AVAILABILITY OF SOIL MOISTURE FOR ACTIVE ABSORPTION
IN DRYING SOIL.1

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There is considerable disagreement as to whether or not water is equally available to plants in drying soil over the entire range from field capacity to wilting percentage. Some workers have repeatedly stated that water is equally available over this range (5, 18, 23, 24) while considerable data have accumulated which indicate that physiological processes in plants are altered as a result of decreasing soil moisture content even before the onset of wilting (1, 2, 4, 6, 7, 12, 16, 21, 25). As indicated by KRAMER (15) some of this disagreement exists because of differences in soil moisture tension-soil moisture content relations for different textural grades of soil. In certain coarse-textured soils most of the water in the range from wilting percentage to field capacity is held with a tension of less than one atmosphere and probably most of it is readily available. In some fine-textured soils, however, less than half of the available water may be held with a force of less than one atmosphere, and water is withheld from plants with appreciably greater energy over the lower part of the available range than over the upper part. Near the wilting percentage a small decrease in moisture content effects an enormous increase in tension.

Data also are available which indicate that active absorption and root pressure specifically are depressed by low soil moisture contents above the wilting percentage. LITVINOV and GEBHARDT (17) have reported a qualitative correlation between drying of soil and cessation of exudation from stumps of detopped plants. Kramer (14) noted that removal of tops of unwilted herbaceous plants was not always followed by expected exudation. However, exudation usually began soon after the soil was watered. Working with coleus, sunflower and tomato, Kramer found that about 45% of the soil moisture between the moisture equivalent and the wilting percentage was unavailable to detopped plants. He concluded that the active absorption mechanism does not absorb against a diffusion pressure deficit greater than one or two atmospheres. The proportion of moisture in the “available range” over which exudation does not take place was essentially similar for clay, sand, and sandy loam. The uniformity of the results obtained indicated that the soil moisture content which limits exudation is determined predominantly by soil characteristics and not by plant characteristics. Using sunflower plants and a uniform, fertile sandy loam, McDERMOTT (19) found that within a range of moisture content just above the wilting per-

1 Contribution No. 781, Massachusetts Agricultural Experiment Station, Amherst, Massachusetts.
centage the detopped root systems exhibited negative exudation. As soil moisture content increased, the rate of negative exudation decreased, reached zero, and was followed by positive exudation which reached a maximum approximately at the moisture equivalent. At soil moisture contents higher than the moisture equivalent there was a decrease in exudation, and this was attributed to poor aeration and accompanying high carbon dioxide content. McDermott (19) found that an equation of the parabolic type expressing the relationship between the rate of exudation and soil moisture content best fitted the results obtained. He reported that about 60% of the soil moisture available to the whole plant when the soil was at the moisture equivalent was found to be unavailable to detopped root systems.

The present study was undertaken to extend the work of these investigators to include New England field soils of varying textural grades and species which had previously not been used as test plants. It is an investigation of the relationship between exudation from detopped plants and soil moisture content.

Materials and methods

Experiments were performed on tomato (Lycopersicon esculentum Mill.), tobacco (Nicotiana tabacum L.), corn (Zea mays L. var. indentata) and bean (Phaseolus vulgaris L.). The soils used were Merrimac Fine Sandy Loam and Suffield Silt obtained from fields on the University Farm, Amherst, Massachusetts. Results of a mechanical analysis by the pipette method (20), wilting percentages (determined with wheat plants), organic matter contents, and moisture equivalents are given in table I.

All plants were started in flats and later transplanted to 4-inch, porous clay pots. The plants were never more than 15 cm. tall at the time of transplanting. At the time of experimentation the plants were four to six

<table>
<thead>
<tr>
<th>TABLE I</th>
</tr>
</thead>
<tbody>
<tr>
<td>MECHANICAL ANALYSIS, ORGANIC MATTER CONTENTS, WILTING PERCENTAGES, AND MOISTURE EQUIVALENTS OF SOILS USED</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Per cent. of dry sample</th>
<th>Merrimac fine sandy loam</th>
<th>Suffield silt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clay</td>
<td>0.002 mm.</td>
<td>9.79</td>
</tr>
<tr>
<td>Silt</td>
<td>0.002-0.05 mm.</td>
<td>49.89</td>
</tr>
<tr>
<td>Fine gravel</td>
<td>retained on 1 mm. sieve</td>
<td>0.05</td>
</tr>
<tr>
<td>Coarse sand</td>
<td>retained on 0.5 mm. sieve</td>
<td>1.02</td>
</tr>
<tr>
<td>Medium sand</td>
<td>retained on 60 mesh sieve</td>
<td>1.14</td>
</tr>
<tr>
<td>Fine sand</td>
<td>retained on 140 mesh sieve</td>
<td>9.04</td>
</tr>
<tr>
<td>Very fine sand</td>
<td>retained on 300 mesh sieve</td>
<td>29.07</td>
</tr>
<tr>
<td>Total mineral fraction</td>
<td>100.00</td>
<td>100.00</td>
</tr>
<tr>
<td>Organic matter</td>
<td>1.91</td>
<td>3.49</td>
</tr>
<tr>
<td>Moisture equivalent</td>
<td>17.38</td>
<td>33.82</td>
</tr>
<tr>
<td>Wilting percentage</td>
<td>4.50</td>
<td>12.35</td>
</tr>
</tbody>
</table>
weeks old and all were at least 30 cm. tall. From the time of transplanting until actually detopped they were watered occasionally with a complete nutrient solution of low osmotic pressure (approximately 0.5 atmos.). Better root distribution was obtained in Merrimac sandy loam but in both soils roots were generally well distributed throughout the soil mass.

On the evening prior to the day on which determinations of exudation rates were to be made, a group of plants selected at random from those available was brought from the greenhouse to the laboratory. If at this time differences in soil moisture content of individual pots were not apparent, unequal amounts of water were added to the soil of the test plants. This assured a greater range for each set of determinations (11). None of the pots was allowed to dry down to a point at which any wilting was evident. The pots were then placed in metal containers, covered with oil-cloth to prevent evaporation from the soil surface, and allowed to stand overnight in the laboratory.

The following morning the top of each test plant was removed about four to six cm. above the soil surface with a sharp razor. A graduated 10-ml. pipette was attached to each stump by means of close-fitting rubber tubing and grafting wax. Enough water was placed in each pipette to make a meniscus easily visible. Suction was applied for a short time to remove any air trapped in the stump, roots, or connections. An initial observation of water volume was recorded in milliliters for each pipette. At the end of a 4-hour period a final reading was made.

All experiments were started at approximately 9:30 a.m. It took approximately one hour to set up 15 plants. Therefore exudation was being measured over a period when it is at a maximum. According to Grosenbacher (8, 9) the period of maximum exudation is at approximately noon. Hagan (10) found minimum negative exudation at this time.

After the 4-hour reading had been recorded, the pipettes were removed and the soil of each pot was sampled for moisture content. A sample of 70 to 80 grams of soil was taken from each pot with a small spatula. As many root fragments as possible were removed. The samples were weighed and oven-dried at 105° C for 48 hours. The moisture content expressed as percentage of dry weight was then calculated.

**Results and discussion**

The rates of exudation plotted against the corresponding soil moisture content are shown in figures 1, 2, 3, and 4. The parabolic curve was derived by the least square technique (22). However, in order to reduce the large number of calculations necessary if each set of values was tabulated individually, averages for both exudation and soil moisture were used in deriving the equations for the eight curves. The equations were differentiated to ascertain the theoretical moisture content at which exudation was a maximum. Equations and theoretical moisture content of maximum exudation for all plants and soil types are given in table II.
### TABLE II

RELATIONS BETWEEN SOIL MOISTURE CONTENT AND RATE OF EXUDATION AND AVAILABILITY OF WATER FOR ACTIVE ABSORPTION*

<table>
<thead>
<tr>
<th>Plant</th>
<th>No. of plants used</th>
<th>No. of grouped headings</th>
<th>Theoretical per cent. moisture at maximum exudation</th>
<th>Per cent. of water in range between W.P. and M.E. which is available to detopped roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merrimac Fine Sandy Loam</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bean</td>
<td>$Y = -0.4374 + 0.0408X - 0.00035X^2$</td>
<td>50</td>
<td>14</td>
<td>58.4</td>
</tr>
<tr>
<td>Corn</td>
<td>$Y = -0.7919 + 0.0802X - 0.00084X^2$</td>
<td>55</td>
<td>15</td>
<td>47.9</td>
</tr>
<tr>
<td>Tobacco</td>
<td>$Y = -1.1525 + 0.1262X - 0.00256X^2$</td>
<td>55</td>
<td>16</td>
<td>24.6</td>
</tr>
<tr>
<td>Tomato</td>
<td>$Y = -4.1955 + 0.3533X - 0.00615X^2$</td>
<td>122</td>
<td>20</td>
<td>28.7</td>
</tr>
<tr>
<td>Suffield Silt</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bean</td>
<td>$Y = -2.5854 + 0.1376X - 0.00166X^2$</td>
<td>54</td>
<td>13</td>
<td>41.2</td>
</tr>
<tr>
<td>Corn</td>
<td>$Y = -8.0468 + 0.4782X - 0.00632X^2$</td>
<td>54</td>
<td>13</td>
<td>37.8</td>
</tr>
<tr>
<td>Tobacco</td>
<td>$Y = -1.2437 + 0.0456X - 0.00028X^2$</td>
<td>60</td>
<td>17</td>
<td>80.6</td>
</tr>
<tr>
<td>Tomato</td>
<td>$Y = -4.3747 + 0.0194X - 0.00162X^2$</td>
<td>73</td>
<td>14</td>
<td>59.9</td>
</tr>
</tbody>
</table>

* $Y = \text{ml. exudation for 4-hour period and } X = \text{soil moisture content on dry weight basis.}
Curves for active absorption for various species in both silt and loam are of the same general type. The curves for silt, however, begin at higher soil moisture contents than those of loam because of the higher water-holding capacity of the silt. Figures 1, 2, 3, and 4 indicate that root pressure is not positive throughout the range from moisture equivalent to wilting percentage. As soil moisture content increases the amount of negative exudation decreases until it reaches zero. With a further increase in soil moisture, exudation becomes positive and eventually reaches a maximum.

**Fig. 1.** Milliliters of exudation plotted against respective soil moisture contents for bean plants in silt and loam.

**Fig. 2.** Milliliters of exudation plotted against respective soil moisture contents for corn plants in silt and loam.

Maximum positive exudation, however, in all cases occurred when soil moisture content was higher than the moisture equivalent. This observation is not in agreement with the data of McDermott (19) for sunflowers in a sandy loam. McDermott found that a maximum was reached at about the moisture equivalent. Reduction in positive rates of exudation for several of the species at excessively high soil moisture content is probably due to decreased aeration and an increase in the concentration of carbon dioxide around the roots (3, 13). It seems likely that the moisture equivalents of Merrimac Fine Sandy Loam and Suffield Silt are not accurate estimates of
their respective field capacities which are probably higher. Since in every case the maximum rates of exudation were at soil moisture contents in excess of moisture equivalent, apparently aeration was not limiting near the moisture equivalent. This indicates that capillary capacity was not exceeded until moisture content was considerably higher than the moisture equivalent. McDermott's (19) determinations of moisture equivalent were probably a better estimate of the field capacity of his soil, and this observation is supported by the fact that he observed effects of decreased aeration at about the moisture equivalent. The discrepancies in the actual percentage of water available as reported by Kramer (14) and McDermott (19) may be partly explained by the fact that although moisture equivalent is often used as an estimate of the upper limit of available moisture, it is very often not an adequate estimate of field capacity which is essentially equal to capillary capacity (26). In certain soils field capacity may be twice moisture equivalent (15).

Figures 1, 2, 3, and 4 indicate that root pressure is negligible, or in fact, negative when soil moisture content is in the lower 60% of the range between wilting percentage and moisture equivalent. In sandy loam, with the excep-
tion of tomato, approximately 58% of soil moisture available to the whole plant when the soil is at the moisture equivalent is not available to the detopped root system. In the calculated curve for tomato in loam (fig. 4) the positive slope is increased by the several exceedingly high negative values at high soil moisture content. If the erratic negative values are disregarded, the curve would cross the zero line for exudation at about 11% soil moisture content. This adjusted curve would then give one comparable to those of the other three species for the percentage of soil moisture available to the detopped plant for exudation.

In silt, tobacco showed very little exudation at any moisture content (fig. 3). Tobacco exhibited positive exudation only in the upper 1.26% of the range of moisture between the moisture equivalent and wilting percentage. Corn (fig. 2) actively absorbed water in approximately 40% of the available range.

A total of 60% of soil moisture in the range from wilting percentage to moisture equivalent appears to be the minimum proportion that is not available to detopped root systems. The results of the present study are in general agreement with the findings of Kramer and McDermott in demonstrating that when soil moisture is depleted to the lower part of the available range, active absorption is depressed. Somewhat less moisture was found to be available for active absorption than reported by Kramer and in a few cases less than reported by McDermott. These differences may be due to the fact that moisture equivalent is used to estimate the upper limit of available moisture. The relationship of moisture equivalent to capillary capacity of the different soils used is not clarified although McDermott's data and those of the present study suggest that the degree of reliability concerned is different.

A statistical analysis indicates significant differences in exudation as conditioned by soil types and species. For loam there is a highly significant difference between corn and all other species. Bean shows a significant difference at the 5% level when compared with tomato. The indication is that the observed differences would be due to chance not more than five times out of 100. However, no statistically significant differences were shown to exist between bean and tobacco or tobacco and tomato.

When the same type of analysis of variance is made for plants grown in silt, tobacco when compared with tomato yields no difference of statistical significance. Tobacco did, however, show a statistical difference beyond the 1% level when compared with bean and corn. Corn, bean, and tomato when compared all exhibited highly significant differences in the total amounts of fluid exuded by plants grown in silt.

When a comparison is made for soil types there exists a difference beyond the 1% level for all but corn. Particle size and organic matter content of the soil probably influence the total amount of exudation exhibited by some species. The reasons for the great variation in amounts of water available to four different species in Suffield Silt are not clear. It may be that decreased aeration is a significant factor and a differential species
response is manifested because of hereditary effects on physiological processes of species concerned.

The very small amounts of exudate produced by all species in both Merrimac Fine Sandy Loam and Suffield Silt further demonstrate the inadequacy of active absorption in supplying tops of plants with water. In no case did exudation exceed 2 ml. for four hours and in most tests exudation was less than this small amount or in fact negative. In 4-hour time tests of transpiration and exudation of tomato plants, it was found that the maximum amount exuded represented only 2.07% of the water transpired per gram of oven dry weight of foliage. That much greater forces for water intake are developed in shoots than in roots is further indicated in figure 5.

Fig. 5. Transpiration-exudation comparison for tomato plants with roots immersed in sucrose solutions of known osmotic pressure.

Tomato seedlings were grown in sand and watered with a complete nutrient solution. The plants were approximately four weeks old when placed in blackened bottles containing various concentrations of sucrose. Transpiration was determined gravimetrically for a 4-hour period. At the end of this period each bottle was refilled and exudation from stumps of excised plants determined with 10-ml. pipettes in the manner previously described. Figure 5 amplifies the results of two comparisons between transpiration and exudation in sucrose solutions. In neither case was any root pressure manifested when the osmotic pressure of the sucrose solution exceeded three atmospheres and even in solutions of the lowest osmotic pressure the amount of exudate was negligible. The pull developed by intact plants was at least equal to 17.8 atmospheres and this was approximately eight times greater than the maximum force developed by the detopped roots in the weakest concentrations of sucrose.
Summary

1. Relationships between exudation from detopped plants and soil moisture content were studied for Merrimac Fine Sandy Loam and Suffield Silt. Species used as test plants were tomato (Lycopersicum esculentum Mill.), tobacco (Nicotiana tabacum L.) corn (Zea mays L. var. indentata), and bean (Phaseolus vulgaris L.).

2. A parabolic relationship was found between exudation and soil moisture content on a dry weight basis.

3. Soil types yielded significant differences for most species tested when total exudation was compared for silt and loam.

4. A total of approximately 60% of soil moisture in the range from wilting percentage to moisture equivalent appeared to be a minimum value which was not available to detopped root systems.

5. Data are presented which indicate that moisture equivalent may be grossly inadequate as an estimate of capillary capacity of soil.

6. Evidence is presented to show the inadequacy of active absorption in supplying tops of plants with water.

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LITERATURE CITED


