



The interrelationship between soil moisture tension and leaf water deficit, and photosynthetic rate of two orchardgrass clones
by An Kao Lee

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE in Agronomy
Montana State University
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Abstract:

We measured relative turgidity and net photosynthesis of orchard-grass (*Dactylic glomerate* L.) leaves undergoing increase soil moisture stress under growth chamber condition (light intensity of 25,000 lux, 15 hrs of light period, 9 hrs of dark period, temperature 21 C). Two clones of orchardgrass which differ in osmotic response during germination were used. Eight propagates were taken from each clone. Soil moisture tension was measured by a thermocouple psychrometer buried at the center of the pots. Relative turgidity of leaves were measured by the technique proposed by Weatherley. Net photosynthesis was measured by Beckman Infrared Gas Analyzer (Model 215A). The results showed a negative relationship between the relative turgidity of the leaves and soil moisture tension. Relative turgidity did not decrease until the soil moisture tension was more than 10 atmospheres. Relative turgidity decreased with soil moisture tension in a like manner for both orchardgrass clones. Wilted plants recovered full turgidity rapidly following watering. A highly significant negative correlation between net photosynthesis and plant moisture stress was established.

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Date March 8 1971

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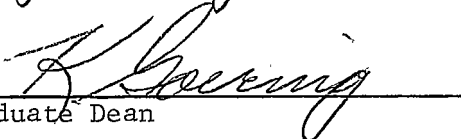
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Bozeman, Montana

March 1971

ACKNOWLEDGMENT

I wish to express my sincere thanks to Dr. Clee S. Cooper, my major professor, for his conscientious guidance throughout my graduate work, Dr. A. H. Ferguson and Dr. J. H. Brown for suggestions and constructive criticism. Special thanks to Dr. E. R. Hehn, the head of the Plant and Soil Science Department, for his encouragement.

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ABSTRACT

We measured relative turgidity and net photosynthesis of orchardgrass (Dactylic glomerate L.) leaves undergoing increase soil moisture stress under growth chamber condition (light intensity of 25,000 lux, 15 hrs of light period, 9 hrs of dark period, temperature 21 C). Two clones of orchardgrass which differ in osmotic response during germination were used. Eight propagates were taken from each clone. Soil moisture tension was measured by a thermocouple psychrometer buried at the center of the pots. Relative turgidity of leaves were measured by the technique proposed by Weatherley. Net photosynthesis was measured by Beckman Infrared Gas Analyzer (Model 215A). The results showed a negative relationship between the relative turgidity of the leaves and soil moisture tension. Relative turgidity did not decrease until the soil moisture tension was more than 10 atmospheres. Relative turgidity decreased with soil moisture tension in a like manner for both orchardgrass clones. Wilted plants recovered full turgidity rapidly following watering. A highly significant negative correlation between net photosynthesis and plant moisture stress was established.

INTRODUCTION

Water stress has manifold effects on the metabolism of higher plants. It reduces plant capacity to synthesize materials; thus decreasing CO₂ assimilation (30, 17). It has been shown repeatedly that decreasing the soil moisture, even within the available soil moisture range, causes a reduction in both transpiration and photosynthesis (1, 2, 15, 23, 28, 30). Ashton stated that the critical factor was the internal moisture condition of the plant rather than a specific soil moisture tension (2). Kramer also emphasized this point stating that "plant growth really is controlled by the internal water balance and the turgidity of the plant." It is not safe to assume that a certain level of soil water stress is accompanied by an equivalent degree of plant water stress. The only way to know whether a plant is being subjected to water stress, as proposed by Kramer (18), is by measuring the water potential of the plant itself.

Other authors have also implied a relationship between water potential of the leaf and that of the growth medium (6, 18). Boyer found a change in the water potential of the leaf tissue followed changes in the potential of the root medium (9); Boyer stated that the availability of soil moisture would affect growth rate by altering the water potential of the leaf (6). Werner reported that as available soil moisture diminished, both the maximum and minimum daily relative turgidity value decreased and the daily range in relative turgidity increased (34.)

Sorghum (Sorghum vulgare L.), Russian sunflower (Holiantus annus L.), cotton (Gossypium hirsulnea L.), and Thespesia populnea L. studied under experimental condition showed that the maximum net photosynthesis was not depressed by increasing water deficit until leaves were at least visibly wilted or visibly curled (12). Leaf water potential and net photosynthesis were also shown to be correlated by Verduin and Loomis (31). Their report, in which a comparison of the rate of apparent photosynthesis of turgid corn (Zea mays L.) leaves with those of visibly wilted corn leaves were made, showed that the rate of apparent photosynthesis of wilted corn leaves averaged 37% of the control with value ranging from 0 to 82 percent.

The present experiment was undertaken to determine the following (1) the relationship between the availability of soil moisture and relative turgidity of the leaves of two clones of orchardgrass (Dactylis glomerata L.); (2) the relationship between the relative turgidity of the leaves and net photosynthesis; (3) if these relationships vary among clones of a species.

LITERATURE REVIEW

Allmendinger et al. (1) studied the effect of soil moisture content on the net CO₂ exchange of apple (Malus pumila L.) leaves over a four week period. Plants were allowed to extract 20, 40, 60, 80, and 100% of the available soil moisture and were then watered to field capacity. They wrote "apple trees growing in the greenhouse did not show a reduction in apparent photosynthesis until more than four fifths of the available soil water had been utilized". The growth of the tree, however, was reduced after it had extracted 80% of the available soil moisture.

Upchurch et al. (30) studied the effect of soil moisture content upon the rate of photosynthesis in ladino clover (Trifolium repens L.). The rate of photosynthesis in ladino clover was not affected by removal of available moisture until the first visible signs of wilting appeared. Under their experimental conditions, these first signs of wilting occurred when approximately 10% of the total available moisture was left in the container. When they delayed irrigation until at least 75 to 85% of the available moisture had been extracted, no change in the rate of photosynthesis was detected preceeding or following irrigation.

Loustalot (23) grew pecan (Carya illinoinsis L.) trees in soil containers under field conditions and measured the CO₂ exchange in part of certain leaves while the plants were allowed to extract the soil moisture from field capacity to the permanent wilting percentage. He found that a more complete exhaustion of soil moisture was required to bring about reductions of photosynthetic activity in the morning

than was required to reduce corresponding reductions in the afternoons.

Babalola et al. (3) by using Monterey pine (Pinus radiata D. Don) seedlings, showed the rate of net photosynthesis as a function of soil water suction for four soil temperatures. Rate of net photosynthesis decreases with increasing soil water suction. The rate of net photosynthesis dropped sharply between soil water suction of 0.35 and 0.70 bar.

The rate of photosynthesis of the cotton plant (Gossypium hirsutum L.) was studied under varying water potential and light intensity of full, 1/2 and 1/4 full sunlight (25). As soil water decreased, photosynthesis first increased slightly and then markedly decreased. At the low soil water potential, rate of photosynthesis under full, 1/2 and 1/4 light intensity was 42, 66, and 52%, respectively, of its original measurement. An increase in photosynthesis was detected within several hours of rewatering. Rate of increase, however, was different under full sunlight and 1/4 sunlight.

Etherington's experiment on soil water and the growth of meadow foxtail (Alopecurus pratensis L.) (13) also showed the influence of soil water potential on photosynthesis. A very small decrease in soil water potential from field capacity was sufficient to depress net photosynthesis.

The relationship of soil moisture content or soil moisture stress to rate of photosynthesis in ladino clover was investigated in con-

ainers under controlled environmental conditions and in field plots by Hagan et al. (15). They showed that rate of photosynthesis continued undiminished until about the time the plant began to show visible signs of moisture stress. These findings are in general agreement with those of Allmendinger (1) on apple leaves and of Loustalot (23) on pecan leaves. However, the work of Schneider and Childers (28) on apple leaves indicated greater reductions in the rate of photosynthesis with decreases within the available moisture range.

Schneider and Childers (28) determined the net CO₂ exchange by attached leaves of small apple trees growing under conditions of decreasing soil moisture in the field and under controlled environmental conditions. They reported that before wilting was evident, the rate of photosynthesis was reduced 55%. When the plant showed definite wilting, there was an 87% reduction in the rate of photosynthesis. When water was applied to the soil in which the wilted plants were grown, the leaves usually attained turgidity within 3 to 5 hours. The rate of photosynthesis, however, did not regain its original magnitude until 2 to 7 days after watering.

Photosynthetic response to moisture stress of three timberline meadow species which vary in drought resistance was studied (22). The three species and order of drought resistance were as follows: Calamagrostis breweri: most sensitive, Potentilla breweri; intermediate sensitive, Carex exserta; least sensitive. With increasing moisture

stress, the order of photosynthesis rate reduction was Calamagrostis breweri > Potentilla breweri > Carex exserta, which was in direct relation to their drought resistance.

A field study of sugar cane (Saccharum officinarum L.) (2) further substantiated this relationship between soil moisture tension and rate of photosynthesis. The rate of photosynthesis does not decrease at a uniform rate during this drying out period. The original rate of photosynthesis is maintained until a significant soil moisture stress develops somewhere between field capacity and permanent wilting percentage and then decreases to a rate approaching zero at the permanent wilting percentage. Several days pass after an irrigation before the plant regains the original rate of photosynthesis.

Holger related the rate of photosynthesis of tomato (Lycopersicon esculentum Mill) and loblolly pine seedlings (Pinus taeda L.) to the diffusion pressure deficit of the leaves (17). The net rate of photosynthesis decreased when the leaf diffusion pressure deficit rose above 4 atmospheres for loblolly pine and above 7 atmospheres for tomato. A diffusion pressure deficit of 11 atmospheres for loblolly pine and 14 atmospheres for tomato decreased photosynthesis to zero. Changes in the rates of photosynthesis for tomato and loblolly pine during increasing water stress were quite similar. This is taken to indicate that photosynthesis is affected by water stress because of an increased resistance to gaseous diffusion.

Boyer (8) compared the rate of net photosynthesis of corn and that of soybean (Glycine max. L.) over a range of leaf water potentials. Corn was known to possess the C_4 -dicarboxylic acid pathway for CO_2 fixation during photosynthesis and soybean did not (20). He showed that soybean was unaffected by desiccation until leaf water potentials were below -11 bars. Rates of photosynthesis in corn were inhibited whenever leaf water potentials dropped below -3.5 bars. The differences in photosynthetic behavior could be attributed solely to differences in stomatal behavior down to leaf water potential of -16 bars in soybean and -10 bars in corn. Below these potentials, other factors in addition to stomatal closure caused inhibition, although their effect was relatively small.

MATERIALS AND METHODS

Two clones of orchardgrass were studied. They had a history of development as follows (10):

In 1959, 50,000 orchardgrass seeds were planted in germinating boxes with blotters wetted with mannitol solution at 9 atmospheres tension. Of these seeds, only 82 germinated. These 82 seeds were transplanted into pots and later transplanted to the field in an isolated crossing block. Plants from seed germinating under high osmotic tension were designated "resistant". An additional 50,000 seeds were germinated in mannitol at a tension of 1 atmosphere. Seeds not germinating after 3 weeks were removed and placed in distilled water. Seeds incapable of germinating at 1 atmosphere, but germinating in distilled water, were transplanted into pots and later to the field in an isolated crossing block. Plants thus established were designated "susceptable". In 1961 seeds were harvested from each plant in each isolated crossing block and tested for germination. Data obtained indicated that the ability of seeds to germinate against mannitol induced osmotic stress was heritable.

Eight propagates were taken from each clone, they were cut back and grown in growth chamber (light intensity: 25,000 lux 15 hrs of light period 9 hrs of dark period, temperature 21 C) in 16 plastic cylindrical cans (15.5 cm in diameter) each contained 1700 gm of Bozeman silt loam soil taken 6 inches beneath the surface layer from the university farm. Vermiculite 2.5 cm in depth was layered on the

surface of the pots to reduce evaporation. Thermocouple Psychrometers were buried at the center of the pots with wire leading through a hole in the pot to the outside. The essential parts of the psychrometer are a porous ceramic bulb whose primary function is to maintain a chamber of fixed dimensions within the soil, and a thermocouple to measure the relative humidity within the chamber (27). The hole in the pot was then filled with wax. When propagates in the growth chamber reached a height of 32 cm (2-3 weeks of growth) we stopped watering and soil moisture tension was measured daily with a battery operated portable electronic voltmeter (Keithley Model 148 Nanovoltmeter). Procedure to make a reading was given elsewhere (27). After all pots reached a soil moisture tension of 20 atmosphere, the study was terminated and plant cut back and watered thoroughly with complete nutrient solution until the next study. The interval between the first and second study and that between the second and third study was approximately 2-3 weeks. The time from the original cut back until sampling was also of the same length, so leaf age was essentially the same.

Net photosynthesis was measured two times in a leaf chamber (16). Two different models of leaf chamber were used in these studies. For the first study, a transparent chamber of a diameter of 4 cm which is surrounded by a water jacket 1.5 cm in thickness was used. Water that circulated between the water jacket of leaf chamber and that of the whole system maintain the temperature in the leaf chamber at 21.1 C.

For the second study, a square shaped chamber 7.75 cm x 3.75 cm x 30 cm in size was constructed. Since for both studies, a layer of circulated water 7.75 cm thick was set between the light source (.333 langley/hr) and the leaf chamber, light should not affect the temperature of the leaf chamber. So no water jacket was constructed around the square shaped leaf chamber used for second study and the temperature inside the leaf chamber, as measured by thermometer, was essentially the same as that in the water bath tank, that is 21.1 C. An infrared CO₂ analyzer which permitted direct and continuous observation of changes in the concentration of CO₂ around the leaf sample was used in this measurement (21). In the whole system, the incoming air is divided into two streams. One of these, after moisture saturation and being kept at 21.1 C by going through temperature constant water bath, goes directly into the infrared CO₂ analyzer and its analysis indicates the initial CO₂ content. The other stream, same temperature and moisture saturation as the first one, first passes through the leaf chamber and then through the infrared CO₂ analyzer. Both streams, before passing through the infrared CO₂ analyzer, must be dried to prevent interference from water vapor. A drying agent must neither absorb nor emit CO₂ and must not create an environment conducive to the growth of microorganisms. In our set-up, indicating drierite (CaSO₄) was used. Net photosynthesis rates were then calculated from

$$P = (\Delta \text{CO}_2 \cdot F \cdot K) / A \quad (16)$$

where P = net photosynthesis as mg of CO_2 assimilated per square dm of leaf area per hour

ΔCO_2 = change in concentration of CO_2 between intake and exhaust as ppm by volume $\times 10^{-6}$

F = air flow through the chamber

$K = (44000 \text{ mg } CO_2) / 22.4 \times (273/294)$, an approximate empirical conversion factor from liters of CO_2 to mg CO_2 for the rotameters used

A = leaf area

The principle of the operation of infrared CO_2 analyzer, as discussed by some authors (21, 5) are given briefly as below:

The Beckman Infrared Gas Analyzer (model 215 A) we used consisted of two energy sources emitting two infrared radiation beams, which are interrupted by a motor driven chopper operating at 10 cycles per second. One beam passes through the sample cell and the other through the reference cell. The beam passing through the sample cell has some of its radiation absorbed by the CO_2 present in it. Difference in the amount of radiation passing through the two cells are detected as a difference in heat. The change in heat in turn causes an electrical differential which is recorded.

The method used for the determination of the relative turgidity of orchardgrass leaf samples was similar to that of Barrs and Weatherley (4). Formula for this calculation is:

$$R. T. = (FW - DW) / (TW - DW)$$

where: RT = Relative turgidity

FW = Fresh weight

DW = Dry weight

TW = Turgid weight

After measurement of soil moisture tension by the use of thermocouple psychrometer, a leaf from each container was taken every morning and cut into segments. The leaf segments were weighed to determine their fresh weight (FW). Segments were then floated on water in closed petri dishes 13 cm x 12 cm x 3 cm in size for 24 hrs without illumination at 21.1 C constant temperature. They were then blotted with paper towels to remove superficial water and weighed to determine the fully turgid weight (TW). Another set of leaf segments taken from the same tiller were used for the calculation of dry weight (DW). These, after determining the fresh weight, were oven dried for 48 hours at 70 C. Calculations of the relative turgidity follows the formula shown above.

An air flow planimeter was used for leaf area measurement. Three to four readings were taken of each leaf and averaged.

RESULTS AND DISCUSSION

The relationship between soil moisture tension and relative turgidity of leaves is shown for three samplings in Figures 1, 2 and 3. A comparison of the curves on those figures show that at the first run, there was no change in relative turgidity as soil moisture tension increased up to 10 atmosphere. From this point on, a sharp decrease in relative turgidity was evident. The second run showed a tendency toward faster and earlier decrease in relative turgidity as the soil moisture tension increased. This tendency became more apparent during the third run. Since in these three experiment leaves were all cut back three weeks before sampling, leaf age should not contribute appreciably to this discrepancy. However, root proliferation increased with time. Observation of the root proliferation after the end of the third experiment showed a thick mat of roots crowded all over the interface between container and soil mass. High root proliferation, especially at the third sampling, could essentially stop unsaturated conductivity of soil water. This might be one of the reasons for change in relative turgidity at low soil moisture tensions at the later sampling. In addition, the mass of roots between the soil and pots could be expected to dry more rapidly than those within the soil. Thus, measurement of soil moisture did not reflect the moisture condition of the roots.

There was no apparent difference in the rate of decrease in relative turgidity among the two clones used (Figures 1, 2, and 3).

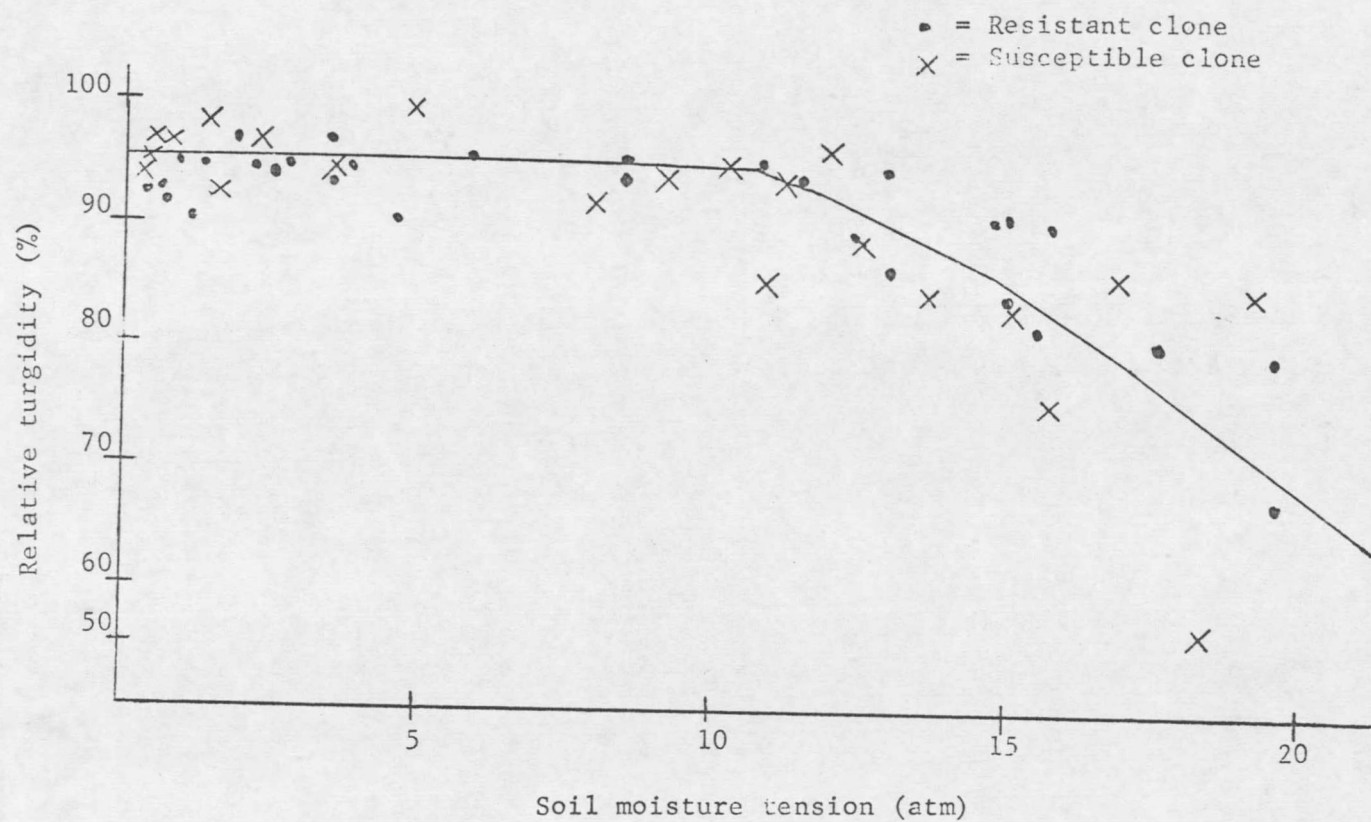


Figure 1. The relationship between soil moisture tension and relative turgidity of orchardgrass leaves. (First sampling).

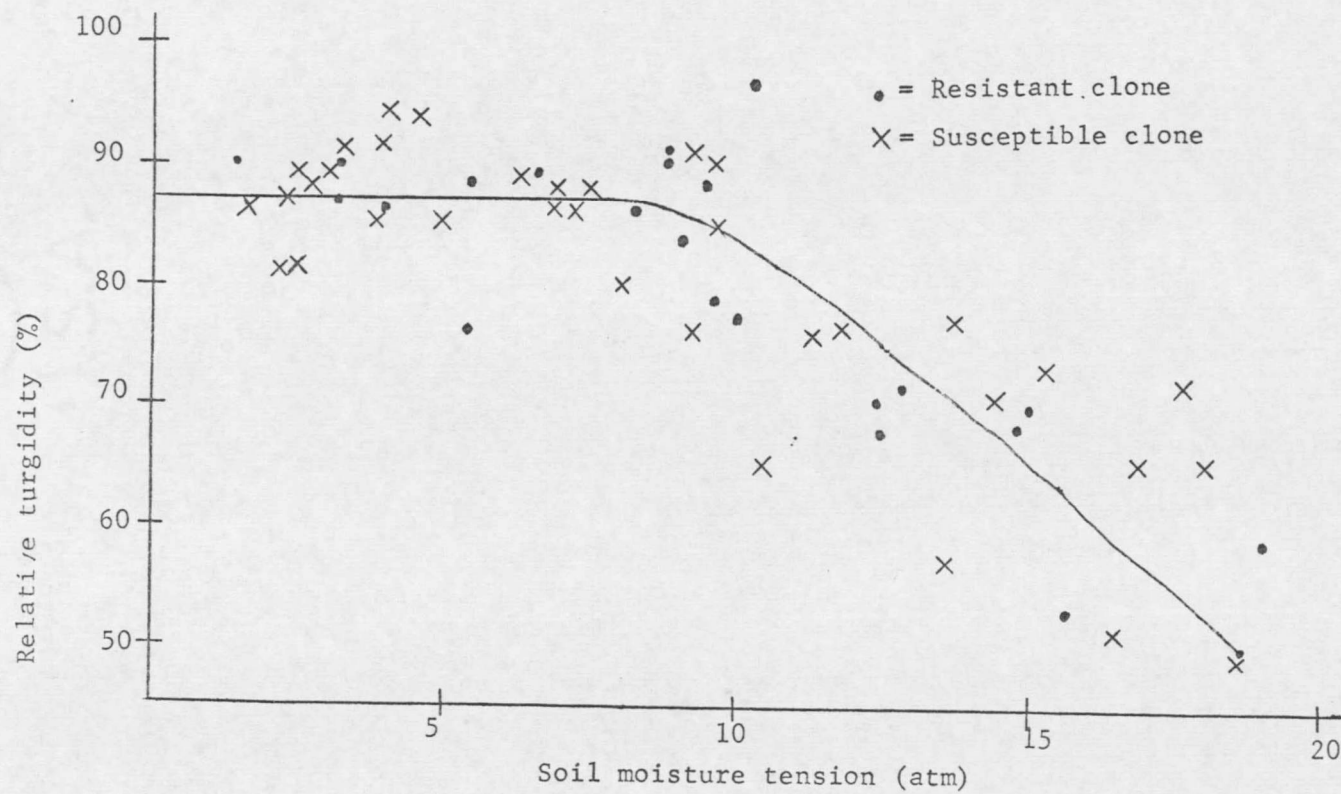


Figure 2. The relationship between soil moisture tension and relative turgidity of orchardgrass leaves. (Second sampling).

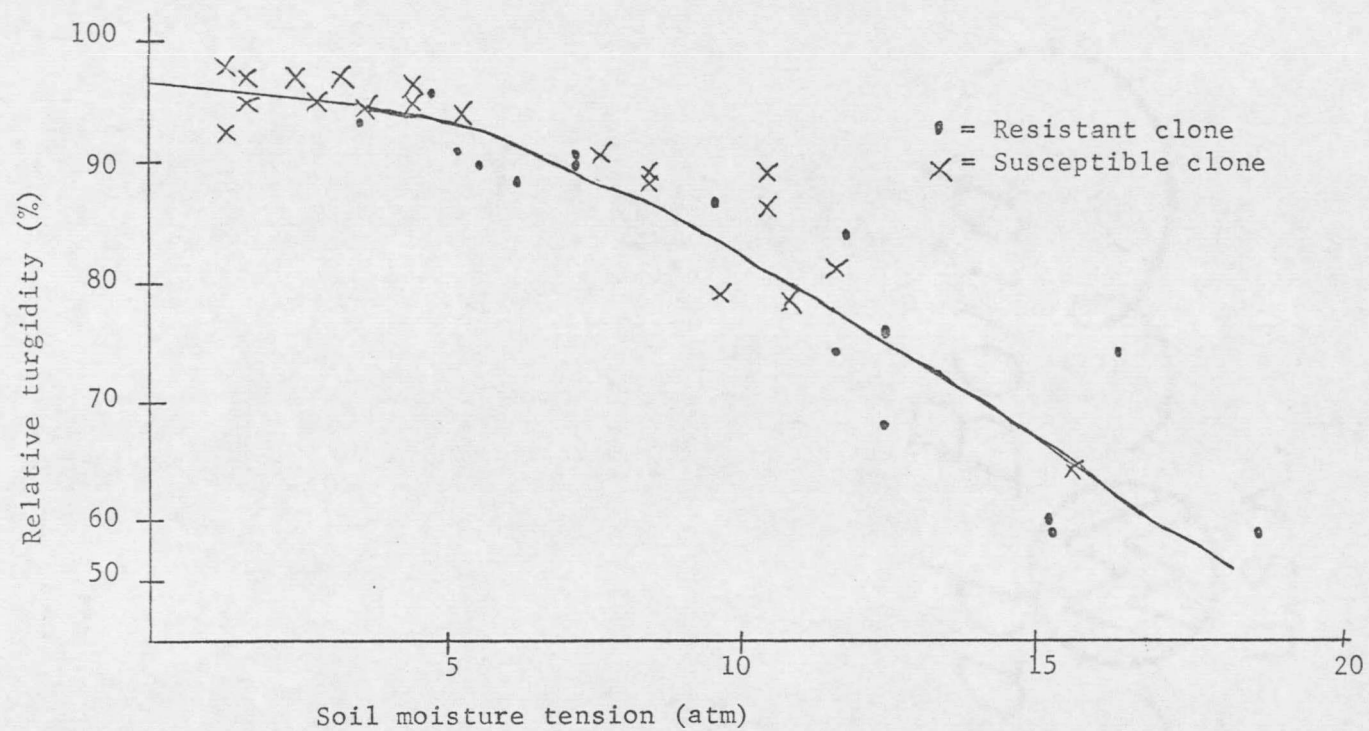


Figure 3. The relationship between soil moisture tension and relative turgidity of orchardgrass leaves. (Third sampling).

Data on the rate of recovery of relative turgidity for these three samplings are summarized in Table 1.

Plants which were wilted and whose relative turgidity dropped down to 53.2 and 38.4%, respectively, for experiment 1 and 2 recovered to their original readings within 24 hours after watering. In the third experiment in which soil moisture tension and relative turgidity were measured twice a day, the relative water content after watering was 131. Relative turgidity reading after watering for 12 hours in this case also went back to the original value.

The relative turgidity method used in this study is the most widely accepted way of expressing the quantity of water in plant tissue. This method, after calibration in terms of potential, may be used to estimate plant water potential (33). The validity of the determination depends on (1) the stability of the calibration (33), (2) the degree of injection of the tissue with water during soaking for turgid weights (14), and (3) on the definition of turgid tissue itself (4, 14). Some plant tissues undergo growth by cell enlargement when turgor rises above a certain level and in the case of leaf tissue at least the cell may not become fully turgid in the sense of having zero water potential (34). Temperature also may have an effect (4, 24).

Experiments relating relative turgidity of leaves to photosynthetic rate were conducted twice. The results were very variable. We found a better relationship between photosynthesis and water deficit express-

Table 1. Amount of recovery of relative turgidity for three experiments. ^{1/}

	R. T. of plant at 0 soil mois- ture tension	R. T. of plant at highest soil moisture tension	R. T. of plant after watering ^{2/}	Relative water content after watering
Exp. 1	95	53.15	95.18	179
Exp. 2	85	38.39	84.84	221
Exp. 3	95	72.16	94.33	131

^{1/} The value in this table are averaged over all samples of the two strains used in this study.

^{2/} The interval between watering and measurement for experiment 1 and 2 was 24 hours and that for experiment 3 was 12 hours.

ed in terms of the amount of water absorbed per cm^2 of leaf area. This relationship is shown in Figure 4 and 5. While the results are still variable, they do show a significant decrease in the photosynthetic rate as the leaf water deficit increased.

In this study, we found that soil moisture tension above 10 atmospheres affected the relative turgidity of leaves. The change in relative turgidity was not accompanied by visual wilting. We could not observe wilting until after 15 atmospheres. Therefore, from our data we can conclude that a plant may be undergoing moisture deficiency even though wilting is not apparent. Under the conditions of this experiment, orchardgrass should have been watered slightly below 10 atmospheres to maintain optimum yield. However, under field conditions, many factors may affect the water balance of this plant. Therefore, one cannot predict optimum time for irrigation. Our data show, however, that internal moisture stress will occur before the commonly expected 15 atmospheres wilting point.

We did not find differences in the response of the two orchardgrass clones used. However, differences might have occurred if a greater number of clones or species have been tested.

Wilted plants recovered full turgidity within 24 hours after watering. We did not measure photosynthesis following recovery. Some authors (1, 17, 23) have shown a lag in recovery of net photosynthesis after plants are brought back to a turgid condition. Thus it is impor-

tant that one irrigate before plants acquire an internal moisture stress great enough to decrease photosynthesis.

Our data were extremely variable. Part of our problem was that each tiller is a distinct entity with its own root system. Thus soil moisture measured in the middle of the pot may not be indicative of that for a tiller growing on the outside. Furthermore, photosynthesis varies with tiller age and it was difficult to select tillers of like age. With the technique used, we do not feel that we could make precise enough estimates of the relationship of leaf water deficit and photosynthesis to compare clones of orchardgrass. Hesketh et al. (12) also showed a poor relationship between leaf water deficit and photosynthesis; but a good relationship between stomata opening and photosynthesis. Therefore, it seems obvious that stomata opening and leaf water deficit are not necessarily closely related. Furthermore, the ability or lack of ability of a leaf to open stomata under stress may not be heritable. Studies of stomatal behavior between clones of a species under various stress conditions might help resolve this question and should be made.

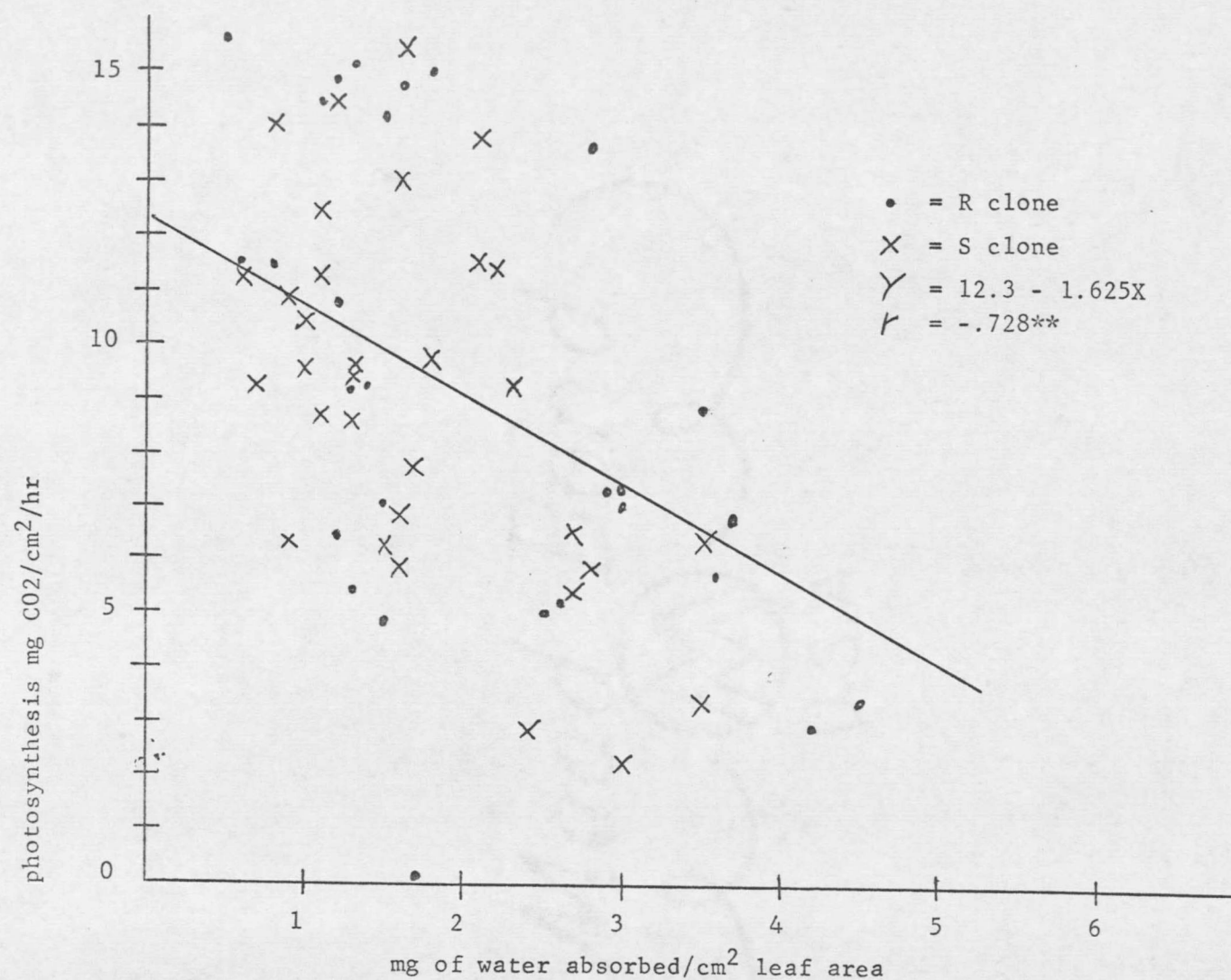


Figure 4 . The decline in photosynthetic rate of orchardgrass with increasing leaf water deficit. (First sampling).

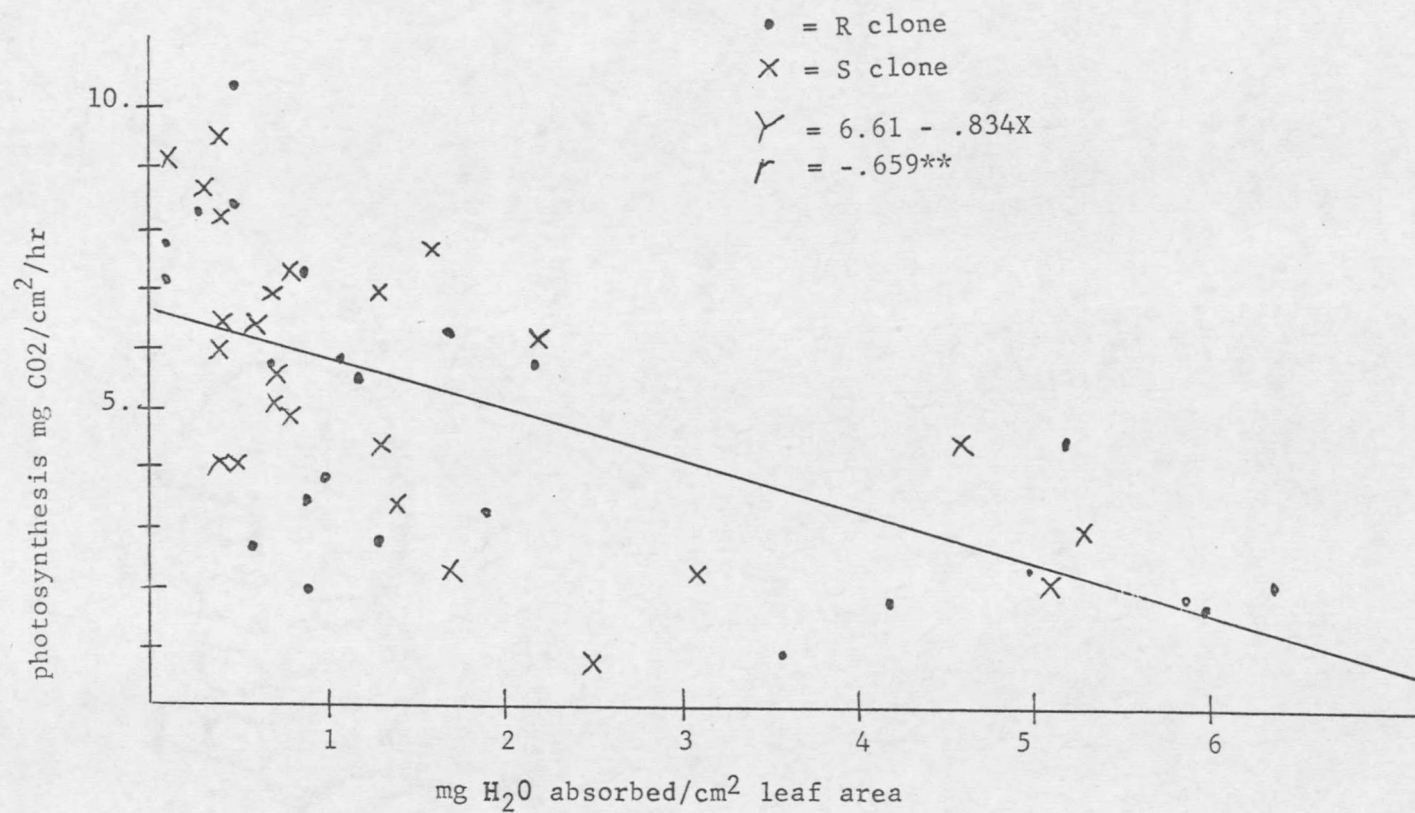


Figure 5 . The decline in photosynthetic rate of orchardgrass with increasing leaf water deficit (Second sampling).

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