 Shoot Growth and Mineral Composition of Leaves and Fruits of Apple as Affected by Relative Air Humidity

By

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Abstract

Shoot growth and water consumption of potted Golden Delicious trees were studied under a controlled environment with respect to two levels of air humidity, soil moisture content, and the availability of nitrogen. In the high-N treatment, high air humidity and high soil moisture content promoted growth; at the low-N level, growth did not respond to the treatments. Water consumption was enhanced at low air humidity but was not affected by the moisture content of the soil.

In potted fruit-bearing Cox's Orange Pippin trees exposed to two levels of air humidity, low humidity reduced shoot growth and, but to a much lower degree, fruit growth. It increased the spur-leaf levels of N, Mg, and, for part of the experimental period, K and Ca, but affected hardly the mineral level in fruits. It is concluded that the amount of the minerals reaching the fruit is determined by the relative importance of the xylem influx during the first few weeks after fruit set and the phloem influx occurring throughout. It is suggested that the xylem supply of the various minerals does not differ greatly; it is probably the main way for the influx of Ca, but for N, K, Mg, and P the phloem influx is completely dominating.

Introduction

The effect of air humidity on the physiology of plants has received relatively little attention, and almost no data are available on trees studied in long-term experiments. It may be expected that via its effect on transpiration, air humidity will have an influence on the amounts of the minerals translocated in the transpiration stream from the roots to the above-ground parts. Information from trees is needed on this point, especially since the occurrence of storage disorders in fruits, such as bitter pit in apple, appears to be correlated with mineral deficiencies (Faust and Shear 1968, Bangerth 1969).

In the present investigation, which was carried out in controlled-environment rooms, a preliminary experiment was performed to examine the effect on shoot growth of air humidity in combination with soil moisture content and nitrogen application. In a second experiment attention was focused on the mineral composition of leaves and fruits as influenced by air humidity.

Material and Methods

Plant material

Experiment 1. In April of 1969, 56 one-year-old Golden Delicious trees (rootstock M IX) were planted in pots provided with sand (capacity 12 litres) and were allowed to grow in the open until the next spring. In June of 1969 each tree received a dressing of 14 g Ca(NO₃)₂. In the middle of May in 1970, the trees were transferred to two controlled-environment rooms, one maintained at "high" (about 75 % during the day, almost 100 % during the night) and the other one at "low" air humidity (45-55 % throughout). Temperature (19°C during the day, 14°C at night), day length (16 hours), and light intensity were equal in both rooms. The illumination consisted of fluorescent lamps (Philips TLM 120W/33, about 1100 W/m²) and some incandescent lamps (about 60 W/m²) giving an intensity of about 25,000 lux at the top of the trees at the start of the experiment. In each room, 4 treatments of 7 trees each were maintained, i.e. two levels of soil moisture content ("high": 18 % by weight, and "low": 10 %) and two levels of nitrogen (+N: 7 g Ca(NO₃)₂ per tree and -N: no nitrogen added). Soil moisture content was controlled by a frequent weighing and watering of the pots. All trees also received a moderate application of the other essential minerals i.e. 0.7 g KH₂PO₄, 0.7 g MgSO₄·7H₂O, 0.007 g MnSO₄·4H₂O, 0.007 g H₃BO₃, 0.016 g CuSO₄·5H₂O, and 0.016 g ZnSO₄·7H₂O. At full bloom, all
Table 1. The effect of the various treatments in Experiments 1 and 2 on mean shoot growth, number of shoots, shoot length and total water consumption. High relative humidity (RH) = about 75 % during the day, almost 100 % at night; low RH = 45-55 % throughout. High soil moisture content (SMC) = 18 %; low SMC = 10 %.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shoot growth/tree cm</th>
<th>Number of shoots/tree</th>
<th>Shoot length cm</th>
<th>Total water consumption/tree, l</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High RH, low SMC, +N</td>
<td>142</td>
<td>9.5</td>
<td>14.5</td>
<td>6.5</td>
</tr>
<tr>
<td>High RH, low SMC, -N</td>
<td>78</td>
<td>7.7</td>
<td>10.2</td>
<td>8.2</td>
</tr>
<tr>
<td>High RH, high SMC, +N</td>
<td>256</td>
<td>12.2</td>
<td>17.1</td>
<td>10.7</td>
</tr>
<tr>
<td>High RH, high SMC, -N</td>
<td>82</td>
<td>7.7</td>
<td>10.5</td>
<td>9.5</td>
</tr>
<tr>
<td>Low RH, low SMC, +N</td>
<td>69</td>
<td>7.5</td>
<td>9.2</td>
<td>10.3</td>
</tr>
<tr>
<td>Low RH, low SMC, -N</td>
<td>59</td>
<td>7.5</td>
<td>7.8</td>
<td>15.8</td>
</tr>
<tr>
<td>Low RH, high SMC, +N</td>
<td>128</td>
<td>9.5</td>
<td>12.1</td>
<td>16.9</td>
</tr>
<tr>
<td>Low RH, high SMC, -N</td>
<td>46</td>
<td>5.7</td>
<td>8.4</td>
<td>15.1</td>
</tr>
<tr>
<td>LSD 5 %</td>
<td>58</td>
<td>3.4</td>
<td>3.9</td>
<td>3.8</td>
</tr>
<tr>
<td>LSD 1 %</td>
<td>76</td>
<td>4.4</td>
<td>5.6</td>
<td>5.1</td>
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<tr>
<td>Experiment 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High RH</td>
<td>289</td>
<td>11.7</td>
<td>23.2</td>
<td>40.1</td>
</tr>
<tr>
<td>Low RH</td>
<td>134</td>
<td>8.3</td>
<td>17.0</td>
<td>54.1</td>
</tr>
</tbody>
</table>

1 Differ significantly at the 1 % level.
2 Do not differ significantly.
3 Differ significantly at the 5 % level.

trees were deblossomed. The experiment was terminated at the end of July, when shoot growth had ceased. It should be stressed that the predetermined moisture content of the soil was taken as an average value of the entire soil mass, and that marked variations may have occurred inside the pots.

Experiment 2. In December of 1970, 30 three-year-old Cox's Orange Pippin trees (rootstock M IX) grown under rather poor nutritional conditions, were planted in pots (capacity 32 litres) containing a mixture of sand and pot soil. In February of 1971, the trees were divided in two equal groups and transferred to the controlled-environment rooms, in which exactly the same conditions were maintained as in Experiment 1. From the end of February, at 4-week intervals each tree was given a total of 16 g Ca(NO₃)₂. An additional application of essential minerals threefold the amounts as were supplied in Experiment 1 was also given. The moisture content of the soil was kept constant at 33 % by weight by frequent weighing and watering. The trees flowered abundantly. All flowers were hand-pollinated, which resulted in a good fruit set. Only a few fruits dropped during the experimental period. The mean number of fruits per tree did not differ greatly (9.1 and 8.4 at high and low humidity, respectively). The experiment was terminated early in July, when the fruits were ready for picking. Throughout the experimental period, samples of spur leaves, fruits, and, during a limited period, full-grown leaves from the basal parts of shoots were taken. Each sample consisted of 15 leaves or fruits. Fresh and dry weight were determined immediately after sampling. All samples were analysed for N, K, Ca, Mg, and P.

Methods of analysis

As concerns N, K, Mg, and P, the methods were the same for leaves and fruits. After digestion in sulphuric acid according to Lindner and Harley (1942), a micro-Kjeldahl method was used for N. K was estimated by flame-photometer, Mg colorimetrically with titanyellow (Van Schouwenburg 1965), and P also colorimetrically with ammoniummolybdate. The flame-photometer method was used for Ca in leaves, whereas, because of the low concentration in fruits, the determination of Ca in fruits was done titrimetrically as oxalate after drying, following by dissolving in hydrochloric acid. All determinations were done in duplicate, the differences between duplicates for N and K being less than 5 % and for Mg, Ca, and P less than 10 %.

Results

Growth. Shoot growth was favoured considerably under high air humidity and high soil moisture content when nitrogen was applied, but no significant effect could be shown in the unfertilized trees (Table 1, Experiment 1). The data on the number of shoots per tree and shoot length showed a similar pattern, but the differences between treatments were only significant in a few cases.

The effect of air humidity was also very clear-cut in
Experiment 2. Total growth, shoot number, and shoot length increased under conditions of high humidity (Table 1). Leaf size was somewhat lower at low humidity but the dry weight percentage was the same at the two humidity levels. Apart from during the first few weeks, when leaf growth occurred, the size and the fresh and dry weights of the sample leaves remained almost constant throughout.

In spite of the weaker shoot growth, water consumption in the two experiments was greater at the low humidity level (Table 1). The effect of soil moisture content on water consumption in Experiment 1 was indirect, through the effect on shoot vigour, since it was only observed in the +N treatments where growth was stimulated at the high moisture level. In proportion to the growth produced, furthermore, the high-N trees consumed much less water than the unfertilized trees.

With respect to fruit growth, Figure 1 shows that both fresh weight and dry weight were slightly reduced at the low air humidity. Dry weight as a percentage of fresh weight was about 0.8 % lower at high than at low humidity throughout, and increased slightly from about 13 % in April to about 17 % in July (complete data not given because of space limitations).

Mineral composition of leaves and fruits. The effect of air humidity on the mineral content of the leaves (on a dry weight basis) was not very pronounced (Figure 2). Spur-leaf levels of N and Mg were highest throughout at low humidity, whereas for K this was only true at the beginning, and for Ca at the end of the experimental period. In relation to time, N decreased gradually to rather low values, but K, at least at high humidity, and Ca both increased in the first few months to reach a more or less constant level. The Mg content
Figure 3. Amounts of N, K, Ca, Mg, and P per fruit at high (solid line) and low (dashed line) air humidity, throughout the experimental period.

showed little variation, but tended to decrease slightly during the last few weeks at low humidity.

Variations in the size and quality of shoot leaves disturbed sampling; therefore, the data for shoot leaves show a large spread and cannot be considered very reliable. Nevertheless, they fit in rather well with the results for spur leaves.

Because of the excessive spread, the data for P are not given.

Since the dry weight of the fruits, in contrast to that of the leaves, increased considerably during the experimental period, the analytical data for fruits are expressed as amounts per fruit (Figure 3). The various minerals increased readily, but the rate of increase was divergent. Particularly Ca remained at a low level, especially as compared with K and N. Nitrogen increased almost linearly with time, but K and Mg showed the same pattern as was found for dry and fresh weight (Figure 1); P occupied an intermediate position. Calcium levelled off at low humidity and even tended to decrease at high humidity. No other effects of air humidity were observed.

Discussion

The internal water balance of the plant as a whole is determined by the relative rates of absorption by the roots and loss via the transpiring leaves. Deficiency of water leads to reduction of growth (Meyer 1956, Barseh 1956, Kramer 1963). Since water deficits may be due to lack of water around the roots as well as to enhanced transpiration, the reduced growth found in the present experiment in the treatments with low soil moisture content and air humidity is according to expectation. However, the trees only responded to treatments when sufficient nitrogen was available. Obviously, the nitrogen level in the soil was the limiting factor for growth in the low-N treatments. The unfavourable effect of low soil moisture levels is confirmed by the results obtained in other studies on woody plants, made both under orchard conditions (Goode and Hyrysz 1970, black currant, Goode and Ingram 1971, apple) and in pots (Kongsrud 1969, apple, Cripps 1971, apple and black currant). Information on the effect of air humidity is contradictory and scarce, however, especially with respect to trees. In long-term experiments...
on cacao, Sale (1970) found a greater stem length but lower total dry weight at high than at low humidity. In contrast, in experiments carried out by Winneberger (1958) the growth of pear buds was completely inhibited at an extremely high humidity. For annuals the situation is also confused, but in general growth or dry weight increase was lowest at low humidities (Michael and Marschner 1962, Krizek et al. 1971).

With respect to the amounts of water consumed in the various treatments, it is remarkable that in proportion to the growth produced, the high-N trees used much less water than the unfertilized trees. This observation fits in with findings of Lüdders and Bünnemann (1970); and Delver (personal communication) also found in apple rootstocks that within certain limits there was a decrease of the ratio between water consumption and dry weight increase at increasing nitrogen levels in the soil. The explanation of this phenomenon is not clear. Since in apple root spread is better and the stem-to-root ratio is lower in poor soils than in fertile soils (Rogers and Head 1969), rooting might vary between treatments.

As only over-all growth was measured in this study and detailed observations were not done, the question of why shoot growth is reduced under conditions that induce water stress will not be discussed. It should be emphasized, however, that both fresh and dry growth of fruits showed much less response to treatments. This may be due to the fact that the water supply to leaves occurs entirely in the xylem, whereas, as shown by Wiersum (1966), xylem translocation of water to fruits of tomatoes and apple is only of importance during a few weeks following fruit set. Thereafter, in Wiersum's view, the fruit is apparently supplied with water via the phloem, as the solvent of the assimilates. Why internal differences of water stress affect phloem translocation of water so little is a matter of conjecture. It is known that, in agreement with the present data, the total of the assimilates reaching fruits is usually little influenced by water stress, but that the rate of movement and consequently the concentration may be quite different (Crafts and Crisp 1971).

It is generally accepted that minerals absorbed by the roots are carried up in the transpiration stream to the above-ground parts. As a consequence it may be expected that the amount of minerals in readily transpiring organs, such as leaves and to a lower degree fruits, is a function of the rate of water loss. Indeed, in short-term experiments it has been shown that transpiration promotes ion absorption (Brouwer 1965), but information from experiments of longer duration is almost unavailable. In the present experiment the enhanced transpiration seen at low humidity increased the level of N and Mg somewhat, and, for part of the season, that of K and Ca, in the leaves (Figure 2), but hardly influenced the mineral levels in fruits (Figure 3). However, apart from the first few samples, only full-grown leaves were analysed. It is quite possible that for young, growing leaves the effects would be more marked.

If the view of Wiersum (1966) mentioned above is correct, the amount of each mineral reaching the fruit is mainly determined by the relative importance of xylem influx during the first few weeks after fruit set and phloem influx occurring throughout. Experiments in which radio-isotopes were applied to leaves of bean plants, have shown that amongst others K, P (Bukovac and Wittwer 1957), and Mg (Steucek and Koontz 1970) are distributed to other parts of the plant; the mobility of Ca consistently appeared to be extremely low (Bukovac and Wittwer 1957, Biddulph et al. 1959). Efforts to increase the Ca level of apple fruits by Ca application to the leaves also failed (Wieneke 1967, 1969, Bangerth 1969), which was interpreted as supporting the hypothesis of Wiersum (1966), i.e. that the supply of Ca to the fruits is almost completely dependent on xylem transport occurring while the fruits are small. In the present study, however, in contrast to the findings of Kohl (1967), the amounts of Ca in the fruits did not level off before maturity was approached (Figure 3), which indicates that xylem influx was not completely eliminated or that a Ca flow via the phloem occurred to some degree. Wiersum et al. (1971) demonstrated phloem movement of Ca in inflorescence stalks of Yucca flaccida when Ca was applied in a high concentration to the base of the stalks.

The other minerals increased to much higher levels than Ca, which must be due to influx via the phloem, because in the xylem sap of apple the Ca, K, and N concentrations are almost equally high and the Mg and P concentrations even much lower (Pollard 1953, Wienke 1969, Jones 1971). It can be computed by combining Figures 1 and 3 that K and Mg increased almost linearly with dry weight, a fact that shows that the phloem influx completely overshadowed the xylem influx. It is in itself an indication for a link between assimilate on the one hand and K and Mg movement on the other. As a similar computation for N reveals that the relation between N level and dry weight is almost linear only in the range from 5 to 20 g and that N increases extra in the very small fruits. This extra increase might be due to a supply of nitrogenous compounds stored in the woody tissues since the previous autumn.

In view of the small effect of relative humidity on the movement of water and assimilate in the phloem, the lack of any marked effect on mineral influx into the fruits is not unexpected. Only for Ca, where the xylem supply dominates, could high transpiration have favoured influx at low humidity. This, however, must at the same time have enhanced the competition between leaves and fruits for water and minerals via the xylem. In the present experiment no evidence was obtained indicating an influence of humidity on the Ca level ex-
cept in almost full-grown fruits, where export tended to occur at high humidity but did not take place at low humidity. This confirms the view discussed by Wiersum (1966) and Bangerth (1969) that when the water supply to the fruits via the phloem exceeds the needs under conditions of low transpiration and retarded growth, backflow of water containing a little calcium may take place via the xylem.

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References

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