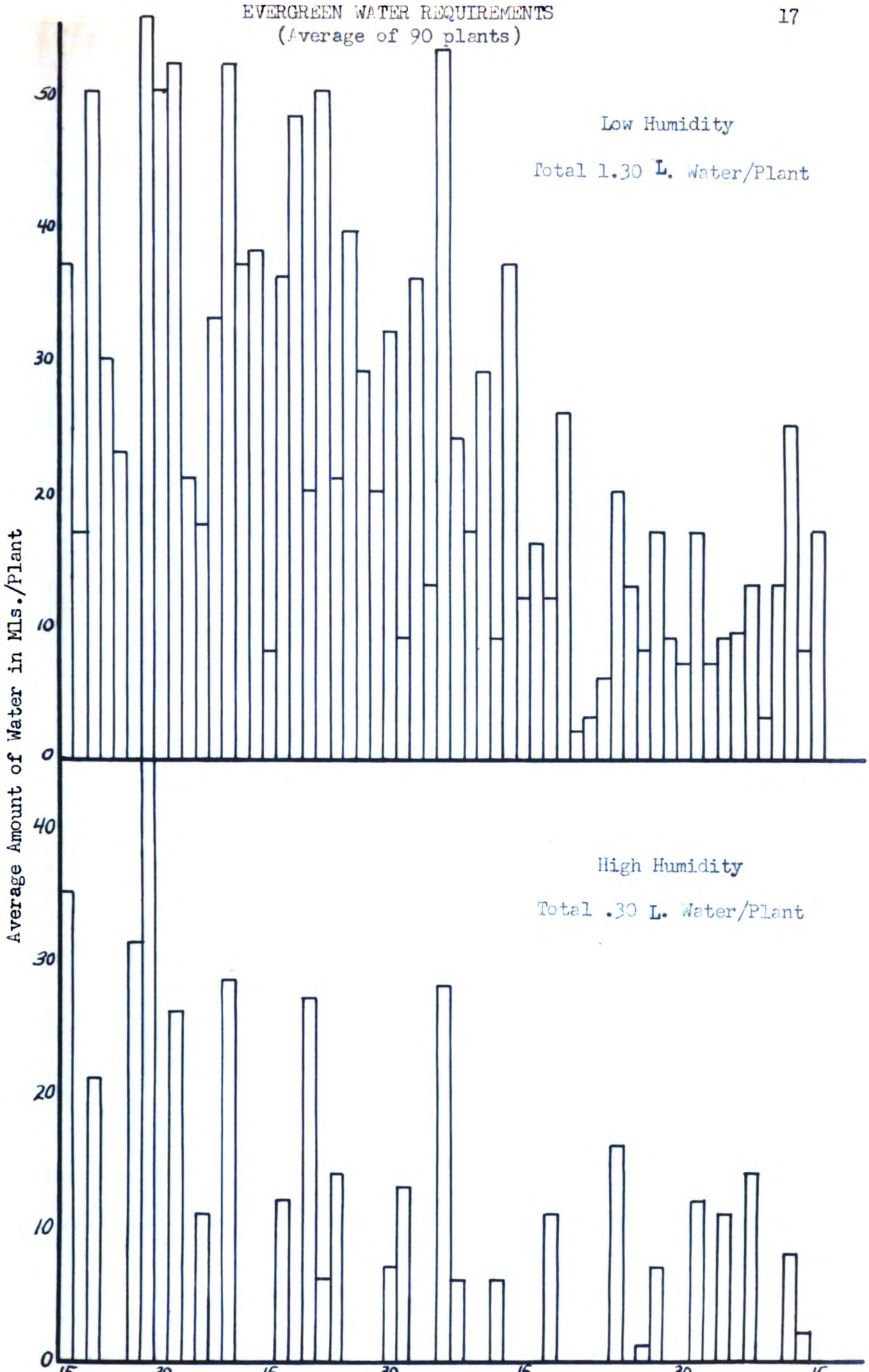
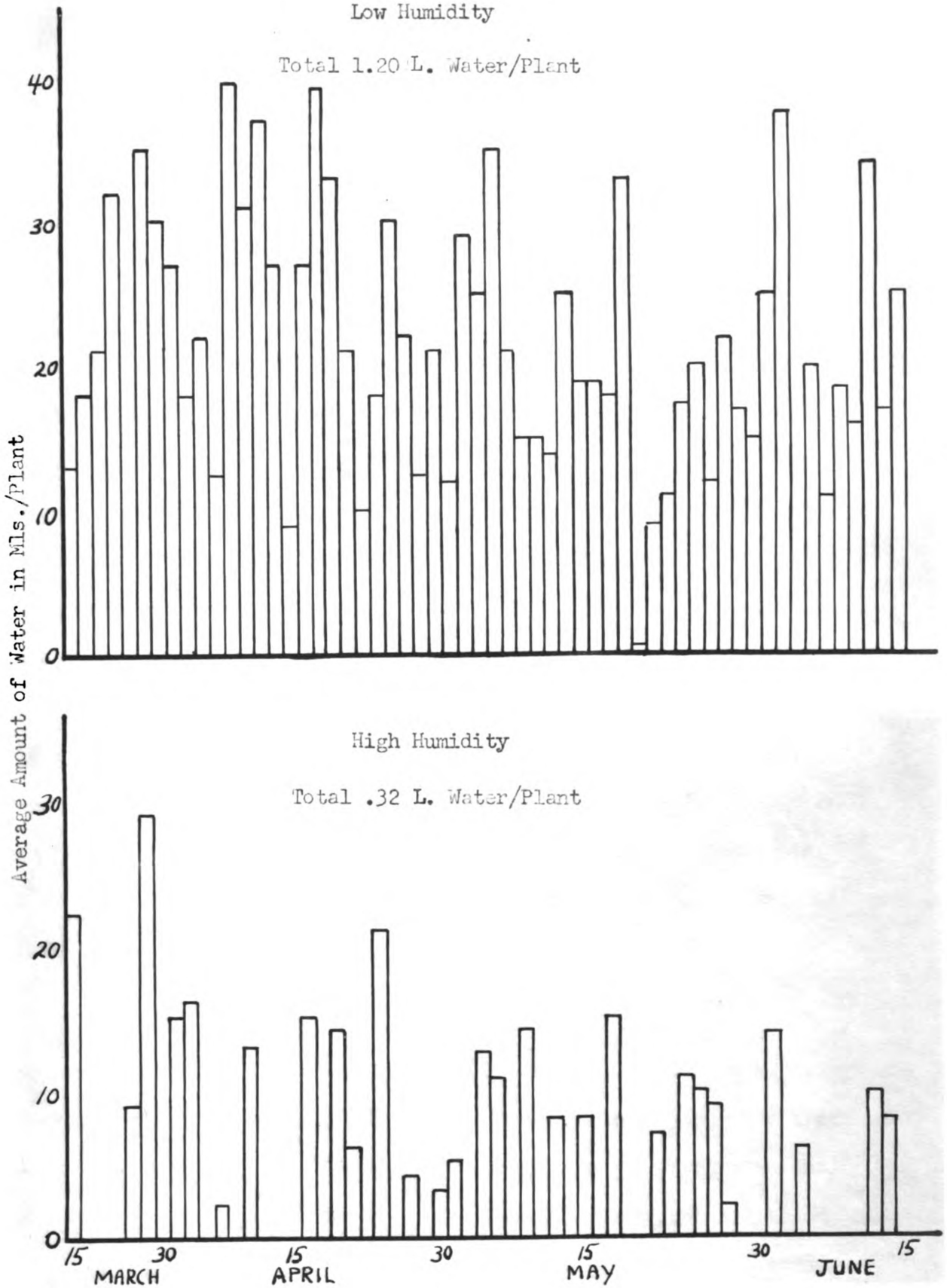

EVERGREEN WATER REQUIREMENTS
(Average of 90 plants)
Low Humidity
Total 1.30 L. Water/Plant
High Humidity
Total .30 L. Water/Plant
Average Amount of Water in Mls./Plant
50
40
30
20
10
0
40
30
20
10
0
15
30
15
30
15

Figure 3

FOLIAGE PLANT WATER REQUIREMENTS
(Average of 40 plants)



Much of this water requirement was due to evaporative water loss from the top of the soil as well as through the sides of the porous clay pots. The evaporation rate was undoubtedly hastened in the exposed chambers by air movement and low humidity which created strong vapor pressure deficits in the surrounding atmosphere. In fact, it was difficult to prevent the plants from drying out during the course of the experiment and occasionally they underwent brief periods of soil moisture shortage. The covered chambers, on the other hand, were protected from these desiccating influences. Condensation of water droplets on the transparent cover was often observed, especially in the mornings. Another factor contributing to the greatly reduced water requirements of plants grown in high humidity might be foliar water intake. This reversal of natural conditions in which the leaves become the principal water absorbing organ of the plant in highly saturated atmospheres has previously been noted (Thut, 1936; Breazeale, McGeorge, and Breazeale, 1950). This effect was so great that maturation, flowering and fruit set of tomato plants has been observed with no other source of water than that absorbed through the leaves from a fog or an atmosphere of 100% relative humidity (Breazeale, McGeorge, and Breazeale).

Growth

Reference to the Survival Record (Table II) shows that a majority of evergreens could not grow in low relative humidity. This was best illustrated by the death of every Taxus cuspidata Andersoni stem cutting in a dry atmosphere whereas all but two survived in a saturated one. The same tendency was exhibited by Taxus cuspidata cavitata and

TABLE II

SURVIVAL RECORD

Group I Plants

	Number of Plants	Dead	
		Low Humidity	High Humidity
1. Taxus cuspidata capitata	7	4	1
2. Taxus cuspidata Andersoni	8	8	2
3. Taxus media Hicksi	9	2	3
4. Juniperus chinensis	10	5	-
5. Pinus nigra	11	10	9

Group II Plants

	Number of Plants	Dead	
		Low Humidity	High Humidity
1. Scindapsus aureus	10	-	-
2. Cissus rhombifolia	10	-	-
3. Peperomia obtusifolia variegata	10	-	-
4. Dracena godseffianna	10	-	-

Juniper chinensis. Pinus nigra seedlings and cuttings of Taxus media Hicksi were evidently not even benefited by high humidity, the pine being the least adaptable to either environment (Table III). However, cause of death in high humidity was pathological rather than physiological in that evidences of primary infection by Phythium followed by secondary Fusarium and Verticillium infections were observed. It was therefore likely that high humidity not only encouraged the entry of Phythium but also facilitated the germination of secondary invader spores. Other workers have reported the growth of mold on bulbs in storage (Rume, 1937) and on packages of stored deciduous tree fruits after a month or two in high humidity (Allen and Pentzer, 1935).

Death of plants in low humidity might possibly be due to the same primary agent but examination of the root systems disclosed no significant reduction in development. Instead, the stems were extremely dry and brittle and a physiological basis for death is most plausible since death was rapid and no fungal mycelia were evident. Unfortunately, not enough plants were included in the experiment to make a statistical analysis possible but it is worth noting that death expectancy for Taxus cuspidata capitata and Juniperus chinensis in low humidity was quite near to being statistically significant.

A marketing potential for the evergreens (Group I) was discouraging. Even in high humidity, terminals produced very long feathery new growth. Similar results to a lesser extent were obtained from surviving plants in low humidity. Growth comparisons are provided in graphic form by Figures 2 through 8. They indicate definite growth differences only for Taxus cuspidata capitata. But regardless of any growth differential in

TABLE III

FRESH WEIGHT; DRY WEIGHT: NEEDLE LEAF THICKNESS

	Low Humidity			High Humidity		
	Fresh Weight Average (Gms.)	Dry Weight Average (Gms.)	Needle Leaf Thickness (Micra)	Fresh Weight Average (Gms.)	Dry Weight Average (Gms.)	Needle Leaf Thickness (Micra)
1. *Taxus cuspidata capitata*	2.37	.77	181.25	2.45	.84	320.00
2. *Taxus cuspidata Andersoni*	----	----	-----	----	----	------
3. *Taxus media Hicksi*	2.70	1.01	253.75	2.30	.83	263.75
4. *Juniperus chinensis*	1.55	.75	343.75	2.03	.93	450.00
5. *Pinus nigra*	5.25	1.95	187.50	4.70	1.65	250.00

Figure 4

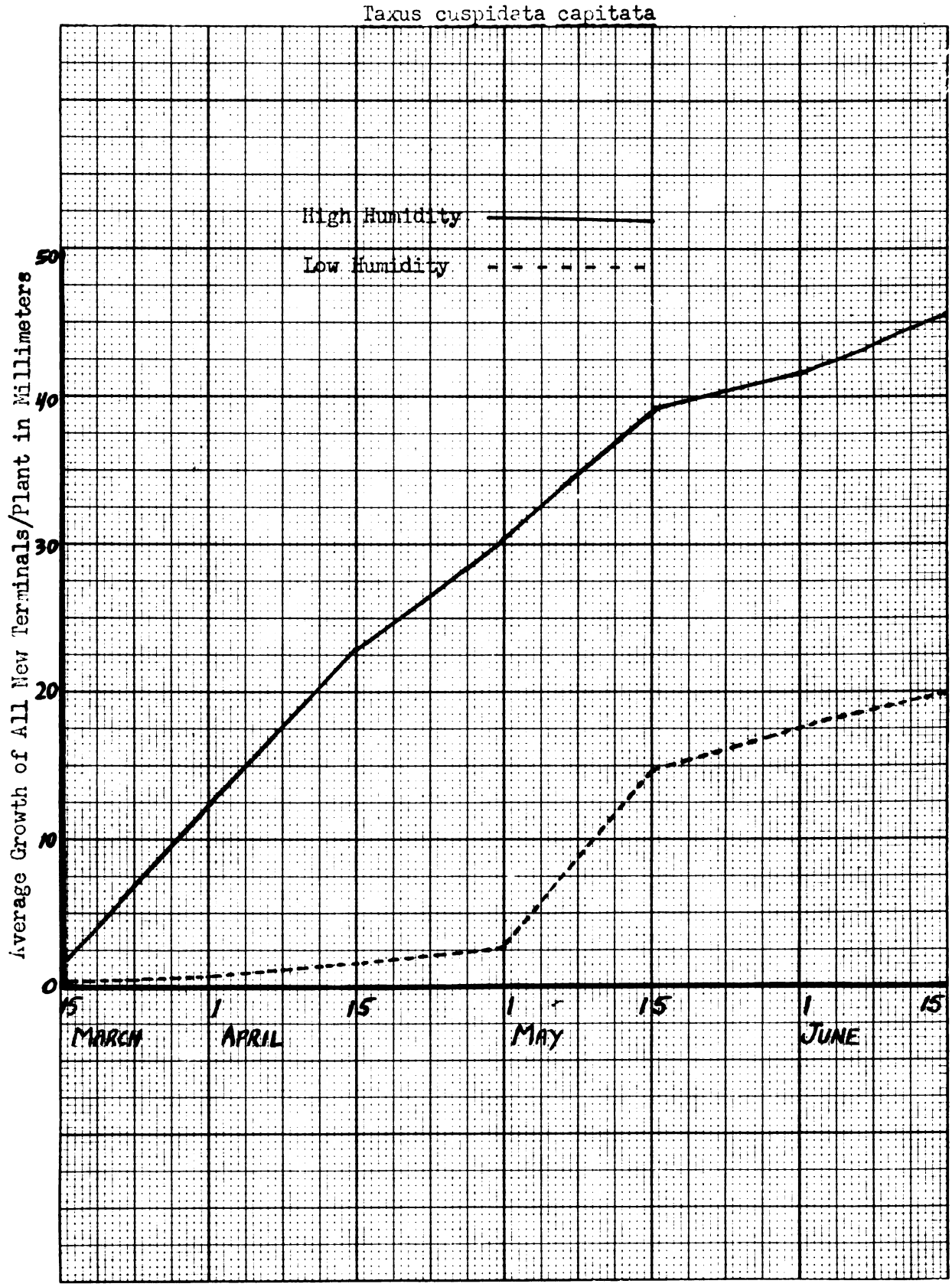

Taxus cuspidata capitata
High Humidity
Low Humidity
Average Growth of All New Terminals/Plant in Millimeters
50
40
30
20
10
0
15
MARCH
1
APRIL
15
1
MAY
15
1
JUNE
15

Figure 5

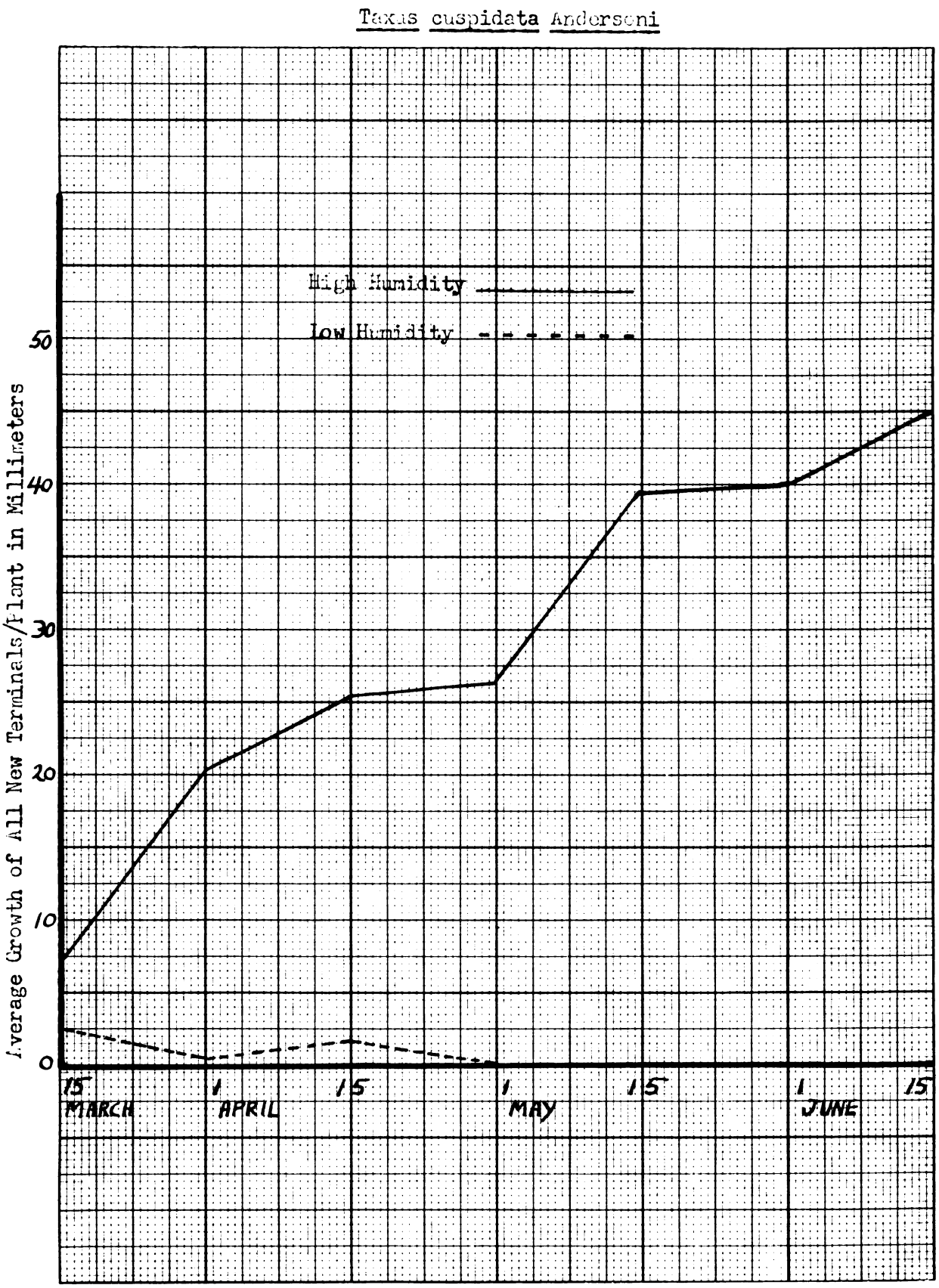

Taxus cuspidata Andersoni
High Humidity
Low Humidity
Average Growth of All New Terminals/Plant in Millimeters
0
10
20
30
40
50
15 MARCH
1 APRIL
15
1 MAY
15
1 JUNE
15

Figure 6

Taxus media Hicksi

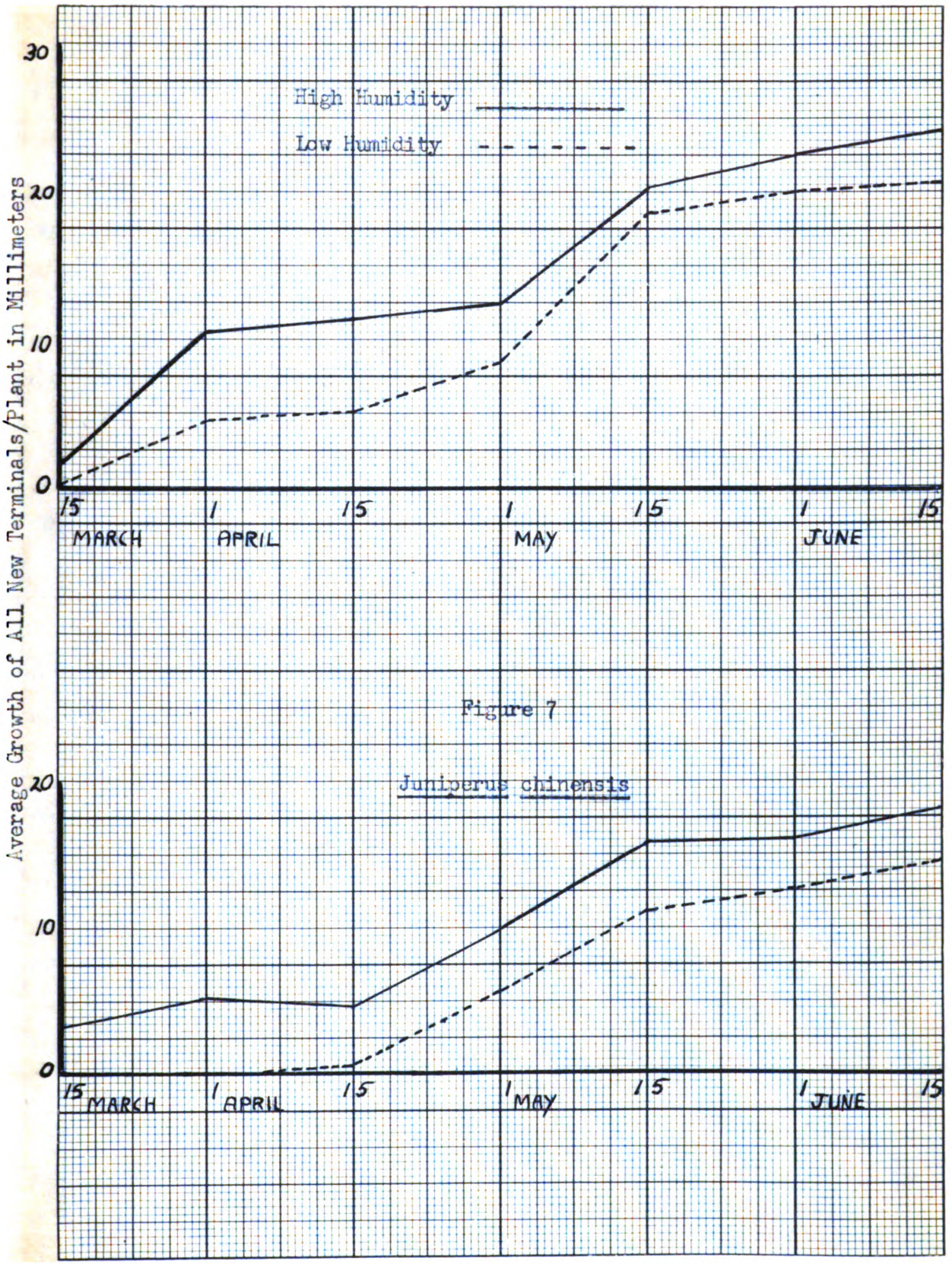
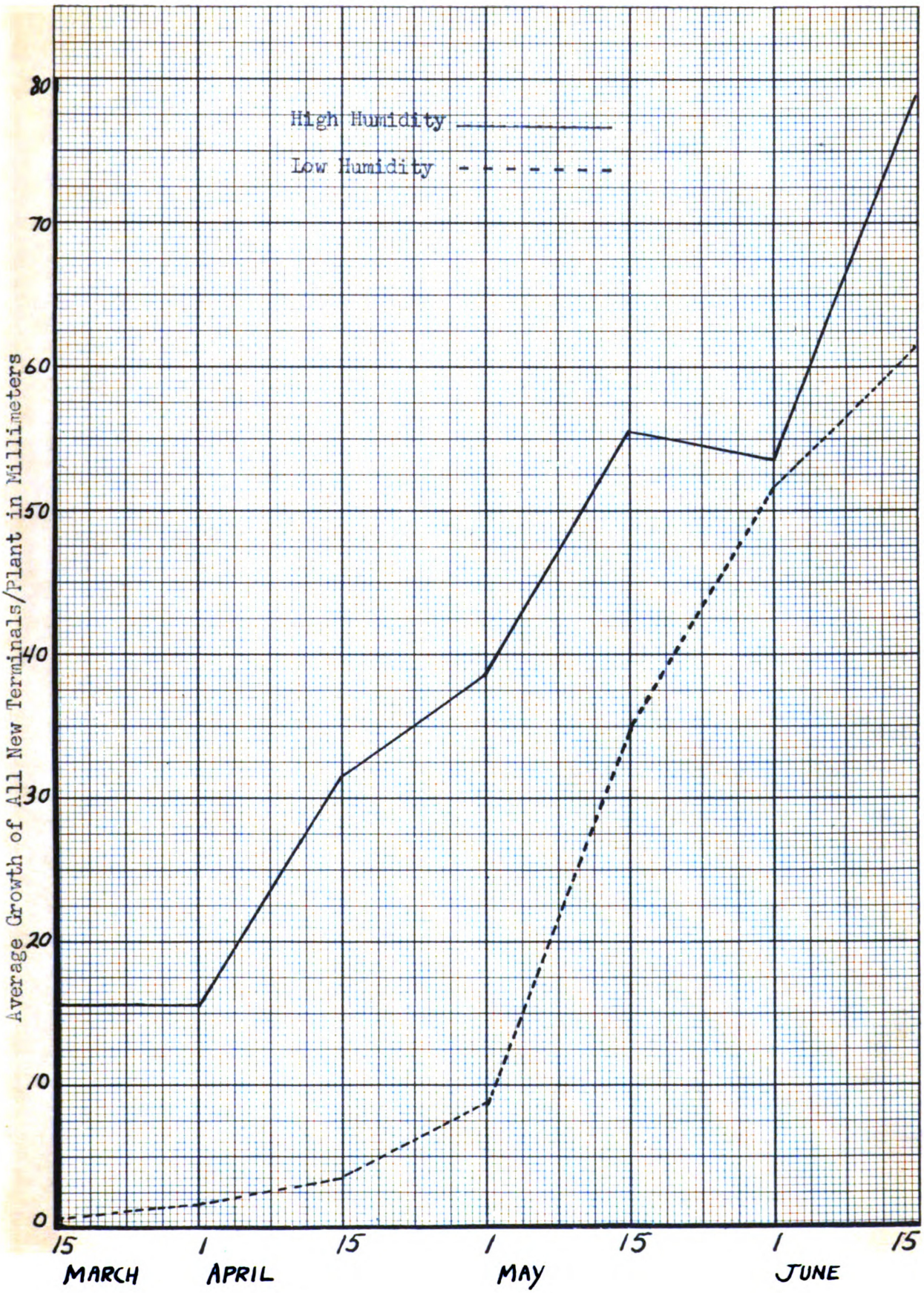


Figure 7

Juniperus chinensis

Figure 8

Pinus nigra



the two treatments, the type of growth was weak and the stems and leaves were pale green. The plants presented little interesting stem structure or lateral branch diversion. Aside from lack of visual appeal, poor growth and death under low humidity conditions would preclude the sale of any indoor plant, no matter how attractive, during the winter months. Consequently, it would seem that the value of small evergreen cuttings and seedlings would not be evident until the plants were more mature.

The broad leaved plants (Group II) responded well to the conditions of high humidity. The 100% survival rate (Table II) in either treatment was not unusual since they were sold commercially for indoor growth in winter and originally come from tropical habitats. While most of these plants responded to the conditions of high humidity (Figures 9 through 12), Peperomia exhibited almost complete absence of new leaf production (Figure 11) in high humidity although the plants were taller with larger and thicker leaves (Table IV). However, in every instance except Dracena, plants grown in high humidity not only made more linear growth but also produced larger, more numerous, and darker green foliage. However, Dracena produced more larger leaves of almost the same thickness in low humidity (Figure 12; Table IV). Yet, this plant was originally found by Godseff in Upper Guinea which is definitely tropical in habitat (Bailey, 1949).

Although anatomical investigation disclosed no significant structural differences, the stiff, leathery texture of leaves from both high and low humidity might be a factor resulting in similar growth. Habitat could possibly be the factor accounting for the lack of

Figure 9

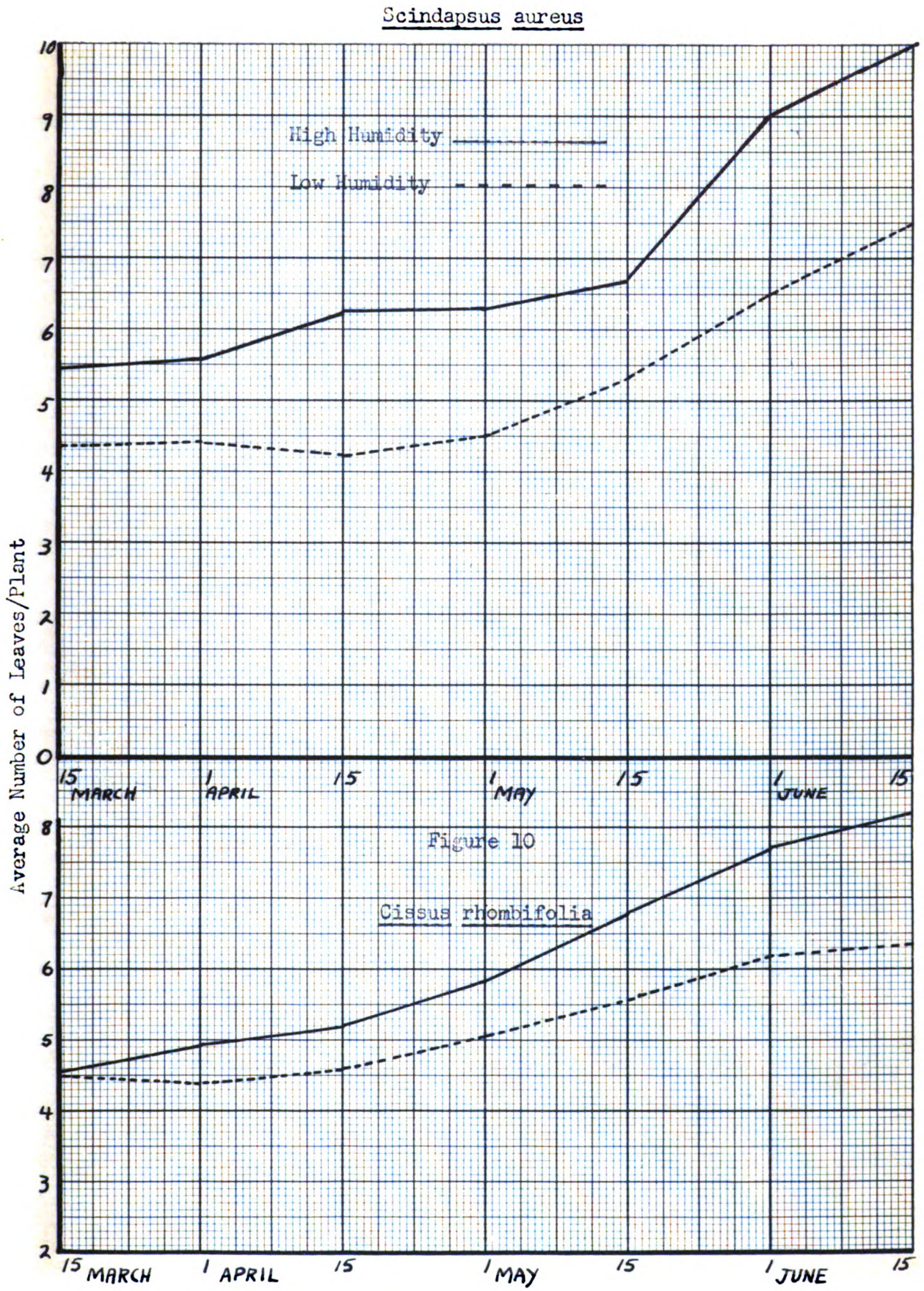


Figure 10

Figure 11

Peperomia obtusifolia variegata

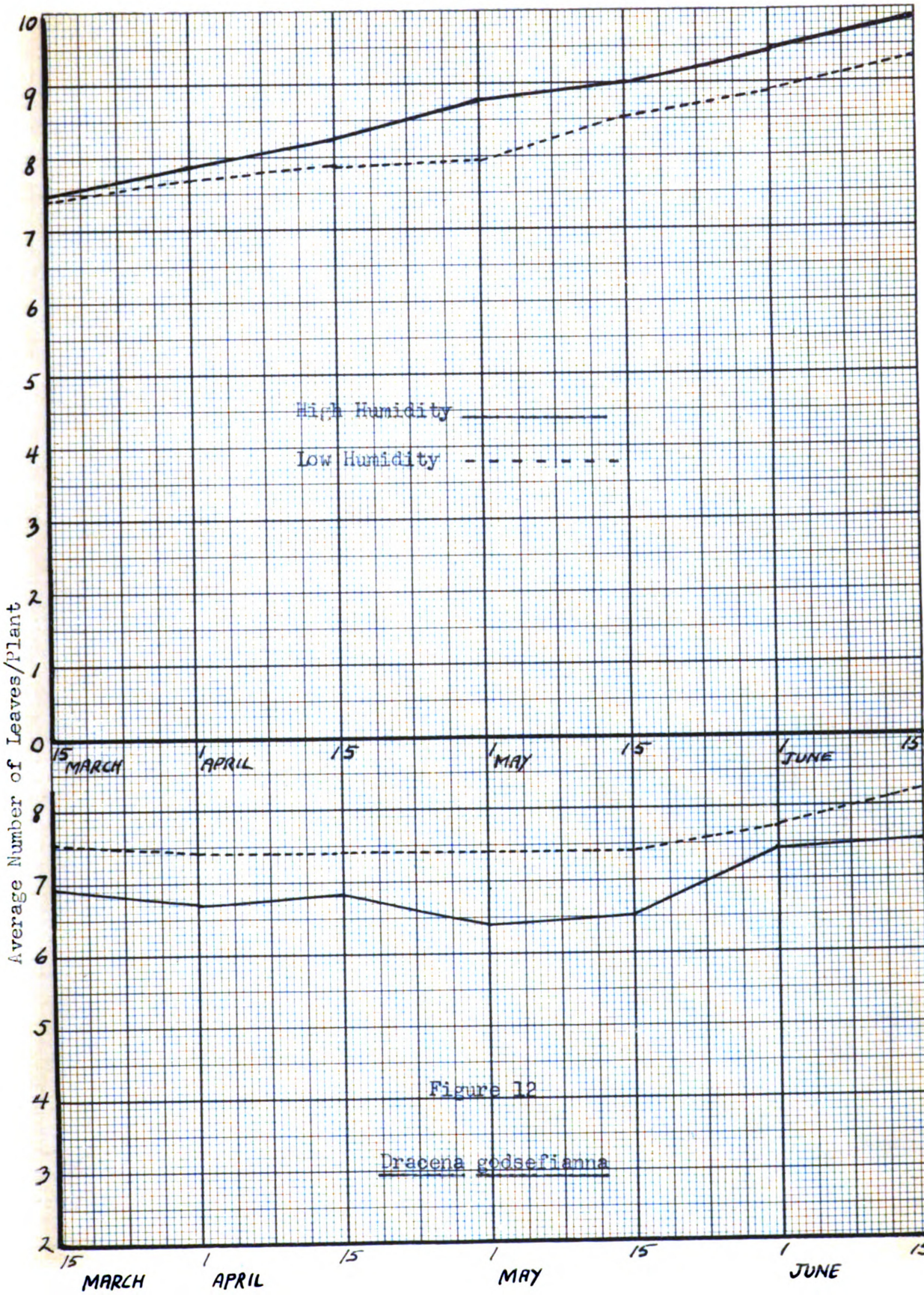


Figure 12

Dracena godsefianna

TABLE IV

FRESH WEIGHT; DRY WEIGHT; PLANT HEIGHT; LEAF AREA & THICKNESS

	Scindapsus aureus		Peperomia obtusifolia variegata		Dracena godsefianna		Cissus rhombifolia		Hepatica	
	Low	High	Low	High	Low	High	Low	High	Low	High
Fresh Weight (Ave. in Gms.)	12.8	22.9	18.2	20.1	3.2	3.2	3.4	5.5	11.4	11.5
Dry Weight (Ave. in Gms.)	1.4	2.1	.89	.92	.8	.8	.7	1.0	2.2	2.2
Ave. Plant Height (in inches	8.9 (to base of tallest leaf)	18.3	2.4 (to highest node)	3.4	3.6 (to top of tallest stem)	3.3	4.9 (to highest node)	9.1	-	-
Ave. Leaf Area ($cm.^2$/planimeter	1118.0	1642.0	800.0	950.0	638.0	597.0	759.0	1082.0	246.0	244.0
Ave. Leaf Thickness (in micra)	242.5	260.0	143.8	176.2	208.8	207.5	103.8	228.8	151.2	173.2

difference between growth of Hepatica (Table IV) in low and high humidity since it is a perennial native to temperate forests. It was evident that most plants grown indoors during winter would benefit by some means of increasing humidity in centrally heated homes. The possibility of fungal infestation would not be great provided there was movement of air.

Anatomy

In transection, the Taxus leaf was elliptical in shape (Figure 13). A single collateral endarch vascular bundle traversed the central bundle region, the xylem tracheids being oriented toward the adaxial side. An obscure bundle sheath separated the vascular and mesophyll tissue. The leaf was enclosed by a light cuticle.

The epidermis of leaves of plants from high humidity (Figure 13, A) consisted of a single row of fairly large rather thin walled cells. The cells varied in size and shape. Many large spherical cells which resembled bulliform cells were observed, especially at the bundle region of the abaxial surface. Conspicuous deposits of deeply staining granular material resembling tannin were common in all epidermal cells except the bulliform type cells. The sunken xeric type stomata were protected by arching subsidiary cells over the guard cells. Subtending the epidermis was a single layer of hypodermis. The cells had abundant protoplasts with large nuclei and numerous chloroplasts but were without evident wall thickenings. The mesophyll cells were parenchymatous and more or less irregular in size and shape, varying from spherical to polyhedral. Chloroplasts and nuclei were prominent as were deeply

staining granular inclusions which resembled those found in the epidermis. Intercellular spaces were large and extensive. As is characteristic of the genus (DeBary, 1884), no dermal glands, resin canals, or other internal secretory resevoirs were observed.

The vein of the leaf was surrounded by an irregular layer of cells which had peripheral walls of greater length than the innermost walls. The fibrovascular strand consisted of a one to several celled serpentine row of extremely thick walled, angular tracheids which adjoined a two to three celled layer of thin walled phloem cells on its lower periphery. These phloem cells were squarish and hexagonal in shape, being located in the approximate center of the vascular bundle and the leaf. Cytoplasm was dense with very prominent nuclei, some of which occupied most of the cell lumen. Immediately subtending the phloem was a three to five celled layer of collenchyma cells.

A single layer of epidermal cells protected leaves of plants from low humidity (Figure 13, B). A rather heavy cuticle covered most of the cells. Pyramidal cap-like peripheral cell walls were characteristic as in leaves from high humidity. Elongated hexagonal cells were prevalent on the adaxial epidermal surface with larger bulliform type spherical cells at the bundle region and tips of the leaf. These cells were also present at the abaxial bundle region although they were smaller and more squarish. Tannin like deposits were observed in all epidermal cells except the bulliform type cells. A definite hypodermal layer of smaller hexagonal cells subtended the abaxial epidermal layer. Cells of the adaxial hypodermis were elongated parallel to the leaf blade surface and so were more rectangular than overlying epidermal cells

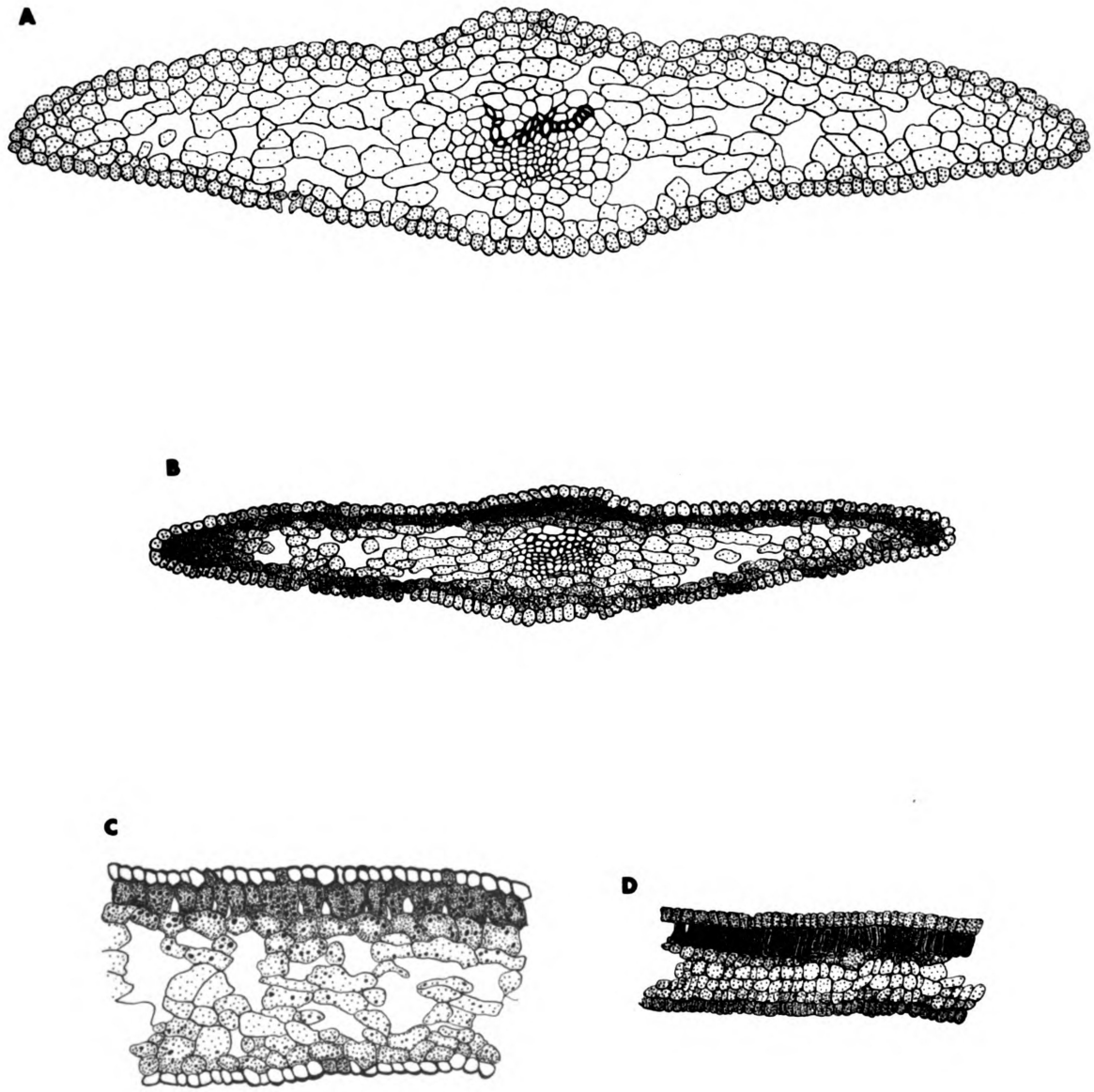


Figure 13

A - Transection of Taxus cuspidata capitata leaves in high humidity

B - " " " " " " " low humidity

C - " " Cissus rhombifolia " " high humidity

D - " " " " " " low humidity

as in leaves from high humidity. No schlerenchyma or wall thickenings of any kind were observed. Protoplasts were densely stained with many chloroplasts and prominent nuclei. Deposits resembling tannin were common. The remainder of the mesophyll was uniform with cells of varied sizes and shapes, ranging from spherical to polyhedral. Very prominent nuclei and extremely abundant chloroplasts were evident. Intercellular spaces were fairly extensive but with densely compacted cells at the central bundle region and tips of the leaf.

A fairly well defined bundle sheath surrounded the vascular bundle region. The large cells contained prominent nuclei and irregular starch grains. The vein of the leaf consisted of the central vascular elements surrounded by laterally and adaxially extending parenchymatous transfusion tissue.

The Cissus leaf in transection was bifacial or dorsiventral with distinct palisade and spongy mesophyll development, protected by a uniseriate epidermis.

Plants from high humidity were protected by a single epidermal layer (Figure 13, C). A thick cuticle completely covered cells on the adaxial surface while abaxial cells had thickened outer walls with less deposition on radial and inner walls. The rounded hexagonal epidermal cells possessed sharp angles only on inner adaxial cell walls and to a much lesser extent on peripheral walls of abaxial cells. The general shape of guard cells was oval in transection with thickened walls above the stomatal pore and between the pore and substomatal chamber. These projections (horn-like structures) were evident on the upper and lower sides of the walls facing the stomatal aperture (i.e., the front

walls). Thin hinges in the wall occurred on the entire back wall and at the mid-point of the front wall.

The single row of thin walled palisade parenchyma cells were elongated at right angles to the leaf surface and were more or less conical with tapered side walls. Walls adjoining spongy mesophyll were shorter and straighter than the sharply serrated upper walls adjoining adaxial epidermal cells. The palisade arrangement allowed room for fairly large lacunar air spaces. Numerous large spherical chloroplasts were usually oriented near the side walls. Thin walled spongy mesophyll cells varied in size and shape. Ovoid to spherical chloroplasts were more numerous in cells adjacent to palisade parenchyma. Intercellular spaces often extended from one epidermal surface to the other.

Leaves of plants from low humidity possessed a uniseriate layer of rectangular epidermal cells (Figure 13, D). Their long axes were oriented at right angles to the leaf blade surface. Cells of the adaxial epidermal surface were longer and usually narrower than the abaxial cells.

The palisade mesophyll consisted of two layers of cells. Long, thin, deeply staining palisade cells subtended the adaxial epidermis. Cells of the lower row were reduced in length. The palisade layers were densely compacted as were the four to five rows of squarish to spherical spongy mesophyll cells. These rows were oriented obliquely parallel to the leaf blade surface. Chloroplasts were numerous but more prevalent near the epidermal surfaces. Intercellular spaces were not observed.

APPLICATION OF RESULTS

Anatomical Agreement

Cissus leaves from high humidity had a greater number of larger chloroplasts both in the palisade and spongy mesophyll than plants grown in low humidity (Figure 13, C and D). Much greater photosynthesizing capacity was therefore to be expected, especially considering that plants from high humidity usually produced larger and more numerous leaves (Table IV). This would tend to offset any reduction in quality and intensity of light, either from the plastic covering or from condensation of moisture on it. Moreover, loosely compacted palisade and spongy mesophyll with large intercellular spaces were clearly characteristic of Cissus as well as the uniform mesophyll of Taxus leaves grown in high humidity (Figure 13, A and C). Conversely, plants from low humidity exhibited small celled, very closely compacted mesophyll with correspondingly greatly reduced intercellular spaces (Figure 13, B and D).

Anatomical Difference

There were, however, significant deviations in anatomical effects from those reported by others. Most outstanding were the greater thickness of leaves grown in high humidity with consequent dry weight increases in most cases (Tables III and IV) and the absence or slight development of a thick epidermal cuticle on Cissus and Taxus leaves from plants grown in low humidity (Figure 13, B and D). In fact,

Cissus leaves from high humidity were covered with a thick cuticle on both surfaces (Figure 13, C). Another difference was the lack of wall thickening in cells of plants from low humidity. For example, sclerenchyma was lacking in the hypodermal layer of Taxus cuspidata capitata leaves in low humidity (Figure 13, B). Determination of the number of stomata per unit of leaf surface area was not attempted.

Transpiration

If more compact chlorenchyma did present an effective obstacle to transpiration (Pool, 1923), reduced transpiration was to be expected. On the other hand, should this compactness result in greater internal evaporative leaf surface area, more transpiration would be anticipated, according to Turrell (1936). Moreover, leaves transpired at a greater rate and even into a saturated atmosphere in sunlight (Briggs and Shantz, 1915; Henderson, 1926). This was due to absorption of infra-red and ultra-violet radiation in addition to heat energy from visible sunlight by the leaves, as well as their heat of respiration, which resulted in higher leaf than surrounding air temperatures. It is further evident from Table I that day temperature of the high humidity chambers averaged about 4°F. higher than in low humidity. This reflected the heating effect of the transparent cover and in combination with high humidity probably also led to higher leaf temperatures and resulting greater differences between leaf and air temperatures in sunlight (Moreland, 1937).

High humidity in diffuse light would have a similar effect (Henderson, 1926). These differences would be accentuated in the still

air of the enclosed atmosphere of the high humidity chambers (Ehlers, 1915; Loreland, 1937), a condition which presumably would lead to an increased transpiration rate as a result of consequent greater vaporization of water within the leaf at least during the day.

This effect may be reversed and reduce transpiration in diffused light or darkness when leaf temperatures lowered as a consequence of heat radiation to space. However, either determinant of transpiration could be modified by the absorption lag created by the resistance to water movement in the living cells of the root (Kramer, 1938), a lag which supposedly accounted for the intake of water vapor from a saturated atmosphere (Thut, 1938). Consequently, if the water content of the leaf was thereby raised, an increase in transpiration in high humidity might be expected, considering the importance that some writers have attached to foliar water content and transpiration rate (Livingston and Brown, 1912; Knight, 1917; Henderson, 1926).

The rate of water loss became greatly retarded below 60% relative humidity or 68°F., according to Bialoglowski (1935). Assuming that all the aforementioned stimulating influences on transpiration were valid and that leaves in high humidity did transpire more, there might be a direct effect upon growth. It would depend upon the resolution of the controversial relationship between transpiration and the absorption of various mineral salts by the plant. Wright (1939) devised a technique that supposedly offset plant metabolism effects on mineral absorption. He concluded that there was a correspondence between increase in transpiration rate and increase in uptake of phosphorus, calcium, potassium, and nitrate ions. He was supported in this

conclusion by several other workers (Haas and Reed, 1927; Hitchcock and Zimmerman, 1935; Freeland, 1936, 1937). On the other hand, earlier investigators have defended the converse proposition that different transpiration rates have no effect upon absorption of mineral salts (Hasselbring, 1914; Muenscher, 1915; Kisselbach, 1916).

If this is true, high transpiration rate of plants in high humidity is of no use in explaining growth differences. However, there is just as much justification for maintaining that the opposite is true. Thus, by transpiring more, plants in high humidity are able to absorb more mineral salts and thereby synthesize more water soluble organic proteins, the elaboration of which entails carbohydrate depletion. In fact, the growth stimulating effect of increasing the amount of nitrate in nutrient solution has been attributed to the depletion of carbohydrates in the top, resulting in more growth (Turner, 1922). Furthermore, thickness of cuticle was not found to have any correlation with rate of transpiration for apple fruits (Pieniazek, 1944). This might mean that the heavy layer of deposition on both epidermal surfaces of Cissus leaves in high humidity (Figure 13, C) would have no deterrent effect on transpiration.

Decrease in dry weight (carbohydrate percentage) followed by hydrolysis of proteins (Nightingale and Robbins, 1928; Nightingale and Schermerhorn, 1928; Nightingale, Schermerhorn, and Robbins, 1928, 1930; Pearsall and Ewing, 1929; Nightingale, 1933) and increased growth has been postulated as accounting for rapid growth in high humidity (Nightingale and Mitchell, 1934). In fact, high dry matter content has been cited as a common low humidity effect (Nightingale et al; Pearsall

and Ewing; Nightingale). Yet, in the present experiment dry weight in high humidity was in one instance almost double that in low humidity (Scindapsus aureus, Table IV). It will be noticed that increased dry weight in high humidity was correlated with more leaves, taller plants, and greater leaf area and thickness, at least for all Group II plants (Table IV).

When dry weight was reduced in high humidity (Dracena godsefianna), correspondingly fewer leaves, shorter plants, and less leaf area and thickness were produced. It is difficult to rationalize how increased dry weight in high humidity may account for better growth if a decrease in dry weight is supposedly associated with better growth of plants in high humidity.

Resolution depends upon the thicker leaves of plants grown in higher humidity which indicates that more dry matter is to be expected. In fact, Pickett (1937) observed that a larger gain in total dry matter per unit area may be produced by leaves with prominent intercellular spaces. Thicker leaves also mean more photosynthetic activity and production of carbohydrates. Assuming that transpiration is maintained at a high enough rate to assure that a constant supply of mineral salts reaches the top of plants in high humidity, it is conceivable that the usual metabolic activity of the leaves (Turner, 1922) would lead to a more rapid growth rate than for plants in low humidity with fewer chloroplasts and reduced transpiration.

SUMMARY

In order to determine the effects of humidity on the growth of plants, 80 tropical foliage plants (4 species) and 45 young evergreen cuttings and seedlings (5 species) were grown for six months in atmospheres of low and high humidity. Half of the plants were placed in chambers covered with transparent plastic ("Saran-Wrap"). The remainder were left exposed in identical chambers.

These chambers were located in a laboratory facing an east window in which temperatures and humidities averaged 74.6°F. and 34.4%, respectively. Average temperatures and relative humidities of 75.2°F. and 91.9%, respectively, were maintained in the covered chambers. All evergreens produced thicker needle leaves in high humidity but a definite growth response in terms of new growth made was observed for only one species.

A definite growth response in high humidity was obtained for most of the foliage plants (with one exception) in terms of greater production of thicker and larger new leaves and taller plants with glossy dark green foliage. Although none of the plants died in low humidity, it was evident that some means of increasing humidity in the home, at least during winter, must be provided before foliage plants can attain their maximum growth. Attention must further be directed to the greater amount of water required by plants growing in low humidity. Failure to prevent extreme soil dryness due to excessive water loss from the sides of clay pots and the soil surface, in addition to

transpiration, led to tissue desiccation and death of a majority of evergreens in low humidity. Death in high humidity was probably pathological since fungal mycelia and spores were observed on the needles and stems of dying plants. Surviving plants were not attractive in appearance. New growth in both high and low humidity was feathery and often insignificant. It was suggested that a marketing potential for these plants exists only after they had matured.

Better growth in high humidity has been attributed to increased transpiration and mineral salt uptake inasmuch as anatomical investigation disclosed no significant differences in leaf structure other than the compact cell arrangement of leaves from low humidity. This in itself may act as a deterrent to transpiration but there were more definite indications that leaves in high humidity transpired more. For example, greater leaf water content, difference between leaf and air temperature, or lack of surrounding air movement led to a higher rate of transpiration. This might have increased the transport of mineral salts resulting in the synthesis of proteins and depleted sugar and starch reserves in leaves of plants in high humidity. The resultant decrease in dry weight was accompanied by proteolysis and release of energy for rapid growth in high humidity.

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Date Due
