EFFECT OF CHEMICAL CONTROL OF STOMATA ON TRANSPIRATION OF INTACT PLANTS

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In the preceding communication it was shown that phenylmercuric acetate sprayed upon detached leaves brings about closure of the stomata and thereby diminishes the diffusion of water from the leaves and of CO₂ into the leaves. In 9 out of 11 experiments, induced closure of stomata reduced transpiration relatively more than CO₂ assimilation as predicted from diffusion theory. This work led to experiments in transpiration control in whole plants grown in containers in the greenhouse.

Success in the greenhouse required, of course, that the plants be sufficiently turgid, well-watered, and illuminated to permit the opening of the stomata in the untreated plants. It also required that the compound reduce transpiration without destroying the leaf.

The experiments reported employed the effective 3.3 and 10 × 10⁻⁵ M phenylmercuric acetate solutions sprayed in the afternoon upon a species whose stomata close uniformly.

Methods.—Each lot consisted of nine tobacco plants (so-called shade-type) 25 to 35 cm tall, growing in about 600 gm of fine sandy loam in waxed paper cups and arranged in a Latin square. The soil surface was covered by paraffin film. The initial soil moisture was the quantity retained after drainage; in some cups the water diminished to the wilting percentage before restoration to the initial state.

The transpiration for one day was determined before spraying, and the later transpiration was expressed as a fraction of this reference amount. The containers were set on shields that rested on a bed of wet sand. Experiments had shown that the stomata of control plants were not fully open in the dry air of the greenhouse, and, as expected under these circumstances, transpiration was scarcely reduced by treatment. In the experiments to be presented, the plants were enclosed in a transparent plastic tent to ensure high humidity and open stomata in the unsprayed plants.

Results.—The plants of the experiment of Table 1 were sprayed on February 27. The next day was cloudy, transpiration was slight, and no treatment effects were seen. During the next four days the sun shone, transpiration was high, and the 45 per cent reduction between plants sprayed with 0 and 10⁻⁴ M inhibition was significant. The next three days were cloudy; nevertheless, transpiration was reduced. The second week of observation had five clear days, and transpiration was reduced by 40 per cent.
Transpiration, day 1-2 had been decreased insignificantly.

The plants of another experiment were sprayed on March 13. On the first day, they transpired rapidly beneath the clear sky, and the loss of water was reduced significantly from a relative rate of 1.25 to 0.84 and 0.43 where the plants had been sprayed by 3.3 and $10 \times 10^{-5}$ M phenylmercuric acetate.

The plants were next permitted to wilt inside the tent, and were then uncovered and removed to a subirrigated bench. On day 22, the mean dry weights of the shoots were 5.7, 5.7, and 5.8 gm where the plants had been sprayed by 0, 3.3, and $10 \times 10^{-5}$ M inhibitor. Thus in an experiment where soil moisture in most containers was exhausted twice, and where the plants were exposed to the dry air of the greenhouse for 12 days, the inhibitor did not reduce dry weight in comparison with the control.

The plants of the experiment of Figure 1 were sprayed on March 28. The extraction of soil water was observed until the plants wilted. On the first day, the loss of water was reduced as before from a relative rate of 0.55 to 0.46 and 0.20. The mean transpirations per plant before treatment were 75.7, 77.8, and 76.6 gm per day. The slope of the line between two points (Fig. 1) is a function of energy available for evaporation, as well as of treatment and of soil water. The leveling of the curve near day 6 is due to exhaustion of soil water and wilting of all plants; here treatment can have no effect.

The inhibitor reduced transpiration as shown by the slower decline of the curve (Fig. 1). On the morning of day 5, two of three control plants, two of three sprayed with $3.3 \times 10^{-5} M$, and none of three sprayed with $10^{-4} M$ inhibitor were wilted. The longer time that the curve for the treated plants remained above a given level on Figure 1 while the curve for the control fell below indicates the benefit that may

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Mean ht., cm, day 0</th>
<th>Transpiration,* day 1-2</th>
<th>Transpiration, day 2-6</th>
<th>Transpiration, day 6-9</th>
<th>Transpiration, day 9-16</th>
<th>Ht. increase, cm, day 0-16</th>
<th>Fresh weight, shoot, gm per plant, day 16</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weather</td>
<td>0</td>
<td>Raining</td>
<td>Clear</td>
<td>Cloudy</td>
<td>Partly cloudy</td>
<td>9</td>
<td>30</td>
</tr>
<tr>
<td>Phenylmercuric Acetate</td>
<td>$0 \times 10^{-5}$</td>
<td>0.07</td>
<td>1.19</td>
<td>0.91</td>
<td>1.52</td>
<td>7</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>$3.3 \times 10^{-5}$</td>
<td>0.08</td>
<td>0.95</td>
<td>0.68</td>
<td>1.28</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>$10 \times 10^{-5}$</td>
<td>0.10</td>
<td>0.66</td>
<td>0.52</td>
<td>0.86</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Transpiration is relative to that of day before spraying.
be derived from this treatment. The time thus gained may compensate for the lower diffusion of CO₂ through closed stomata.

An inhibitor has enabled us to close stomata at will, and hence, to demonstrate the relation between stomatal resistance and both photosynthesis and transpiration. In the greenhouse, this inhibitor has consistently and markedly reduced transpiration. The physiology of these experiments has already been dealt with, but the possibility of application demands comment.

Discussion.—The clear demonstration that less than one ounce of a compound in 100 gallons of water diminishes transpiration of tobacco plants in the greenhouse encourages the hope that a considerable reduction in water use may be attained in the field or forest. Great problems lie ahead, of course. For example, finding compounds effective for a species and compatible with our use of the plant will be a difficult task. The possibility of benefit, however, is also great.

Conceivably, prolonging the duration of a well-hydrated condition (Fig. 3) may permit a plant to survive a drought that otherwise would injure it. Even yield increases are conceivable if the weather caused leaf hydration to vary in the appropriate sequence and severity; in fact, Blandy 2 has reported yield increases where phenylmercuric chloride was sprayed on disease-free plants and transpiration was decreased. The ratio of lowering of photosynthesis to transpiration will be most advantageous where compounds are specific for stomatal closure and where resistance M of the water barrier in mesophyll cells is great.

If the plant survived, even though growth were inhibited, transpiration reduction might be useful. For example, inhibition of forest growth may be less costly than the benefit of increased water yield. In the forest the disappearance of net radiation in the canopy is three times as great as that at the ground, 3 and three portions of evapotranspiration likely occur in the canopy for each portion of evaporation below. If the canopy could be retained intact but with the stomata closed, the leaves would probably become warmer, more energy would be lost by convection and a yet unknown portion of water saved from the canopy's three portions of evapotranspiration.

Summary.—Spraying phenylmercuric acetate on the leaves of tobacco plants in the greenhouse consistently diminished transpiration, usually more than half, while the effect on growth varied with environment.

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1 Zelitch, I., and Waggoner, P. E., these PROCEEDINGS, 48, 1101 (1962).