THE EFFECTS OF WIND- AND DROUGHT-STRESS ON THE INTERNAL WATER RELATIONS OF WINTER WHEAT I. GROWN WITH ROOTS SPLIT BETWEEN SOIL AND NUTRIENT SOLUTION IN A GROWTH CHAMBER II. GROWN IN DIFFERENT ROW DIRECTIONS IN THE FIELD

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CHAPTER I

INTRODUCTION

The effect of wind- and drought-stress on plants is known to have detrimental effects. There is a preponderance of literature on the subject of moisture stress and its qualitative effects. However, little attention has been given to the quantitative effects of wind- and drought-stress. It is difficult to ascertain how environmental mechanisms interact with biological processes under wind- and drought-stress conditions. Due to the complex interaction these factors, quantitative relationships between the leaf-water potential, stomatal resistance, growth rate, and transpiration rate are difficult to derive. Also, these parameters are intimately associated with both plant and physical processes. Hence, cause and effect relations are rather inconclusive.

Transpiration is a process governed by the rate of diffusion of a gas (water vapor) out of the leaf (Gayle and Mayber, 1968). It is well known that the rate of transpiration is governed by the degree of opening and/or closing of the stomata. However, determining the motivating force by which stomata respond is the subject of considerable controversy and has led to a number of hypotheses.

A popular view of the soil-plant-atmosphere continuum, SPAC as used by Philip (1966), is that the flow of liquid water is initiated by evaporation from leaves, which in turn, lowers leaf water contents, decreases leaf-water potentials, and generates a water potential gradient which extends progressively through the plant water system and into into the soil (Slayter, 1967). According to Gardner (1960) and Cowan (1965) this is a physically unified and dynamic system in which flow processes occur independently, but linked via the SPAC as Philip (1966) points out. We shall assume that the absorption of water by plants is a passive process. Water moves, in this case, from regions of higher to lower potential energy, as it moves through the SPAC. The potential energy continuously decreases until the water reaches the point in the leaves at which evaporation occurs. This study will concentrate mainly on the plant-air portion of the SPAC, although inferences will be drawn from the data regarding resistances in the rooting media.

The internal water relations of wheat grown in the field and growth chamber, as affected by wind, were studied in two separate experiments. In the growth chamber experiment, the internal water relations of wind- and drought-stressed wheat plants were studied. In addition, the effect of soil and nutrient solution media on plant water relations of wind- an drought-stressed plants was measured. Plants were grown with roots split between soil and nutrient solution in both wind and still air. During the first 16 days of the experiment, the soil was well watered. During the last 22 days of the experiment, the soil was not watered. Leaf-water potential, stomatal resistance, transpiration rate, growth rate and leaf area were measured periodically throughout the experiment. At harvest, root and leaf dry matter and root length were determined.

In the field experiment, the objective of the study was to determine row direction orientational effects on the internal water relations of winter wheat. Specifically, this included observable differences in the variation of water potential and stomatal resistance in leaves of wheat, planted in four row directions (north-south, east-west, northeast-southwest, northwest-southeast) and exposed to the strong prevailing winds in central Oklahoma. It is important to determine the water potential and stomatal resistance of plants because growth occurs only when potentials are high and resistances are low.

CHAPTER II

LITERATURE REVIEW

In approaching the detrimental effects of both wind- and drought-stress, it is necessary to consider them separately even though there is an intimate relationship. These environmental considerations are present in all areas of the world where agriculture is practiced. Research on improved management and breeding of plant has led to increased yields. However, methods for increasing the water-use efficiency and resisitance to wind damage have been, at best, somewhat discouraging. In order to provide ample food for the increasing world population, problems of controlling evapotranspiration and reclamation of arid and semi-arid regions for agricultural use must be overcome.

In the past much of the research on plant response to drought stress has been based on soil moisture rather than plant status. Kramer (1969) suggests it is absolutely necessary that plant water stress be measured directly in all future drought research in order to thoroughly understand plant response to drought under various conditions.

An even more insurmountable compilation of research has been done regarding the effects of drought stress and its influence on plant physiological processes. Most have dealt with the transpiration stream and the internal water status associated with it. In recent years there have been some excellent reviews on the subject, e.g. Barrs (1968), Kramer (1969), Slayter (1967), Jordan and Ritchie (1971), Hsiao and Acevedo (1974), Idso (1968). Physical-mathematical models of water trasport have been developed for some years (Philip, 1957; Gardner, 1960; Cowan, 1965; Denmead and Millar, 1976). Some of these models shall be discussed later.

For years it has been know that moisture is the greatest limiting factor in wheat production in Oklahoma (Finnell, 1928; Finnell, 1933; Daniel, 1935; Mathews and Brown, 1938). Droughts are a result of a variation in precipitation coupled with high temperatures and winds, which can cause unprofitable returns and total crop failure. Simultaneous measurements on micrometeorological and physiological processes in response to moisture deficits are few. This is due to the difficulty in divorcing the response of plant processes to drought-stress from that of micrometeorological stress, i.e., wind and temperature stress.

Drought Stress

As Idso (1968) points out, the term water (moisture) stress has become somewhat nebulous. Therefore, the term drought stress will be used to indicate a prolonged or chronic shortage of moisture. Although drought stress is an influencing factor of most plant processes and has varied effects, it is a function of physical processes within the soil (source) and the atmosphere (sink). The plant is a vehicle by which water is translocated from its source to the sink, via the SPAC.

Hillel (1971) considers that the resistance of water vapor diffusion between the leaves and the atmosphere may be 50 or more times greater than the resistance of the plant and soil. Philip (1966) concurs that the major portion of the overall potential difference in the SPAC occurs between the leaves and the atmosphere. Regardless of the atmospheric conditions over a relative humidity range from 0 to 98 per cent, Idso (1968, p. 2) points out that "the difference in free energy between the soil-root interface and the mesophyll cells must remain essentially constant, as the slope [of this part of the free energy gradient] is a property of the plant and not of the soil or atmosphere."

According to Kaufman and Hall (1974), water flow through plants is driven by water potential gradients, which result from water stress in leaves generated by transpiration. Therefore, they felt that the flow of water through a plant is primarily controlled by the climate and plant factors that influence gaseous flow fro leaf to atmosphere. They said that other plant factors and the soil influence the flow of water indirectly through feedback effects of stomatal aperture.

Total Soil Water Potential

The total soil water potential, ψ_{Ts}, as defined by Baver et al., (1972) is:

$$\psi_{T_s} = \psi_m + \psi_g + \psi_p + \psi_\pi + \psi_\eta$$

where ψ_m, ψ_g, ψ_p, ψ_π, and ψ_η are the matric, gravity, pressure, osmotic, and overburden potentials, respectively. Of these potentials, have the greatest relevance in soil-plant-water relations. The ψ_s potential may be defined as:

$$\psi_s = \psi_m + \psi_\pi$$

where the subscript s refers to stress, which is the common term that is used to identify potential associated with water availability to plants (Baver et al., 1972). Other potentials beside the matric and osmotic potentials influence water uptake by plants, but their effect is small. Under nonsaline conditions, matric potential is the most important component of the total soil water potential.

The potentials of interest in plants, which combine to give the total plant water potential, ψ_{Tp}, may be defined, according to Kirkham et al. (1969), as:

$$\psi_{Tp} = \psi_\pi + \psi_m + \psi_t + \psi_g$$

where ψ_π, ψ_m, ψ_t, and ψ_g are the osmotic, matric, turgor, and gravitational potentials, respectively. The matric potential in plants is associated with capillary absorption forces which, in a plant, are forces such as those at the cell walls. The magnitudes of the matric and gravitational potentials are small compared to those of the osmotic and turgor potentials and in most plant-water relation studies they are neglected.

Cowan (1965) states that the relationship between leaf-water potential and stomatal resistance is of intrinsic interest and also is important in constructing transpiration models for the SPAC. The movement of water in the SPAC occurs in response to a potential difference and is in the direction of decreasing energy, (i.e., from the soil, into the plant root, and through the xylem to the leaves). Gardner points out that as soil-water content decreases, the soil- and leaf-water potentials also decrease. Development of lower leaf-water potentials to meet increases in transpiration rate in drying soil, may require lower leaf-water contents and lower leaf turgor potentials (Slayter, 1967). Only under conditions of extremely severe desiccation is direct control by nonstomatal mechanisms, such as epidermal waxes, hairy leaves, and leaf curling, possible, and then there is also likely to be complete stomatal closure (Slayter, 1966).

A considerable amount of literature indicates that leaf-water potential and transpiration both decrease as soil water is depleted (Hagan et al., 1957; Slayter, 1966; Ehlig and Gardner, 1963 and 1964). A simultaneous decrease of leaf-water potential and transpiration rate of a number of species as soil-water potential decreased after irrigation was noted by Gardner and Ehlig (1963) and Ehlig and Gardner (1964). However, Stoker and Weatherly (1971) measured leaf-water potential of solution grown cotton and sunflower plants over a wide range of transpiration rates. They found that a small increase in transpiration from zero resulted in a rapid decrease of leaf-water potential. But, thereafter, water potential remained constant. To explain this, they proposed that resistance to flow of water from the soil to the leaves changes with flow rate such that no increases in gradient for flow are required as transpiration increases. If so, then considerable differences exists among species in the mechanism by which water flow through plants is accomplished. Such a mechanism(s) is not yet known.

As soil-water content (and soil-water potential) is progressively reduced during a rainless period of weather, there is a concomitant drop in the level of plant water potential (Slayter, 1969). That is, plant water potential cannot be higher than soil-water potential. Hence, there is a base level of plant water potential and internal water deficit which is limited by the level of soil water potential.

There are consistent relationships between the leaf-water potential and other aspects of the internal water status of plant leaves. Gardner (1973) observed that in a large number of cases under greenhouse conditions the plant leaf-potential during the day tends to remain at a rather constant amount below the soil-water potential, regardless of the value of the latter. Where the soil-water potential surrounding the plant root is no lower than about -1 bar, the turgor pressure of the plant depends more strongly upon the transpiration rate than upon the soil-water potential. In this range of soil-water potentials, it is not expected that the potentials at the soil-root interface is usually substantially lower than the average soil-water potential (Gardner, 1960). He concluded that the internal water status of a plant leaf appears to depend more on the transpiration rate than upon the soil-water potentials.

Transpiration and Internal Water Relations

Idson (1968) concurs and considers that transpiration is chiefly determined by the leaf-air free energy difference. He said it is evident that the soil-moisture control of this process is less than 10 per cent effective.

Ehlig and Gardner (1964) determined the relationship between transpiration and the internal water relations (i.e., relative water content and diffusion pressure deficit) for pepper, trefoil, sunflower, andcotton. They found that below a characteristic diffusion pressure deficit value for each plant, the transpiration rate was proportional to potential evapotranspiration. Above this value, the transpiration rate tended to decrease rapidly at first and then more slowly, with increasing diffusion pressure deficit. The relative rate of water loss from initially turgid detached leaves decreased markedly with decreasing water content. A water content of about 90 per cent of that at full turgor corresponded to a diffusion pressure deficit of about 10 to 15 bars. Leaves of all species displayed large decreases in the rate of water loss over relatively small differences in water content.

The correlation between transpiration rate and leaf-water potential under non-limiting conditions (sufficient water, nutrients, light, temperature, and CO_2) is based on the assumption that the relationship between flux and potential follows a sequence of steady states (Kaufman and Hall, 1974). However, as demonstrated by many workers (e.g., Gardner, 1960; Slayter, 1966; Cowan, 1965), the system is actually in a dynamic state with respect to the transpiration stream and plant water relations.

Stomatal Regulation

Plants cannot live without water. The availability of water is a critical consideration in arid and semi-arid environments to agriculturalists. Sullivan and Eastin (1974) state that in order to accomplish plant modification for more efficient water use, when plants are grown under conditions of limited water availability, it is necessary that we have a complete understanding of the physiological responses to drought stress including those factors which contribute to drought resistance. It is widely recognized that the loss of water from plant surfaces (transpiration) occurs through the stomata. However, the role of stomata in regulating the rate of transpiration has been a matter of controversy since von Mohl (1856) first described the movement of stomata. Subsequent research has yielded a myriad of conclusions regarding stomatal control, and, hence, factors controlling transpiration (Brown and Escombe, 1900; Penman and Schofield, 1951; Knight, 1917; Lloyd, 1908; Maskell, 1928; Stalfelt, 1932; Livingston and Brown, 1912; Gregory et al., 1950; Heath, 1948 and 1950). More recently articles by Milthorpe and Spencer (1957), Barrs and Kelper (1967), Gardner (1960), Ketellapper (1963), Idso (1968), Cowan (1965), Slayter (1966), and Kanemasu and Tanner (1969), for example, have elucidated much of the present understanding of factors influencing stomatal movement. These factors shall be discussed later.

Ritchie (1971) and Ritchie and Burnett (1972) have shown that the evaporation rate is dictated primarily by micrometeorological factors, i.e., the atmospheric demand, when soil water is non-limiting and plants provide full cover. However, as soil water is depleted beyond a threshold value, evaporation rates fall below the evaporative potential. Evaporative potential is the maximum amount of water that can be lost (evaporated) under given meteorological conditions. When soil water becomes limited, the relation between soil water content and evaporation rate depends on soil water transmission characteristics and plant properties (Gardner, 1960; Gates and Hanks, 1967; Gardner and Ehlig, 1963) as well as the evaporative demand (Denmand and Shaw, 1962; Palmer et al., 1964).

Kanemasu and Tanner (1969) found that the abaxial and adaxial stomata of snap beans (Phaseolus vulgaris L.) react differently to water deficit in both the field and growth chamber. The stomata on the abaxial surface are not significantly affected at leaf-water potentials greater than -11 bars. But with a further decrease in leaf-water potential, the resistance rapidly increases. However, the resistance of the adaxial stomata increases sharply at a leaf-water potential of about-8 bars and is constant at higher water potentials. The average stomatal resistance for both surfaces of the leaf, which is the major diffusive resistance to water vapor, to a first approximation, acts as an on-off switch and helps to prevent further decline in leaf-water potential. They concluded that the relation between the leaf-water potential and the stomatal resistance links the soil-water potential to the transpiration stream. Such information is needed for soil-plant-atmospheric models.

For turgid plants exposed to normal levels of CO_2, the main regulator of the stomatal aperture and, therefore, of the leaf diffusion resistance is the illuminance of the leaf (Dale, 1961; Slayter and Bierhuizen, 1964; Ehnler and van Bavel, 1968). Numerous experiments in both the field and laboratory have shown that stomata respond rapidly to light. That is, the stomat open in the light and close in the dark. Williams (1954),however, found that closing is the more rapid process. It may be measurable 15 seconds after darkness (Virgin, 1956). However, recent data do not substantiate this

(Kirkham). Ketallapper (1963) states taht the rate of opening is also influenced by light intensity and this varies with species. Kanemasu and Tanner (1969) found that the adaxial (upper) stomata of bean required more light to open than abaxial (lower) stomata. Ehrler and van Bavel (1968) worked with eight plant species grown in Hoagland solution and increased illuminance, as a single variable in a controlled environment, in a stepwise manner. They found that illuminance was a regulator of stomatal aperture and, therefore, of the leaf diffusion resistance.

Growth

Water-stress literature made available in the recent past clearly establishes that growth is extremely sensitive to small water deficits. In some species, any reduction in the water potential of tissue reduces growth. Cell growth, as defined by Hsiao and Acevedo (1974), is an irreversible enlargement or expansion of cells and, although seemingly physical, this definition incorporates inplicitly all metabolic aspects of growth.

Green (1968) working with Nitella, monitored growth and turgor pressure with micromanometers in the internodal cell and found that any change in turgor pressure causes immediate changes in growth and developed an equation to describe the extreme sensitivity of growth to turgor pressure as it related to water deficits.

In examining the problem as to whether or not a reduction in the hydrostatic pressure (turgor pressure) is the important effect of water stress in growth, Hsiao et al (1970) noted that changes in water potential of the root media can bring about virtually instant changes in leaf elongation in 10 day old maize. In separate experiments, Acevedo et al. (1971) found the water potential of the youngest leaves was within 1.5 bars or less of the water potential of the next oldest leaf at several stress levels. They concluded that watering a soil slightly deficient in water brings an almost instant increase in turgor in the leaf cells and, hence, an increase in cell growth.

Gardner (1973) emphasizes the experimental evidence is now convincingly in favor of a very intimate coupling between transpiration and photosynthesis through stomatal control of gaseous exchange between the plant leaf and the surrounding atmosphere. This approach requires that one be able to relate the plant leaf-water potential to the soil-water potential and the trdanspiration rate and the stomatal resistance or conductance to the leaf-water potential.

Root Growth

Root growth is generally favored over shoot growth under water stress as indicated by often observed increases in the ratio of root to shoot (El Nadi et al., 1969; Hoffman et al., 1971). In some cases, drought stress appears to enhance root growth not only relative to shoot growth, but absolutely. Ficks et al. (1973) suggest such absolute increases would be important in determining the yield of root crops, (e.g., sugar beets). Hsiao and Acevedo (1974) state that it is tempting to hypothesize that the better growth of roots under moisture stress is due to their spposedly greater abilility to adjust osmotically. They found that increased amounts of assimilates made available by the reduces sink strength in the shoot permitted osmotic adjustment and extra growth in the roots. However, they did not explain how smaller leaves can make more assimilates, but suggested the stress induced preferential root growth may possibly constitute an adaptive mechanism. Supposedly, the better the root proliferation, the more exhaustively soil water is utilized by the plant. This would enable the plant to function and survive at a lower water status.

A number of researchers concur that extensive root systems are advantageous to plants grown under drought stress and extensive rooting are two of a number of plant characteristics that lead to higher yields under drought conditions (Reicosky and Ritchie, 1976; Hurd, 1974; Cowan, 1965; Ritchie and Jordan, 1972; Gardner, 1960; Taylor and Klepper, 1975; Downey and Mitchell, 1971; Ritchie et al., 1972; Ehlig and Gardner, 1964).

The importance of the root system for the maintenance of water balance in the plant has been emphasized by Weaver (1926). In studying cereal crops, most workers have found that the greater the depth of adequate moisture in the soil, the greater the root penetration and that drying of the upper soil layer increases growth of roots in deeper layers (Kmoch et al., 1957; Weaver, 1926; and Hurd, 1974).

Salim, Todd, and Schlehuber (1965) showed that the extent of root growth of cereal plants was highly correlated with the soil moisture level. They found that the penetration of cereal roots was dependent upon the depth to which the soil contains moisture above the permenant wilting point. The amount of leaf growth gave very little indication of the amount or depth of penetration of the roots. The more drought hardy varieties and species had longer seminal roots and usually more of them. Leaf growth continued on most plants after root growth ceased because of lack of moisture and this tendency was greatest in the most drought susceptible plants. They concluded that these two factors coupled together, i.e., less leaf growth with increased root growth would be advantageous to plants growing in water deficient areas.

Root Density

Kmoch et al. (1957) studied the root development of winter wheat as influenced by soil moisture and nitrogen fertilizer. They found that roots attained a depth greater than 3 feet when soil was wetted to a depth of 4 or 6 feet, as compared with 2.5 feet for wetting depths of 0 and 2 feet. Roots which developed under less favorable moisture conditions were finer and had longer branches than roots that developed under favorable moisture conditions. A dense network of of roots developed in the soil which had received no supplemental moisture, even though soil moisture tension was above 15 atmospheres at depths greater than 12 inches. Roots were observed as deep as 13 feet where moisture conditions were favorable. Nitrogen fertilizer increased root weights at all moisture levels and nearly all soil depths and permitted more complete utilization of subsoil moisture.

Gardner (1960) states that water uptake does not occur at a constant rate, but rather, undergoes diurnal fluctuation. Uptake is more nearly a sinusoidal function of time, with a suction at the plant root fluctuating about a mean value which increases approximately as soil moisture content decreases. The rate of uptake of water per unit length of root is proportional to the total transpiration rate and inversely proportional to the total length of the root system. The more extensive the root system, the lower is the rate of uptake per unit length of root, assuming a given rate of transpiration. He continues that the water transmitting properties of the soil undoubtly play an important role in determining the optimum rooting habit, from the standpoint of rooting density, as well as depth of root zone.

Denmead and Shaw (1962) point out that the density of rooting can be a factor responsible for the early reduction of transpiration as soil dries. When atmospheric stress is great, transpiration begins to decrease almost immediately upon reduction of soil moisture content below field capacity. They concluded that for a low density of rooting, transpiration may indeed densities, however, transpiration is maintained for some time and is almost completely independent from the soil moisture condition.

Root Resistance

Newman (1969a, 1969b) attempted to explain differences arising in the literature between the relationship of soil water availability and evapotranspiration rates on the basis of differences in the resistance involved when water moves to an individual plant root from the soil around it. He concluded that there appears to be no definite evidence for appreciable rhizosphere resistance in soils with a soil-water potential above the permenant wilting point. The experimental evidence, therefore, does not conflict with the conclusion, reached on theoretical grounds, that for many species the rhizosphere resistance will not become appreciable until the soil is near or beyond the permenant wilting point and that appreciable rhizosphere resistances occur much less often than is commonly supposed.

In determining the importance of plant resistance, Barrs and Klepper (1968) report that in pepper, plant resistance to water flow is located unequivocally within the roots. They found a diurnal variation in root resistance associated with cyclic behavior and this resistance is affected by poor aeration.

Skidmore and Stone (1964) state that stress can only occur if there is appreciable resistance to water flow within the plant causing the rate of water loss to exceed the rate of uptake. They suggest that the main resistance to flow in the plant, capable of causing leaf-water stress, is situated in the root.

Wind Stress

The atmosphere manifests its influence on plant growth and regulation of water use in many ways. The relative humidity, temperature of the air, evaporative demand, latent heat of vaporization, sensible heat, and wind are all basic products and components of the atmosphere. Each of these have marked influences on soil-plant water relations.

It is commonly believed that the main effect of wind on leaf performance is to alter the boundary-layer diffusive resistance between the ambient air, regulating diffusion of CO_2 and water vapor to and from the leaf (Grace, 1974). According to Monteith (1965), the rate of flow of air, particularly at low wind speeds (0-1 $m \cdot sec^{-1}$), can exert a controlling influence on photosynthesis and transpiration.

Few studies show the effects of wind on plant-wind relations. In an attempt to examine the effects of an increase in wind speed from 1 $m \cdot sec^{-1}$ to 3.5 $m \cdot sec^{-1}$, Grace (1974) found an increase in transpiration, a decrease in stomatal and cuticular resistance and leaf water content, and a decrease in the boundary-layer diffusive resistance. In all samples, high-wind treated leaves lost more water than those not subjected to high wind speeds.

Stomatal Resistance

In an earlier study, Grace and Thompson (1973) showed that wind reduces cuticular and stomatal resistance in tall fescue (Festuca arundinacea). Knight (1917) and Stalfelt (1932) obtained rapid transpiration rates at low wind speeds and no further increase as the wind speed rose to about 1 $m \cdot sec^{-1}$. Martin and Clements (1935) found that the effect of wind on the transpiration rate of Helianthus annuus depended on the velocity and had the same relative effect at night as during the day, while Seybold (1932, 1933) concluded that wind had no effect on stomatal transpiration, but only on the cuticular component, particularly in hydrophytes.

In order to understand the mechanisms by which wind protection changes the rate of transpiration, Brown and Rosenberg (1970) reported that sugar beets generally had a lower stomatal resistance in shelter, compared to exposed sugar beets. Similarly in earlier studies, Rosenberg (1966) and Rosenberg et al. (1967) found that stomata on leaves of sheltered beans (Phaseolus vulgaris) remain open more widely than those of unprotected plants. However, data were insufficient for computing diffusive resistance.

Wind can influence growth characteristics and plant form (Grace, 1975; Rosenberg, 1974; Todd et al., 1972; Evans, 1955; Whitehead, 1962). At high to moderate wind speeds, Hill (1921), Finnell (1928), Martin and Clements (1935), and Whitehead (1957) found that these wind speeds reduced growth. However, the results of Deneke (1931) showed an opposite effect of wind. Uptake of CO_2 and, hence, assimilation rate increased with wind speed. In these experiments, leaves or shoots were grown in wind speeds equivalent to about 0.0005 to 0.9 $m \cdot sec^{-1}$.

Growth Characteristics

To reconcile these results, Wadsworth (1959) undertook laboratory experiments to determine an optimum windspeed for plant growth. Rape (Brassica napus) plants were grown in a wind tunnel so that low windspeeds could be controlled. He found that the relative growth rate (RGR) of plants less than 1 cm tall increased with wind speed; plants 1 to 4 cm tall grew optimally at the wind speeds tested; and, the largest plants, 4 to 7 cm tall, showed a decrease in RGR as windspeed increased. Also, as windspeed increased, the leaf area decreased. However, the change in leaf area was not great so changes in the net assimilation rate generally parallell to those in RGR. The wind speed value for optimal growth has not been determined accurately. But measurements with smoke blown on plants suggests that the value lies around 0.3 $m \cdot sec^{-1}$ (Wadsworth, 1959).

Yamoaka (1958) studied the rate of evapotranspiration (ET) from shoots of Myrica rubra subjected to different windspeeds and found ET increased with windspeeds from 0 to 1 $m \cdot sec^{-1}$ under conditions of low illumination.

Hunt et al. (1967) found that the rate of net photosynthesis increased with windspeed, while ET did not, for vegetative stands of alfalfa and orchard grass in a small wind tunnel. Consequently, water use was most efficient under the highest wind regime.

Transpiration

Stalfelt (1932), using single detached leaves suspended in an analytical balance case, obtained a very rapid increase in transpiration with wind up to a velocity of 0.166 $m \cdot sec^{-1}$, a slower increase from 0.166 to 0.5 $m \cdot sec^{-1}$, but no further increase as the wind rose to 1.0 $m \cdot sec^{-1}$. The maximum increase was 140 per cent of the value with no wind. Fibras (1931) obtained similar results with low transpiration rates for cut shoots with a wind velocity of 3.75 $m \cdot sec^{-1}$, but with high rates (shoots in direct sunlight), wind caused a decrease. Briggs and Shntz (1916) concluded from their studies that a correlation between environmental factors and transpiration rates existed. During the growing season, only 2 to 6 percent of the water loss could be attributed to the action of the wind.

Martin and Clements (1935) emphasized that nearly all work in the field of wind research has been done with cut shoots or leaves, which rarely give dependable results, while that with rooted plants has, for the most part, been under natural conditions with no attempt to control wind velocity. In studying the effect of artifical wind on growth and transpiration in *Helianthus annuus*, Martin and Clements used a combination of methods by growing plants in cans, under "neutral" conditions, and produced artificial wind by means of large fans. They found that the effects of wind on the transpiration rate depended on the velocity. With velocities up to about 2 mph (0.899 m•sec^{-1}), the transpiration rate increased, at the onset of wind, and maintained this value as long as the wind acted. For velocities above this, however, there was usually a high increase in transpiration for the first few minutes after the wind was turned on, followed by a fall, which in turn was followed by a gradual increase. The initial increase in the rate of water loss rose with increasing velocity, reaching 138 per cent in the case of the 16 mph wind (7.19 m•sec^{-1}). This caused slight wilting of the leaves and closure of the stomata with consequent reduction in the transpiration rate. They also presented evidence that the closure of the stomata was partly mechanical (flapping leaves causing abrasions) and partly due to lowering the say content of the leaves. Winds greater than 5 mph (2.25 m•sec^{-1}) practically always induced closure of the stomata and winds lower than 2 mph (0.899 m•sec^{-1}) almost never caused closure. Winds between 2 and 5 mph (0.899 to 2.25 m•sec^{-1}) reduced closure only part of the time. The data also indicated that stomata may close to about one fith of their maximum opening without affecting the transpiration rate markedly. It should be noted that these results were for short-time treatments.

Sheriff (1974) found a transient change in the rate of water uptake of leaves or shoots of plants, in a direction opposite to that of the subsequent change. This transient change occurred if the plant's environment was suddenly altered (i.e., wind stressed). The transient effects seened not to be linked with stomatal changes, in contrast to results obtained by Raschke (1970).and Raschke and Kühl (1969), but were probably due to changes in the values of leaf water path parameters.

Mechanical Damage

The most noticeable effect of wind stress on higher plants, particularly in cereal grasses, is lodging. Thompson (1974) reported other aspects of mechanical damage in *Festuca arundinacea* Schreb. subjected to wind-treated plants had consistently higher specific fold lines frequencies than the control plants. Through the use of stereoscan electron microscopy, severe damage to the leaf surface resulting from leaves rubbing over each other was detected.

The significance of surface abrasions in relation to increased transpiration is discussed by Grace (1974). The reduction in cuticular and stomatal resistance (hence, increased transpiration) as a result of wind stress may be attributed to increased number of collisions between neighboring leaves with consequent development of abrasions and surface wear. Hall and Jones (1961) noticed a similar result in *Trifolium repens* leaves in abrasive contact with the ground, whereby much of the epicuticular wax was lost.

The findings by Grace and Thompson (1973) showed that after a period of exposure in a wind tunnel, wind-treated plants had reduced rates of photosynthesis and lower leaf diffusion resistances. Subsequent studies by Grace (1974) concurred and added that all samples of high wind-treated leaves lost more water than those not subjected to high windspeeds. This can be explained, according to Grace, partly in terms of mechanical damage incurred by the plant. Grace also suggested that guard cells opened at high windspeeds because less pressure was exerted on them by epidermal cells remaining intact, which were able to bulge into some of the space relinquished by their flaccid wind-damaged neighbors. This may explain why the leaf water deficit required for stomatal closure is so high in the case of wind-treated plants.

As to the quantitative damage caused by leaves rubbing over each other, Thompson (1974) suggested that measurements of an indirectly-affected parameter, such as a diffusive resistance or transpiration rate, may be more meaningful than trying to assess the adverse affects of mechanical damage due to wind stress by visual observation.

Row Directional Orientation Effects

Experiments regarding the effect of row directional orientation on growth of wheat in windy areas are few. In Oklahoma, winds are strong and during the active growing season of winter wheat in the spring, they prevail from a southerly direction. Wheat on the leading edge of a field perpendicular to the wind is shorter than wheat in the interior of the field or on edges not facing the wind. However, this phenomenon is not unique to wheat, but other crops, such as corn, as well. This effect is especially pronounced in the Panhandle of Oklahoma where winds are stronger than in central Oklahoma (J. F. Stone, personal communication). It is reasonable that wind should affect growth of crops planted in different row directions. Lemon et al. (1963) showed for corn that rows perpendicular to the wind teneded to generate more turbulence than rows parallel to the wind.

Yield

Recently it has been reported that the direction of rows of field crops may affect crop yield. Pendleton and Dungan (1958) have shown that spring oats drilled in north-south direction yielded significantly more grain than those seeded in east-west direction in four out of seven years. In the remaining three years, the increase was in favor of north-south plantings. Similarly, Dungan (1955) found that maize crops sown in north-south lines produced green fodder, unhusked ears per plant, unhusked ears per acre and plant height significantly more than crops sown in east-west lines. Sandhu (1964) in studying the effect of row direction on the growth of bajra (<u>Pennisetum</u> <u>typhoides</u>) found that due to north-south rows, the percentage increases in height per plant, forage and grain yield per acre was 2.5, 5.8, and 8.3 respectively, as opposed to east-west rows. However, these increases were not statistically significant. Other experiments have been done, without considering the effect of wind, using crops (barley, corn, pearl millet, oats, wheat) oriented in different row directions. These experiments all gave the same result. Yield was greater with north-south rows than east-west rows (Austenson and Larter, 1969; Donald, 1963; Patil and Bhardwaj, 1976). However, two studies with barley and corn showed no effect of row orientation on yield (Yao and Shaw, 1964; J. C. Smith, 1976. The effect of row direction and row spacing on several agronomic characters of winter barley. M.S. Thesis. Univ. of Georgia, Athens, Georgia. pp. 30). Both studies were done in non-windy areas (Iowa and Georgia).

Light Interception

The reason for the better growth in north-south rows has been associated with better light interception. For example, Pendleton and Dungan (1958) in Illinois showed that light intensity between rows of oats was higher from 1000 hours to 1400 hours in the north-south rows than in the east-west rows, but lower in the earlier and later parts of the day. Soil moistusre was higher in the east-west rows, but whether because of soil shading or less water use by the crop was not determined. Allen (1974) concurred and developed a model which predicts that north-south rows should have the greatest light penetration (provided rows are distinct). Chin Choy et al. (1977) in Oklahoma found that peanuts (<u>Arachis</u> <u>hypogaea</u> L.) grown in 30 cm wide, north-south rows lost less water to evapotranspiration than those in

30-cm east-west rows, 90-cm north-south rows, or 90-cm east-west rows. Row direction, therefore, in association with row width (spacing), had an effect on evapotranspiration. Net radiation was lower in narrow rows than wide rows. Because less radiant energy penetrated to the soil level with the narrow rows compared to wide rows less water was evaporated from the soil. The water conserving effect of narrow rows has been noted by others (Chin Choy and Kanemasu, 1974; Adams et al., 1976; Chin Choy et al., 1977). In addition, a peanut plant in the 30-cm east-west rows probably lost more water than a peanut plant in the 30-cm north-south rows because, not only was it competing for water with closely-spaced plants, but also it was facing directly into the prevailing southerly wind.

The internal water status of wheat grown in different row directions has not been reported in literature. The studies of soil water and row orientation (Pendleton and Dungan, 1958; Chin Choy et al., 1977) suggested that moisture availability to plants may be affected by row orientation.

CHAPTER III

METHODS AND MATERIALS

Experiment I

Plant Culture

Certified winter wheat seeds (Triticum aestivum L. 'Osage') were placed in two wooden germination trays (30 x 61 x 10 cm) containing 1:1 sand/vermiculite mixture and allowed to germinate in a Horblit growth chamber (Denver, Colorado) at the Controlled Environment Research Laboratory, Oklahoma State University, Stillwater, Oklahoma. Temperature controls were set at $18^{\circ}C$ (day) and $16^{\circ}C$ (night). The relative humidity varied from 72 to 99 percent. The light quantum flux density, provided by cool-white fluorescent and incandescent lights was 148 $mE \cdot m^{-2} \cdot sec^{-1}$ at the top of the plants from 0600 to 1800 hours. For three weeks, 500 ml of water was added to each germination tray every other day. The trays were then placed in a cold room (vernalization chamber) at the Oklahoma State University Agronomy Research Station, Stillwater, Oklahoma, for six weeks. Temperature in the vernalization chamber was held at $5.6^{\circ}C$ and 300 ml of one-tenth strength Hoagland solution (Kirkham et al., 1969) was applied biweekly.

After vernalization, the trays were put back in the Horblit growth chamber and allowed to grow for one week, during which time 200 ml of half-strength Hoagland solution were added daily. Subsequently, the seedlings were extracted from the sand/vermiculite mixture and placed in 15 x 15 cm (OD) test tubes containing full-strength Hoagland solution for one week.

Upon removal of the seedlings from the test-tubes, 36 plants were selected for the ensuing experiment. Selection was based on equivalent size, growth stage, and health. These plants were then transferred to containers, described below, which held the split roots.

Apparatus and Design

The split root containers consisted of two 1127 cm^3 (23 x 7 x 7 cm) Oklahoma State University milk cartons (Tulsa Paper Company, Tulsa, Oklahoma) connected by water-proof contact cement. Twelve paired cartons were constructed to accommodate three plants each. Roots were split between soil and soil, soil and nutrient solution, and nutrient solution and nutrient solution. The vegetative portion of the plants was supported by No. 10 cork stoppers with a 1.3 cm hole. Each stopper was positioned on top of the paired cartons so that half of the roots from the three plants would grow in one side of the paired cartons and half of the roots would grow in the other side. No carton had drainage holes.

Full-strength Hoagland solution (Ψ_{π} = 0.8 bar) was used for roots split in nutrient solution. The nutrient solution was aerated using an air pump (Hush III Aquarium Pump, Model 83, Metaframe Aquarium Products, Maywood, NJ). The soil was a Kirkland silt loam obtained from the top 30 cm layer at the Oklahoma State University Agronomy Research Station, Stillwater, Oklahoma. It was sterilized in an autoclave. Each carton with soil contained 1330.6 + 0.1 g of soil. Cartons containing nutrient solution and soil were covered with black plastic and paper towels, respectively, to minimize evaporation.

There were two treatments. One treatment was subjected to wind and the other received no wind. Wind treatment began on February 15, 1977. Both treatments had two replications, three paired cartons per replication. To separate the two treatments, a plywood barrier (195 x 91 x 1 cm) was placed in the center of the growth chamber, along the lengthwise axis. Wind was generated by a 33 cm diameter electric fan (Type No. 73646, Emerson Electric Company, St. Louis, Mo.). Wind speed determined with an anemometer (Taylor Biram Type 3132, Chicago, Ill.), was 6.3 and 3.4 $m \cdot sec^{-1}$ for the plants nearest and farthest from the fan, respectively. Wind speed on the side of the plywood barrier without the fan was less than 0.4 $m \cdot sec^{-1}$. Plants were rotated from front to back daily to ensure that all plants were rotated from front to back daily to ensure that all plants were receiving equal amounts of wind throughout the experiment. Plants not receiving wind were rotated in the same way. The plants were subjected to wind

24 hours per day throughout the entire experiment which lasted from February 15 to March 24 (38 days). Pan evaporation was measured daily for both treatments. The average pan evaporation rates for the wind and no-wind treatments were 65.2 $ml \cdot day^{-1}$ and 17.5 $ml \cdot day^{-1}$, respectively.

Procedure

Both treatments with plants having roots in soil were well-watered for the first 14 days. Amounts of water added to the soil and nutrient solution were recorded. After 14 days, no water was added to containers with soil. The experiment was concluded on March 24, 22 days after soil containers had received no water. Nutrient solution was added to cartons with nutrient solution the last 22 days and amounts were recorded.

Measurements

Plant height measurements began on the first day (February 15) and were made every three days during the experiment. Three measurements of each split-root setup were taken from the base of the plant to the top. Height values reported are the mean of six values (three measurements x two replications).

Leaf area was measured using a LI-COR Leaf Area Meter (Model LI-300, Lambda Instrument Crop., Lincoln, Neb.). Measurements were conducted weekly throughout the experiment. At each measurement time, three leaves from each split-root setup were measured. Leaf area values reported are the mean of six samples (three leaves x two replications).

Leaf-water potential measurements were conducted about every four days starting on February 21 using a pressure bomb (Model 3005, Soil Moisture Equipment Crop., Santa Barbara, Calif.), similar to the design of Scholander et al. (1965). At each sampling time, three samples from each split-root setup were taken. Potential values reported are the mean of six samples (three samples x two replications).

Stomatal resistance measurements were determined on every weekday of the experiment using a LI-COR LI-65 Autoporometer and LI-20S Diffusion Resistance Sensor (Lambda Instrument Crop., Lincoln, Neb.) as designed and calibrated by Kanemasu et al. (1969). Stomatal resistance values reported are the mean of six samples (three samples x two replications).

For plants in nutrient solution, transpiration rates were ascertained by adding nutrient solution on weekdays to the same level (1 cm below top of carton). Amounts added were recorded and a transpiration rate was determined in $ml \cdot day^{-1}$. Moisture content of the soil was determined with a moisture probe (Moisture Meter, Green Thumb Products, Apoka, Fla.). The probe was calibrated by determining gravimetrically the moisture content of the soil at different readings on the scale of the moisture probe.

The stage of growth for the plants was determined by visual observation in accordance with the scale devised by Feckes (1941) for the growth stages of cereals. Such observations for each split root setup were made weekly throughout the experiment.

Determination of the relative growth rate (RGR) was calculated from plant height data. The RGR was computed every three days. The first day of the experiment, February 15, was established as the baseline for computing the RGR.

Fresh- and dry-weight measurements were made at the end of the experiment. Leaves and roots were weighed separately immediately after harvest. After the fresh weights were obtained, the leaves and roots were oven dried at 75°C and weight to obtain dry weight. Subsequent evaluation for per cent water content and leaf to root ratio was calculated for each split-root setup (three plants).

Root length determinations were conducted using a method of estimating total length of root in a sample by Newman (1966) and March (1971). This required a line grid of $\frac{1}{2}$ inch (1.28 cm) squares drawn on paper laid under a 7.68 cm petri dish. A sample of the roots was selected and placed in the petri dish. Roots were manipulated so that they filled the measuring area. No rearrangement of the roots was required after teasing out concentrations for easy counting. Intersections were systematically counted and divided by two to give inches of line (or inches of roots). Five counts for each set of roots per carton were made and averaged to obtain the value for root length.

EXPERIMENT II

Design

The study was conducted from October 11, 1976 to June 13, 1977 at the Oklahoma State University Agronomy Research Station, Stillwater, Oklahoma, Plot #6200, S $\frac{1}{2}$ Sec. 16, T16N, R2E. Certified winter wheat seed (Triticum aestivum L. em Thell. 'Osage') was planted on two adjacent plots, each measuring 50 x 50 m. Wheat was planted, with 18 cm between rows, in four directions: north-south (NS), east-west (EW), northeast-southwest (NE-SW), and northwest-southeast (NW-SE). Therefore, there were four treatments. The NS and EW treatments measured 50 x 3 m and the diagonal treatments measured 70 x 3 m. There were 21 plants per meter. Planting dates were October 11, 1976 and October 23, 1976 for the two plots.

The soil was a Kirkland silty loam (Okla. Agric. Expt. Stn. Processed Series P-315, 1959) which is classified as a Paleustoll (Gray and Roozitalab, 1976). Phosphorus fertilizer (0-46-0) was incorporated into the soil on October 9, 1976 at a rate of 270 kg/ha. Nitrogen fertilizer (46% urea) was applied on March 15, 1977 at a rate of 250 kg/ha.

Measurements

Sixteen areas, each measuring 15 x 1.5 m, were harvested, eight areas in each plot. Each half of a row-direction treatment was harvested (i.e., the N side of NS plots, the S side of the NS plots, etc.). Test weight and yield of each harvested area were determined.

Meteorological data were provided by the Oklahoma State University Agronomy Research Station Class AB Weather Station, Stillwater, Oklahoma (NOAA. Okla. Climatological Data, 1976-1977; NOAA. Local Climatological Data. Tulsa, Okla., Oct., 1976-June, 1977). Pan evaporation data were available only between April 1 and September 30. Water in the soil profile at the weather station was determined using a Nuclear Chicago P-19 neutron probe (Chin Choy et al., 1977).

Plant height was recorded weekly from the data of emergence to harvest (for all treatments for the north-plot). (Plant height data for the south-plot were unavailable for three months due to the uncertainty of crop growth shortly after planting.) Concurrent measurements of stomatal resistance, leaf-water potential, and leaf area were conducted on April 12, 19, 27, and May 5, 11, and 19, 1977, at 1000, 1300, and 1600 hours.

Stomatal resistance measurements on the upper surface of flag leaves were made using a LI-COR LI-65 Autoporometer and LI-20S Diffusion Resistance Sensor (Lambda Instrument Crop., Lincoln, Neb.) as designed and calibrated by Kanemasu et al. (1969). Eight leaves in each of the four row-direction treatments in each of the two plots were measured at each time. Stomatal resistance values reported are the mean of 16 measurements per treatment.

Leaf-water potential measurements were conducted using a pressure bomb (Model 3005, Soil Moisture Equipment Corp., Santa Barbara, Calif.), similar to the design of Scholander et al. (1965). At each sampling time, four samples from each treatment in each plot were taken. Potential values reported are the mean of eight samples.

Leaf area was measured using a LI-COR Leaf Area Meter (Model LI-300, Lambda Instrument Corp., Lincoln, Neb.). Leaf-area measurements were conducted at 1000 hours, at which time four samples were taken from each treatment per plot. Leaf-area values reported are the mean of eight samples.

Environmental Parameters

Environmental parameters considered for April 12, 19, 27, May 5, 11, and 19, 1977, were dry- and wet-bulb temperatures, relative humidity, wind speed, solar radiation, and cloud cover. Each parameter was measured at 1000, 1300, and 1600 hours.

Dry- and wet-bulb temperatures were measured using a sling psychrometer (Model 1328A, Taylor Instrument Co., Rochester, N.Y.). Temperatures were converted from Farenheit to Celsius to determine relative humidity values using a relative humidity chart (U.S. Army Field Manual, FM-16, Chart VIII, 202 p.).

Wind speed was measured using a Taylor Biram's Type Anemometer (Model 3132, Taylor Instrument Co., Rochester, N.Y.). Wind speed values were obtained by holding the anemometer 30 cm above crop height for one minute. Values were converted to $m \cdot sec^{-1}$.

Solar radiation was measured using a LI-185 Quantum/Radiometer/Photometer and LI-200S Pyranometer Sensor (Lambda Instrument Corp., Lincoln, Neb.) as patterned after Kerr et al. (1967). The pyranometer sensor was placed at crop height using a 7.6 cm diameter mounting and leveling fixture.

Cloud cover values were based on a scale of zero to ten, or clear to overcast, respectively. The values ascribed to particular cloud cover conditions were determined by visual observation in accordance with the standards set by the National Oceanic and Atmospheric Administration (NOAA. Local Climatological Data. Tulsa, Okla., Monthly Sum., Oct., 1976-June, 1977).

The 1976 to 1977 growing season for winter wheat was characterized by a very dry fall and a wet spring. Total precipitation during the study was 50 cm. February and March were the windiest months. Winter air temperature was mild with an average low of -2.4°C for the month of January.

CHAPTER IV

RESULTS AND DISCUSSION

Experiment I

Potential

Figure 1 shows the potential of water in the leaves of the split-root plants grown with and without wind. Values obtained during the experiment have been averaged and are presented in Table 1. Both with and without wind, potentials of the plants with roots all in solution (highest potentials) and roots all in soil, especially after water was withheld from the soil beginning on March 3. Before soil drought, leaf potentials of plants with roots in all soil were 2 and 3 bars lower than those of plants with roots all in solution for plants in wind and out of wind, respectively (-9.2 - (-12.4)=3.2; -9.8-(-12.1) =2.3, Table I). Soil matric potential, therefore, appeared to have a 2 and 3 bars effect on leaf water potential for plants in wind and out of wind, respectively. The effect of soil matric potential on leaf potential of plants with roots split between soil and solution was intermediate between its effect on potentials of plants with roots all in soil or all in solution. These results are at odds with those of Meyer and Gingrich (1964) who trimmed the root system of wheat

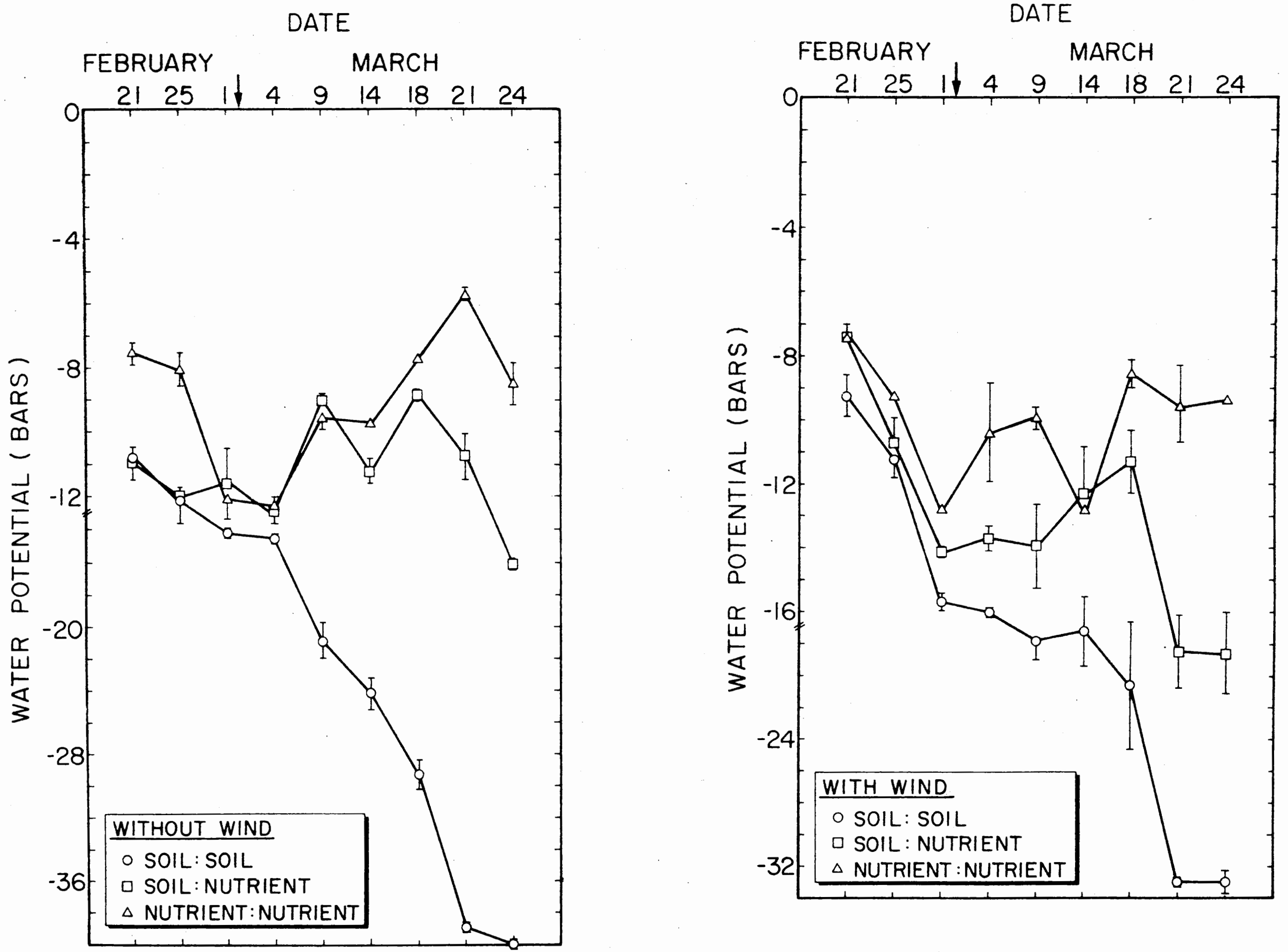

Figure 1. Leaf-water Potential of Wheat Plants with Roots Split between Soil:Soil, Soil:Nutrient Solution, and Nutrient Solution:Nutrient Solution

TABLE I

AVERAGE LEAF WATER POTENTIAL AND STOMATAL RESISTANCE OF SPLIT-ROOT WHEAT PLANTS

	No Wind			Wind		
	Soil:Soil	Soil:Soln	Soln:Soln	Soil:Soil	Soil:Soln	Soln:Soln
			Leaf Potential (bars)			
Pre-drought	-12.4	-11.5	- 9.2	-12.1	-10.8	- 9.8
Drought	-28.0	-11.5	- 9.0	-22.9	-14.7	-10.1
			Stomatal Resistance ($sec \cdot cm^{-1}$)			
Pre-drought	4.5	1.6	0.8	2.7	1.4	0.4
Drought	15.1	2.5	0.6	13.2	4.9	0.5
			Water Added ($ml \cdot day^{-1}$)			
Pre-drought	34/34	15/165	91/90	48/48	29/194	119/127
Drought	0/0	0/208	110/111	0/0	0/214	116/117
			Height Change (cm)			
Pre-drought	11.2	21.6	21.6	9.5	11.9	1.7
Drought	9.1	16.5	10.4	3.7	18.7	1.4
			Leaf Area Change (cm^2)			
Pre-drought	3.7	7.2	6.1	4.0	4.5	3.5
Drought	-13.6 (loss)	13.2	14.7	-13.3 (loss)	2.5	9.6
			Root Length (cm)			
At Harvest	2062/1458	5655/737	1804/1217	1641/1825	221/925	1800/1365

For experimental conditions, see legend of Figure 1. Water added to the two sides of the containers, height, and leaf-area change during the pre-drought and drought periods, and root length at harvest also are given.

seedlings to two roots and found no effect on the leaf relative turgidity, which indicated leaf water status, when one root was subjected to a 1 bar stress using Carbowax 6000 and the other root was in nutrient solution. In this experiment, the water status of the leaf was affected by the root medium (soil compared to nutrient solution).

Gingrich and Russelll (1957) compared the growth of corn seedlings subjected to either an osmotic stress or a moisture stress and found that growth was suppressed more by a given moisture stress than by a comparable osmotic stress. The results of this experiment euggest that this is true at very high potentials. Even though full strength Hoagland nutrient solution was used (-0.8 bar), potentials were higher in plants with roots in nutrient solution than plants with roots in soil with a matric potential of (about) -0.3 bar.

When plants grown under the same split-root treatment and placed in wind were compared to plants grown with no wind, there was essentially no difference in potential. This was true both before and after water was withheld from soil (e.g., compare -12.4 and -12.1 bars; -28.0 and -22.9 bars; -11.5 and -10.8 bars, Table I).

The potential difference between the root medium and the leaf was much larger (more than 8 bars) than the difference in leaf potential of plants with roots all in solution or all in soil (2-3 bars) (e.g., -0.3-(-12.4)=12.1 bars; -0.8 - (-9.2)= 8.4 bars, Table I). Even when plants were grown in nutrient solution or well-watered soil, the highest average plant water potential measured was -9.0 bars (Table I).

Gardner and Ehlig (1963) found that the average plant (birdsfoot trefoil) leaf potential was about 9 bars below the soil potential when the soil potential was high. When the soil potential reached -15 bars, the leaf potential was about -28 bars. At the end of this experiment, when the soil was dry, leaf potential of plants with roots all in soil was -32.9 and -39.9 bars for plants in and out of wind, respectively. Even when soil potential was high, there was an appreciable resistance to water movement in the plant.

Stomatal Resistance

Figure 2 illustrates the stomatal resistance of the adaxial surface of leaves of the split-root plants grown with and without wind. Values obtained during the experiment have been averaged and are presented in Table I. The matric potential had an effect on stomatal resistance. Leaves of plants grown in soil and solution, both with and without wind, and both before and after soil drought, had stomatal resistances which were usually between those of leaves of plants grown all in soil or all in nutrient solution. Plants grown in nutrient solution had the lowest stomatal resistance.

Stomatal resistance of leaves of plants in wind was slightly less than resistances of leaves of plants grown with no wind except for plants with roots split between soil and solution after soil drought was imposed (Table I). Stomatal resistance of leaves of these plants in wind was two times greater than that of leaves of plants grown

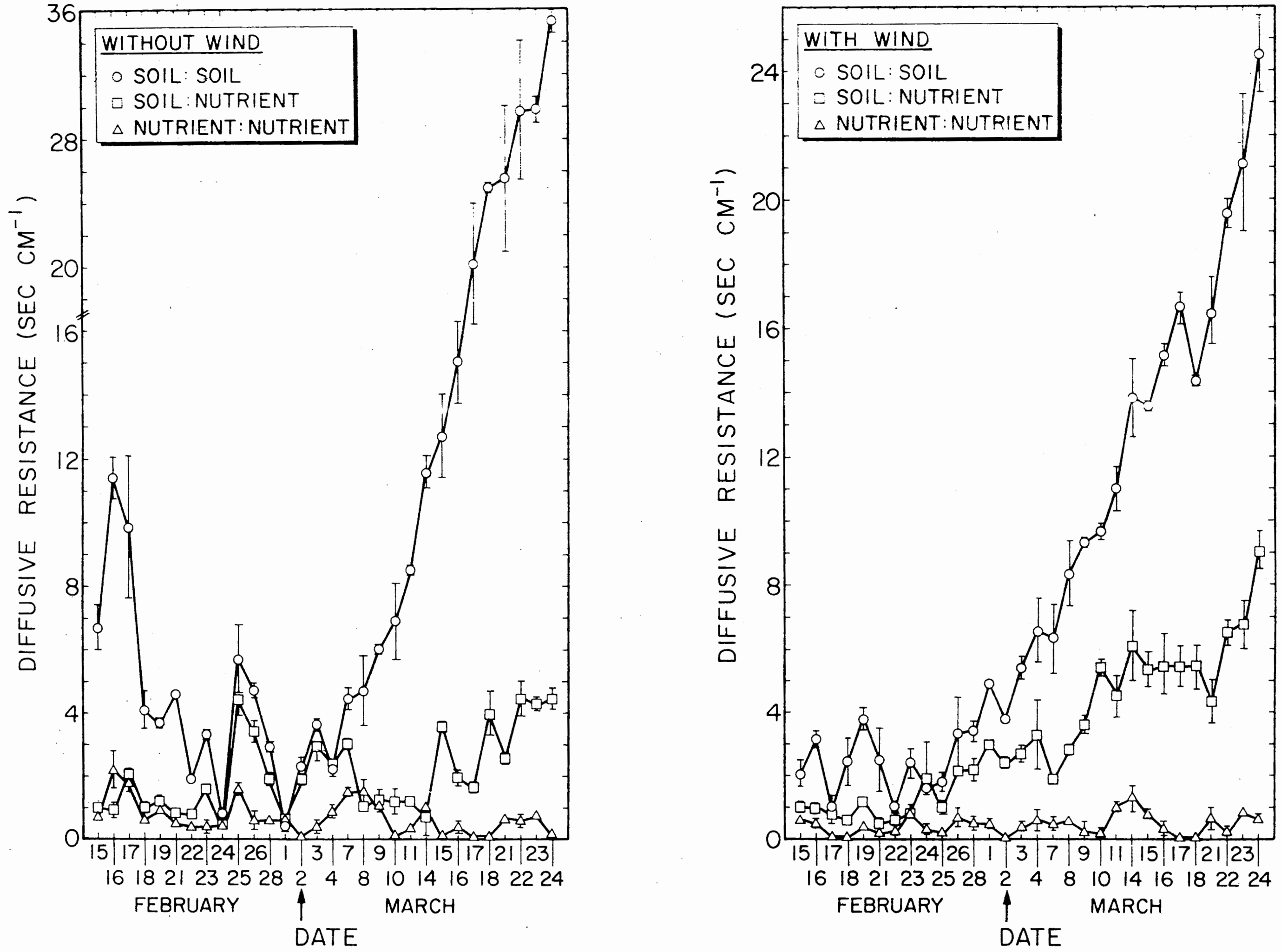

Figure 2. Stomatal Resistance of Split-root Wheat Plants

without wind (4.9 vs. 2.5 sec•cm^{-1}, Table I).

Water Added

The average daily amount of water added to the cartons, both before and after water was withheld from the soil, is shown in Table I. Figure 5 shows the amount of water added to split-root wheat plants before and after water was added. Plants grown all in nutrient solution, both with and without wind, used about 2.6 times more water than plants grown all in soil (91 and 90 vs. 34 and 34 ml•day^{-1}; 119 and 127 vs. 48 and 48 ml•day^{-1}, Table I). For plants placed in nutrient solution and soil, 7 and 10 times more water was added to the nutrient solution side of the cartons than to the soil side for the wind and no-wind treatments, respectively (194 vs. 29 ml•day^{-1}; 165 vs. 15 ml•day^{-1}, Table I). Similar results were obtained by Marais and Wiersma (1975) who split soybean roots horizontally between an upper soil layer and a lower quartz-gravel layer bathed in nutrient solution. They noted that the free water supply from the lower compartment resulted in a relatively slow rate of water extraction from the upper soil level. Wind was not a factor in their experiment. In this experiment, more water was added to plants in the wind than to plants out of the wind for all split-root treatments.

Total water added was similar for plants with roots split between solution and solution and between soil and solution (e.g., 91 + 90 ml•day^{-1} = 15 + 165 ml•day^{-1}, Table I). Plants with roots all in soil

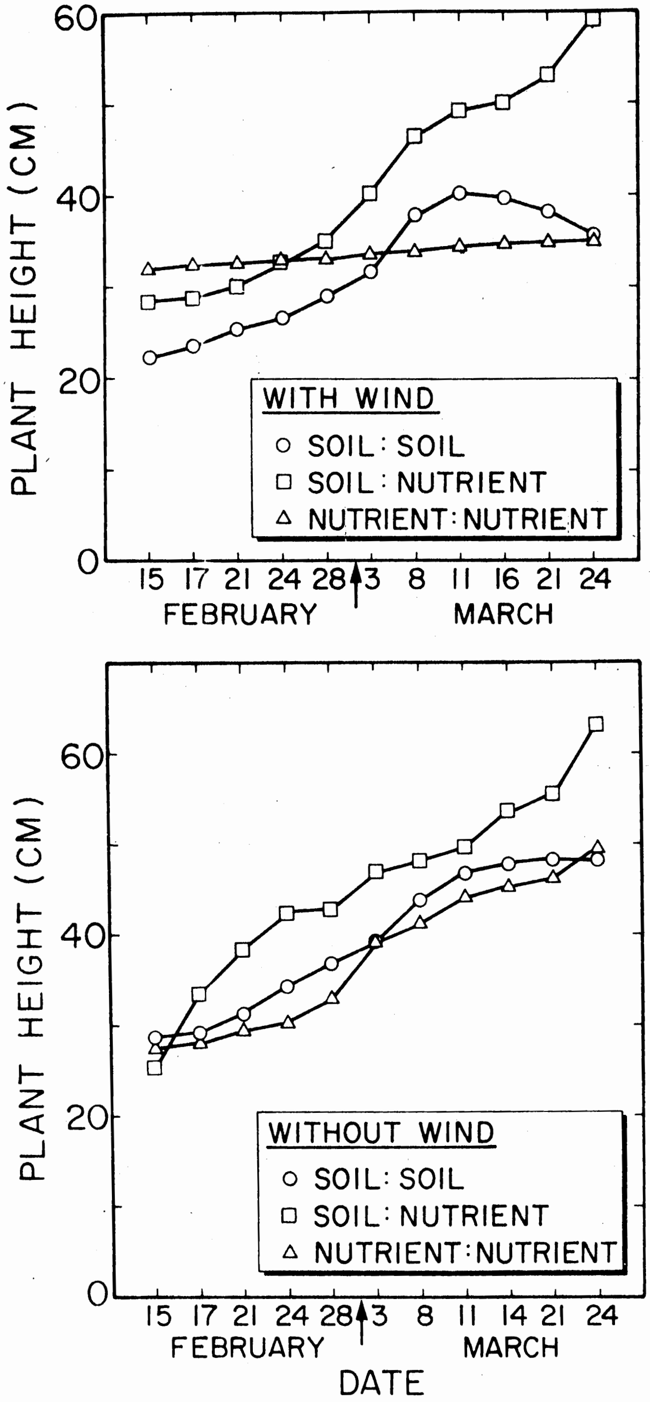

Figure 3. Height of Split-root Wheat Plants

used the least amount of water before water was withheld from the soil.

If one assumes that water flow though the plant is proportional to the potential difference between the root medium and the leaf water potential, an apparent total resistance, R, can be calculated for the root, stem, and leaf using $\frac{\Delta\psi}{\Delta W}$ R where $\Delta\Psi$ is the difference between the potential of the root medium and the water potential in the leaf tissue, and ΔW is the amount of water lost from the containers over a specified period of time (Kirkham et al., 1969). In this experiment before soil was allowed to dry, the soil potential (matric) was about -0.3 bars and the potential (osmotic) of the nutrient solution was -0.8 bars. Using average values from Table I for the amount of water lost, and also for water potential of the leaves before water was withheld from the soil, values for R can be estimated for (1) a plant with all its roots in soil, (2) the portion of a split-root plant with roots in soil, (3) the portion of a split-root plant with roots in nutrient solution, and (4) a plant with all its roots in nutrient solution. The approximate values of R for plants in wind and out of wind thus calculated are listed in Table II.

The apparent total resistance to water movement varied even though the soil and nutrient solution were at similar potentials (-0.3 and -0.8 bars). For plants grown with no wind, R was an order of magnitude greater on the soil side of a plant with roots in soil and nutrient solution than on the nutrient solution side (0.06 vs. 0.72 bar ml^{-1}.

day^{-1}, Table II). For both plants in wind and out of wind, R was about four times greater for plants grown all in soil compared to plants grown all in nutrient solution. Wind reduced R. Water was less available from the soil than from the nutrient solution. The reason for the increased resistance to water flow under the soil conditions is not known. In the well-watered soil, there was probably close contact between the roots and the soil. So it is unlikely that a gap between the soil and roots, such as that discussed by Gardner and Ehlig (1962) caused the resistance. It appeared that the soil reduced the permeability of the root membranes.

Growth

Height. Figure 3 shows the height of plants grown with and without wind as a function of time and Table I shows total height change during the experiment. Plants with roots split between solution and solution and between soil and soil grew about the same in height before water was withheld from the soil (11.7 and 11.2 cm, Table I). Plants with roots split in soil and solution, both with and without wind, grew the tallest compared to plants with roots in soil and soil or solution and solution. Before water was withheld from the soil, wind had little effect on the height of soil-grown plants, but it reduced height of plants in soil and solution and in solution and solution about 2 and 12 times, respectively (Table I). After water was withheld from the soil, wind had little effect on the soil and solution grown plants, but it

TABLE II

APPARENT TOTAL RESISTANCE TO WATER MOVEMENT IN SPLIT-ROOT WHEAT PLANTS

	Resistance, $bars \cdot ml^{-1} \cdot day^{-1}$	
	No Wind	Wind
All Soil	0.35	0.25
Soil side of soil:soln plant	0.72	0.36
Soln side of soil:soln plant	0.06	0.05
All solution	0.09	0.07

For experimental conditions, see legend of Figure 1.

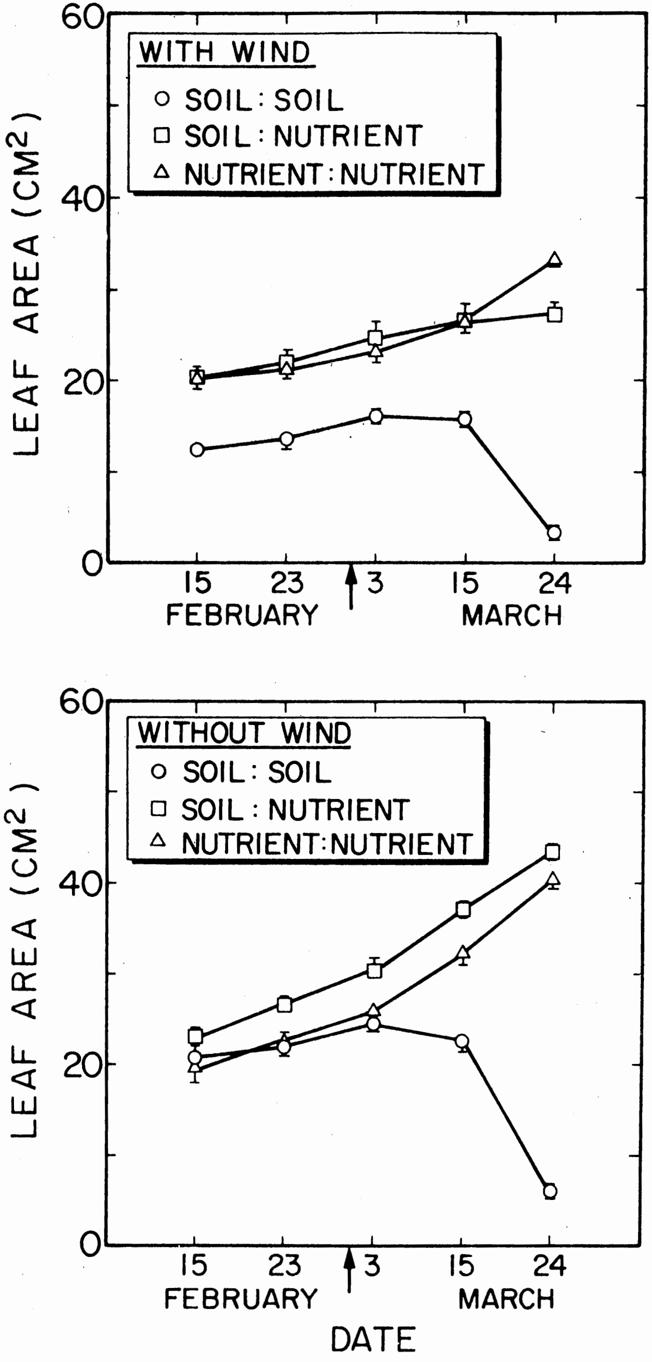

Figure 4. Leaf Area of Split-root Wheat Plants

reduced height of the plants in soil and soil and in solution and solution by 3 and 11 times, respectively (Table I). These results are at variance with those cited by Grace (1975) in a review article on wind. He quoted papers (e.g., Macklon and Weatherley, 1965) which showed that wind speed reduced growth of plants in soil, but not of plants in nutrient solution. In this experiment, wind reduced height of plants grown all in nutrient solution and all in soil. Wind reduced growth of plants in solution by approximately the same amount during the first and second parts of the experiment (12 and 11 times, respectively) because conditions were essentially the same during the entire experiment for these plants. As expected, the combination of wind and water stress reduced growth of plants with roots in soil and soil more than wind stress alone.

Grain Yield

No plants yielded grain except for those grown in soil and nutrient solution and placed in wind. These plants yielded 14.5 g of grain.

Leaf Area

Leaf area results (Figure 4 and Table I) were similar to height results except that leaf area was not as drastically reduced by wind as height was for plants grown in solution and solution. Also, for plants in soil and solution, leaf area was reduced five times by wind

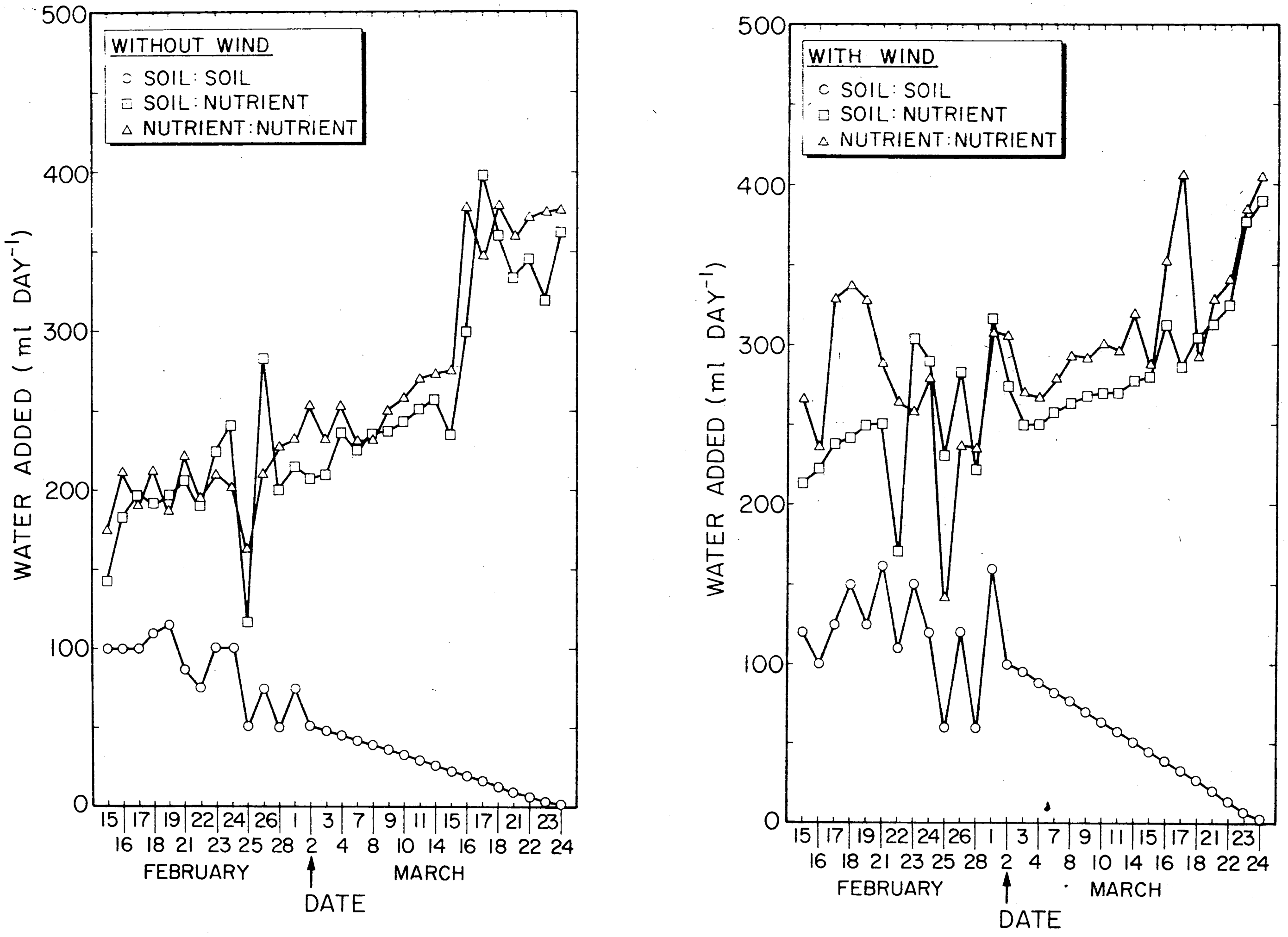

Figure 5. Water Added to Split-root Wheat Plants

after water was withheld, while height was not reduced. These plants responded to the combination of wind and water stress by reducing leaf area, not height. Because most water is lost through the stomata on leaves, and not through stems, it is reasonable that a plant conserves water by reducing leaf area and not height. Leaf area was larger on plants with roots all in solution than that of plants with roots all in soil.

Root Length

Table I shows the total length of roots in the cartons at harvest. Root density can be calculated by dividing root length by carton volume (1127 cm^3). Plants grown all in soil or all in nutrients solution had approximately the same total length of roots. Wind did not significantly change root length for these plants. However, for plants with roots split between soil and solution, and grown with no wind, root length was about seven times more in soil than in nutrient solution (5655 vs. 737 cm, Table I). These results vary with the suggestion that growth of roots into soil may be slower than that into nutrient solution because growth in soil is hindered by mechanical impedance (Newman, 1969a). Wind had little effect on length of roots on the solution side (925 vs. 737 cm, Table I), but length of roots on the soil side in wind was 25 time less than length of roots on the soil side with no wind (221 vs. 5655 cm, Table I). Plants with roots split between soil and solution and placed in wind had a root length four times less than that of the roots in nutrient solution (221 vs. 925 cm, Table I). Volk (1947) found that corn roots, split between a moist sand layer and a soil layer, grew into air-dry soil and increased the moisture content of the soil. However, Hendrickson and Veihmeyer (1947) reported that roots did not increase the soil moisture content of dry soil. In this experiment, roots of plants grown with no wind proliferated in the soil which was drying out, rather than in the nutrient solution. No increase in moisture content was observed in the soil as it was drying. Roots must have been adjusting osmotically to the drier conditions and water did not move from the roots to the dry soil (Newman, 1974). Plant turgidity was maintained when part of the roots were in solution, so translocation of substances from shoots to roots and root growth could continue even though part of the roots in soil rather to roots in solution. Plants with roots in soil and solution, and grown in wind, developed more roots in solution than soil. The wind stress increased the amount of water lost from these plants and reduced growth. Turgor was probably lower in these plants. With wind, translocation of substances to the roots was apparently limited because there were few roots, especially on the soil side of the soil and solution containers.

Taylor and Klepper (1975) said that water uptake is directly proportional to root density. Similarly, Cowan (1965) postulated that low density of rooting may be associated with high internal plant resistance because of the small area of root cortex available to absorb water from the soil. In this experiment, plants with the highest apparent resistance (0.72 bars$\cdot$ml$^{-1}\cdot$day^{-1}, Table II) had the highest root density (5655 cm/1127 cm^3 = 5.0 cm/cm^3). However, Gardner (1966) has pointed out that soil potential decreases more rapidly in regions of high root concentration than where roots are fewer. Eventually this results in proportionally more water being taken up from the regions with fewer roots than initially. He also cautioned (Gardner, 1966) that in a confined root system, such as the containers used in this experiment, the proliferation of roots may be such that the larger more permeable roots may tend to act in parallel with smaller roots offering greater resistance and, in effect, by-pass the smaller ones. This could result in erroneous calculations of the amount of water taken up per unit length of root.

Experiment II

Wind

Table III shows the environmental conditions during the study, including the direction, amount, and duration of wind. About seven times more wind blew in the NS direction than in the EW direction. In fall and winter (October-February), most wind came out of the north. In the spring (March-June), most wind came out of the south and southeast.

TABLE III

ENVIRONMENTAL CONDITIONS DURING ROW ORIENTATION EXPERIMENT

Monthly Data

Month	Rain	Average Temperature	Average Evapotranspiration	Average Water in Profile to 120-cm Depth	Wind
	cm	^{o}C	$cm \cdot day^{-1}$	cm	km
October	4.1	12.6	-----	25.8	4261
November	1.7	6.0	-----	27.8	
December	0.4	3.5	-----	31.8	
January	1.0	- 2.4	-----	35.3	
February	4.0	6.4	-----	37.0	
March	6.1	11.2	-----	35.8	
April	6.8	16.7	0.56	36.7	4383
May	23.8	22.3	0.66	37.5	4547
June	2.1	26.7	0.72	31.7	3952

Wind Direction, Amount and Duration

Direction	Amount	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total
	km	-------------------------------No. of days									------------------------------------
North	7309	2	7	11	11	8	1	3	2	0	45
South	9489	1	9	10	5	4	5	10	12	4	60
East	411	0	0	0	0	1	1	0	1	0	3

TABLE III (Continued)

Wind Direction, Amount and Duration

Direction	Amount	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total
	km	No. of days									
West	2027	0	1	1	2	4	2	1	0	0	11
Northeast	2302	2	3	1	2	3	0	0	3	4	18
Southwest	5171	0	5	3	3	4	5	6	1	5	32
Northwest	4208	1	4	5	4	2	8	2	2	0	28
Southeast	6146	3	1	0	4	2	9	8	10	0	37

Daily Data

Date	Time (hr)	Relative Humidity (%)	Wind $m \cdot sec^{-1}$	Solar Radiation $W \cdot m^{-2}$	Cloud Cover (0-10 with 0=no clouds)
12 Apr. (day 102)	1000	67	1.48	$1.80z10^3$	7
	1300	66	1.87	$2.84x10^3$	6
	1600	72	2.14	$3.96x10^4$	4
19 Apr. (day 109)	1000	64	2.02	$1.92x10^3$	8
	1300	65	2.53	$2.47x10^3$	9
	1600	68	4.81	$1.86x10^3$	10
27 Apr. (day 117)	1000	75	2.62	$2.45x10^3$	3
	1300	76	3.06	$1.92x10^3$	9
	1600	74	6.62	$2.67x10^4$	0
5 May (day 125)	1000	75	9.11	$2.20x10^3$	7
	1300	71	10.12	$1.47x10^3$	10
	1600	74	8.60	$1.03x10^3$	10

TABLE III (Continued)

		Daily Data			
Date	(hr)	Relative Humidity (%)	Wind $m \cdot sec^{-1}$	Solar Radiation $W \cdot m^{-2}$	Cloud Cover (0-10 with 0=no clouds)
11 May (day 131)	1000	45	5.56	2.63×10^3	3
	1300	43	6.07	1.94×10^4	3
	1600	42	4.04	1.86×10^3	6
19 May (day139)	1000	74	6.07	1.36×10^3	8
	1300	65	7.08	1.74×10^3	9
	1600	64	6.12	1.69×10^3	9

Growth

All plants emerged about the same time (14 days after planting). Figure 5 shows the height of the plants oriented in the different directions during the 234-day experiment (Julian days 296-365; and 1-164). Plants placed in the NS rows grew taller than plants placed in the EW, NE-SW, and NW-SE rows. Plants oriented in the EW, NE-SW, and NW-SE directions were similar in height.

Figure 6 shows the leaf area of the plants oriented in the different row directions as a function of time. Plants placed in the NS rows had the largest leaf area, even though the difference was significant only on days 109, 117, and 131. Leaves of plants in the NW-SE rows tended to have the next-to-largest leaf area.

Growth is often reduced in the wind due to mechanical damage (Thompson, 1974), increased plant respiration (Todd et al., 1972), or stomatal closure which reduces photosynthesis (Grace, 1974). Leaf area, in particular, is a sensitive indicator of stress. Plants shed leaves and produce smaller leaves when they are exposed to an environmental stress such as wind. Leaves were more vulnerable to wind damage when plants started to grow rapildy in the spring (after the February 27 and day 58 height measurement, Figure 5). The larger leaf area of the plants oriented in the NS and NW-SE directions suggested that these leaves were least affected by the wind. Leaves of plants in the NE-SW rows, which were perpendicular to prevailing SE winds (Table III) had the smallest leaf area. In non-windy Georgia, Smith,

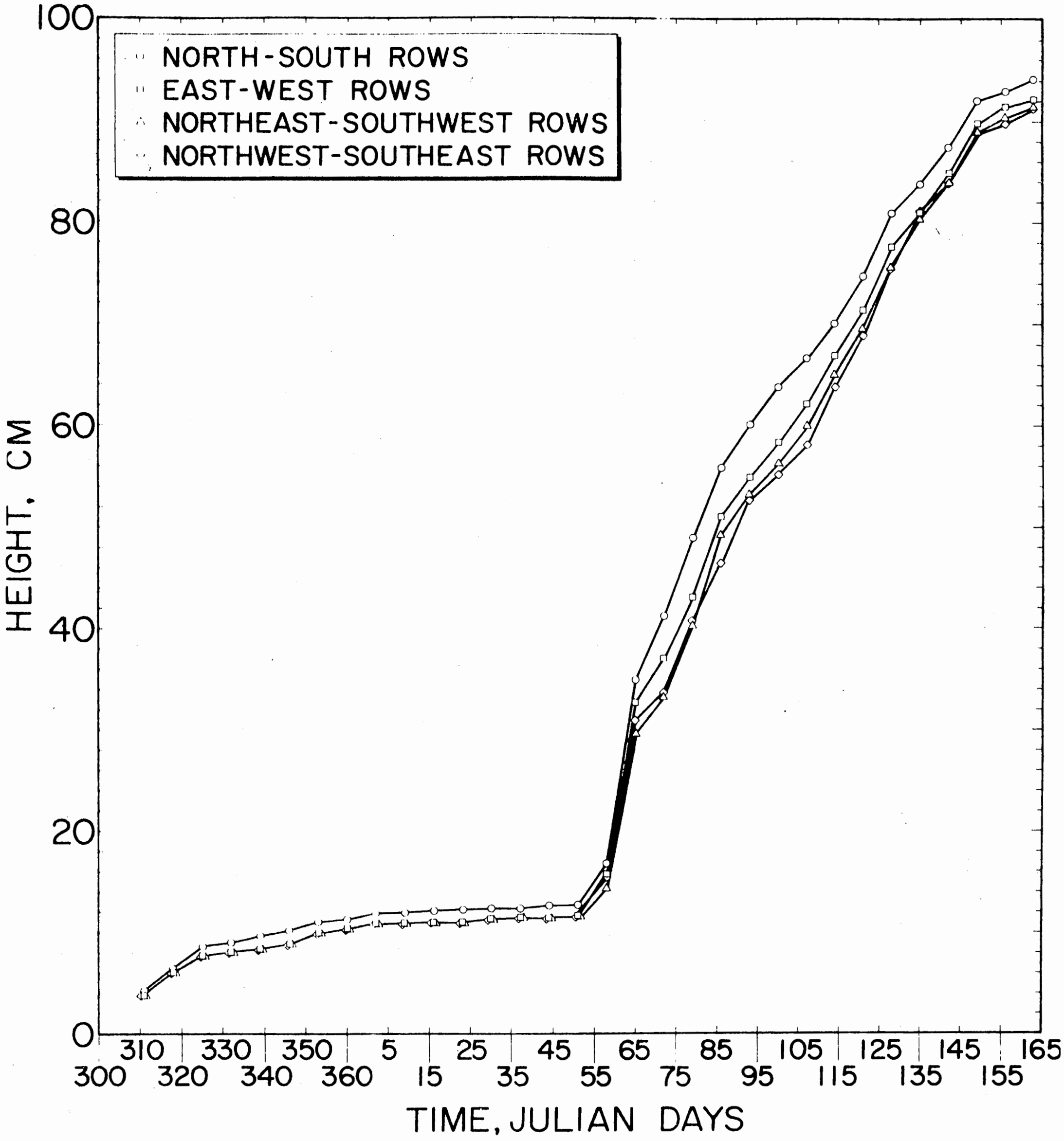

Figure 6. Height of Field-grown Winter Wheat Plants Oriented in NS, EW, NE-SW, and NW-SE Rows

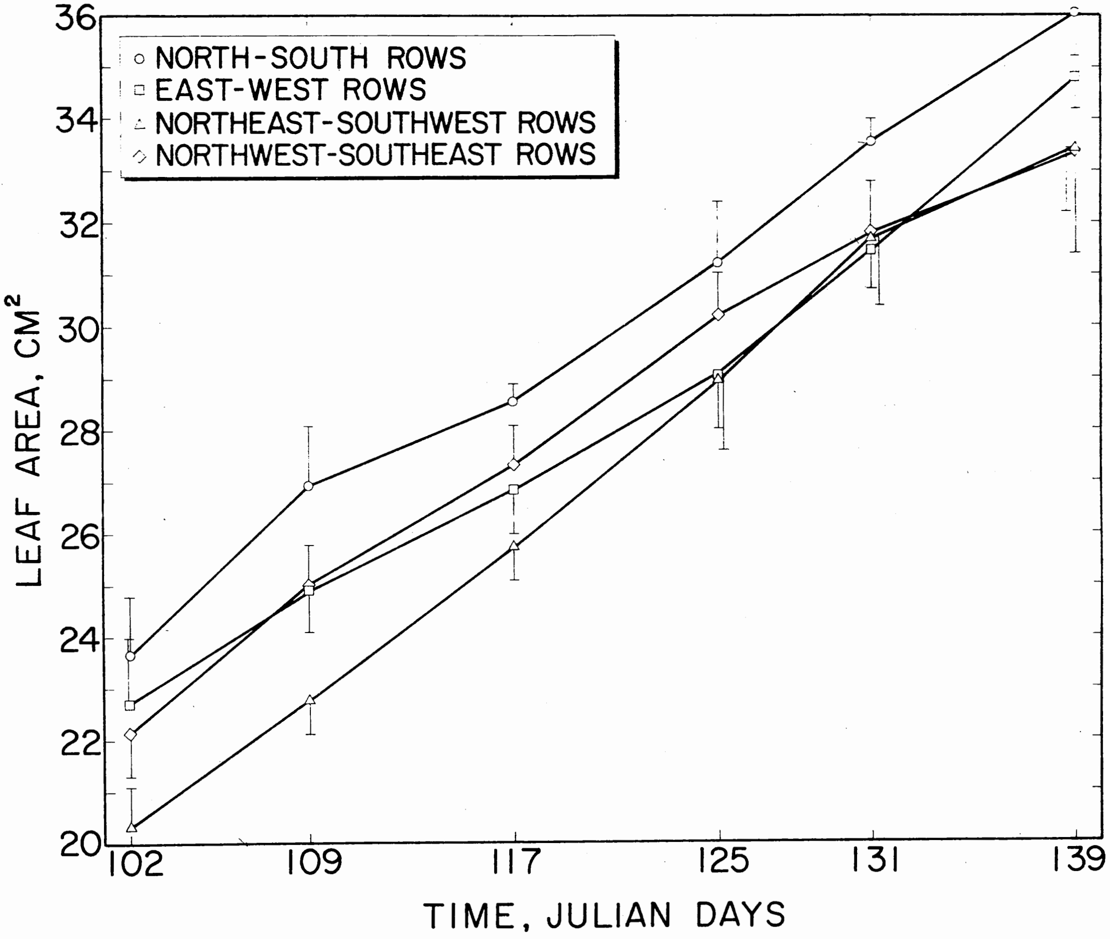

Figure 7. Leaf Area of Field-grown Winter Wheat Plants Oriented in NS, EW, NE-SW, and NW-SE Rows

in the thesis previously cited, found no effect of row direction on leaf area.

Light was a factor which permitted the better growth in the NS rows in the fall and winter. But light, in combination with wind, appeared to have an effect on growth in the spring after the wheat started to grow fast and extend high above the ground. Between March 6 and 20 (days 65 to 79), rows became less distinctly visible. The canopy appeared uniform if one stood outside the plots. If one walked into a plot, rows were still clear. The constant wind also masked the rows. The effects of light should have become less important after the rows were no longer distinct. All plants should have been equally shaded. In addition, in the wheat canopy, the lower leaves senesced so that only the top two leaves were green after the beginning of May. Light penetration into the canopy, therefore, became less critical as the season progressed. In crop such as cotton, where the rows remain distinct, light has an effect on the rate of growth of plants oriented in different row directions (Allen, 1974; Baker and Meyer, 1966). But the height data in this experiment suggested that wind, rather than light, was more important in determining growth in the spring. After March 6 (day 65), differences in height between plants in the NW rows and plants in the other three row directions became more pronounced than differences in height were in the fall when plants were near the ground (Figure 5).

Leaf Water Potential

Figure 7 shows the leaf water potential determined three times on three days in April and three days in May. The environmental conditions for these six days are listed in Table III. Leaves of plants oriented in the NS direction had the highest (least negative) water potential after day 102. Leaves of plants oriented in the EW, NE-SW, and NW-SE directions tended to have similar leaf water potentials. On day 109, 117, and 125 leaves of plants oriented in the EW direction usually had the lowest potential while leaves of plants oriented in the NS direction had the highest potential. As the season progressed, differences in leaf water potential of plants in the NS direction and leaves of plants in other directions become more pronounced.

The 30-cm NS and EW rows of Chin Choy et al. (1977) may be comparable to the NS and EW rows of this experiment. In both experiments, row orientation was not obvious after a certain period of growth. (The 90-cm rows in the study by Chin Choy et al. remained distinct even at harvest.) There was more water in the soil profile with 30-cm NS peanut rows than with 30-cm EW peanut rows. Leaves of wheat oriented in the NS rows had a higher potential than leaves of wheat oriented in the EW direction. The higher potential of the NS wheat leaves corresponds with the greater apparent water availability in the NS rows of Chin Choy et al. (1977).

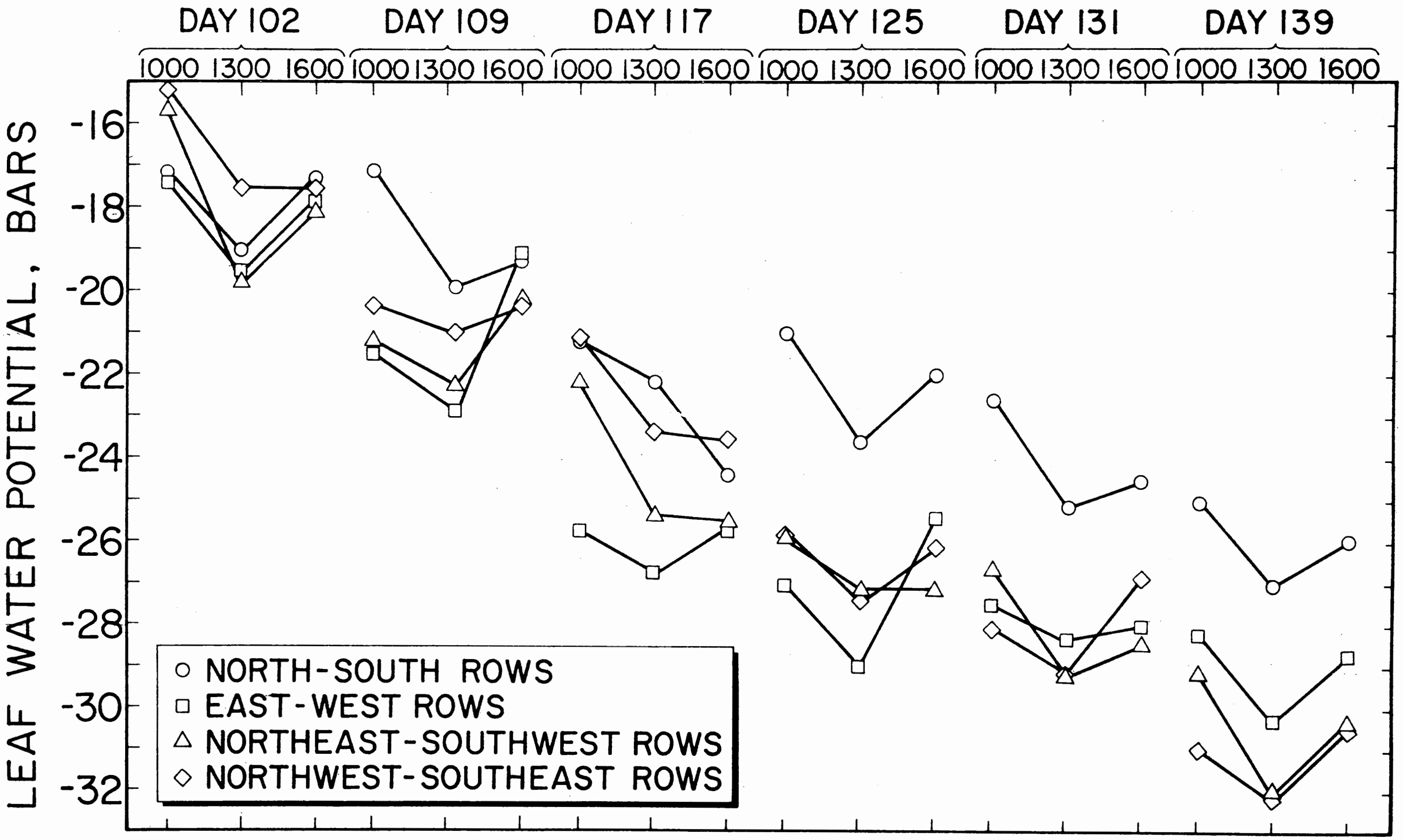

Figure 8. Leaf-water Potential of Field-grown Winter Wheat Plants Oriented in NS, EW, NE-SW, and NW-SE Rows

Stomatal Resistance

Figure 8 shows the stomatal resistance of the upper surface of the flag leaves determined concomitantly with leaf potential (Figure 7). Stomatal resistance of plants oriented in the NS direction was lowest at the 1300-hour readings expect for day 139. Also, 1000-hour stomatal resistance values of plants oriented in the NS rows tended to be low compared to those of plants oriented in other directions. Plants oriented in the NW-SE rows had the highest stomatal resistance at all times, except at 1000 hours on day 109 and 1600 hours on day 131. In addition, leaves of plants oriented in the NW-SE rows had the highest potential at the beginning of measurements in the spirng (day 102, April 12) and ended up with the lowest water potential at the last measurement time (day 139, May 19)(Figure 7). The data suggested that the plants oriented in the NW-SE rows were experiencing an unknown stress that became more pronounced with time.

The stomata were most widely open at the 1000-hour reading. Stomatal diffusive resistance increased as the day progressed (Figure 8). In Oklahoma, winds usually get stronger as the day progresses and are calm at night. Most carbon dioxide uptake for growth probably occurred in the morning when winds (and stomatal resistance) were low. Wind must have reduced growth by causing mechanical damage to the plants rather than by causing high transpiration rates leading to decreased turgidity. Stomata were closed when winds were strongest and large amounts of water probably were not lost from the leaves.

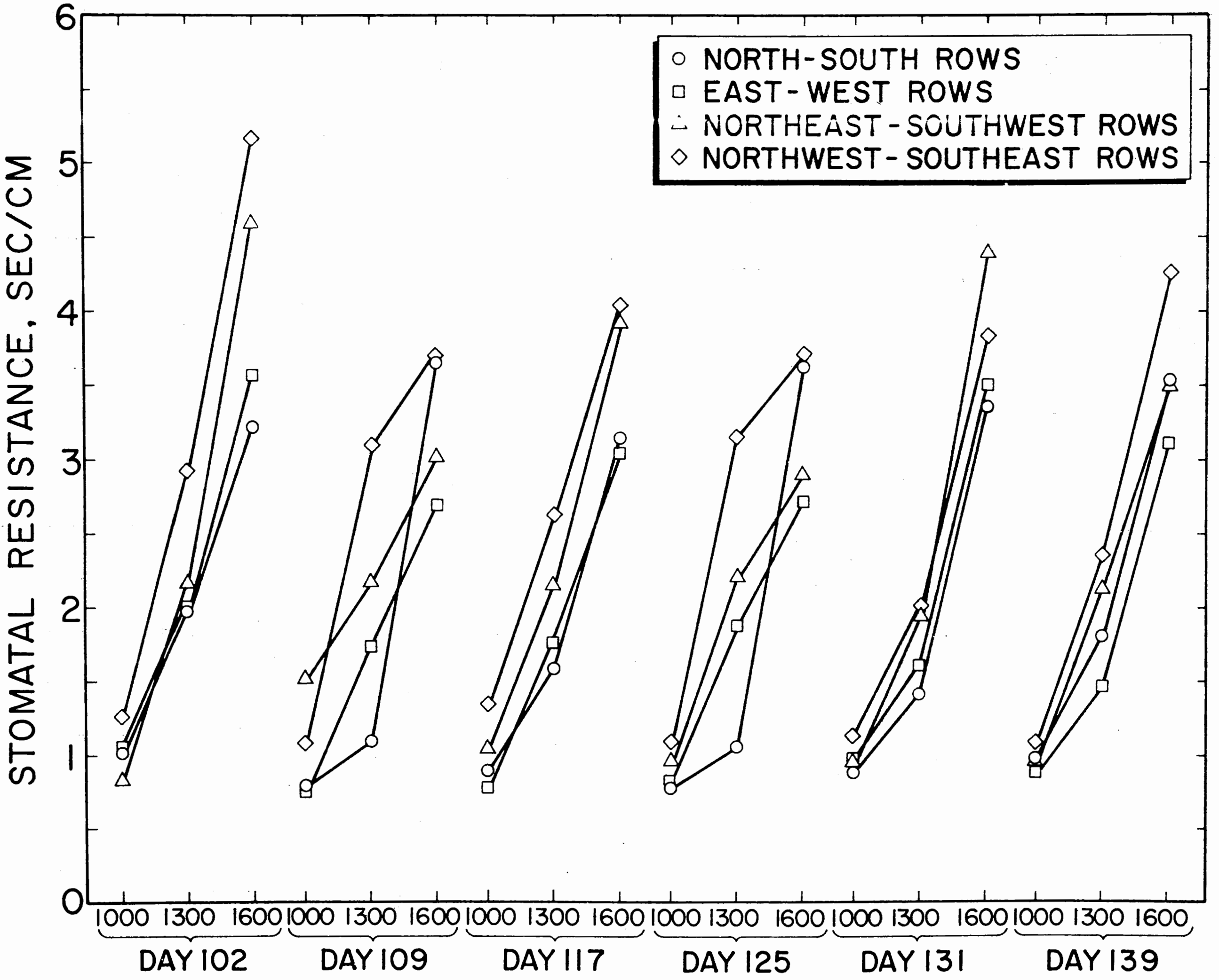

Figure 9. Stomatal Resistance of the Adaxial Surface of Flag Leaves of Field-grown Winter Wheat Plants Oriented in NS, EW, NE-SW, and NW-SE Rows

The high irradiances (1030 $W \cdot m^{-2}$ or greater, Table III) suggested that light had little effect on stomatal opening and, hence, rate of growth. At irradiances greater than 600 $W \cdot m^{-2}$, wheat stomata, under nonstress conditions, are widely open (Denmead and Millar, 1976).

Yield

Table IV shows the test weight and yield of the grain 234 days after planting of the wheat oriented in four directions. No difference was noted in test weight of wheat sown in the different directions. Pendleton and Dungan (1958) observed the same result with oats.

Differences in yield among the four orientations were not significant. Pendleton and Dungan (1958) reported that increases in yields of oats in NS rows occurred only in four out of the seven years of their study. On an average for the seven years, oats in NS rows yielded 6.9 bu/A^{-1} (about 450 kg/ha^{-1}) more than oats planted in EW directions. If the present experiment were repeated for several years, significant differences in yield might be observed in some years. As Donald (1963) pointed out, there are many cereal areas in the world where a difference of a few per cent in production might make NS planting worth while.

In Canada, farmers normally plant in NS rows to control erosion caused by westerly winds (Austenson and Larter, 1969). In the windy Southern Great Plains, farmers traditionally have been advised to harrow and drill in EW rows, which leaves ridging crosswise to the

TABLE IV

YIELD AND TEST WEIGHT OF FIELD-GROWN WINTER WHEAT PLANTS ORIENTED IN NS, EW, NE-SW, NW-SE ROWS

	Yield	Test Weight	
Row Orientation	kg/ha^{-1}	kg/l^{-1}	(lb/bu-1)
North-south	2480 ± 170	0.85 ± 0.02	(56.6 ± 1.3)
East-west	2780 + 560	0.85 + 0.04	(56.8 + 2.6)
Northeast-southwest	2810 + 230	0.86 + 0.03	(57.3 + 2.1)
Northwest-southeast	2660 + 170	0.86 + 0.02	(57.6 + 1.7)

prevailing south and north winds (Malin, 1944). This practice blows dirt upon roots, not away from them, protects tender plants, and resists soil erosion. In the Southern Great Plains, the advantage of increased growth of wheat planted in NS rows would be offset by in increased wind erosion. However, a farmer could harrow in the EW direction. This might reduce soil erosion until the wheat grew enough to protect the soil from blowing.

CHAPTER V

SUMMARY AND CONCLUSIONS

The effects of wind on the internal water relations of wheat plants grown in the field and growth chamber were studied in two separate experiments. In addition to wind effects, drought stress effects were studied in the growth chamber experiment. Row directional orientation effects were observed in the field experiment.

Wheat plants grown in the growth chamber had roots split in soil and soil, soil and nutrient solution, and nutrient solution and utrient solution. There were two treatments. Half of the plants were grown in a 4.8 $m \cdot sec^{-1}$ wind and half were grown without wind. During the first 14 days of the experiment, the soil was well watered. During the last 16 days of the experiment, water was withheld, and at the end of the experiment, the soil was dry. The results showed that the growth of wheat plants was increased if the root system was part in solution and part in moist soil, rather than all in moist soil or all in solution. Idso (1968) reported that growth may be increased by keeping the water content of the soil as high as possible. This experiment suggested that the "high" value for maximum growth is zero matric potential for part of the root system. Under field conditions, this would be difficult to achieve unless roots would grow into free water below a soil zone. In this experiment, some soil in the root zone was essential for a high growth rate. The soil provided a firm support for the plants which might have been critical for maximum growth. It is interesting to note that plants with roots all in nutrient solution and placed in wind were the shortest (Fig. 3, Table I).

There is great debate as to whether the dominant resistance to water flow is in the soil or in the plant. Newman (1969a) and Reicosky and Ritchie (1976) review the evidence. The results of this epxeriment suggested that, even under well-watered conditions, the soil has an effect on water flow through the plant. But the plant itself has a much greater resistance to water flow than that caused by the soil. Reichosky and Ritchie came to a similar conclusion. This experiment did not locate the sight of resistance in the plant lies in the root rather than in the stem or leaf (Barrs and Klepper, 1968; Boyer, 1971; Hansen, 1974; Hansen, 1974; Newman, 1969a,b; Newman, 1974; Reicosky and Ritchie, 1976; Skidmore and Stone, 1964; Taylor and Klepper, 1975; Tinklin and Weatherly, 1966; van Bavel, 1976).

In the field experiment, wheat was planted in north-south, east-west, northeast-southwest, and northwest-southeast directions to determine the effect of row orientation on height, leaf area, leaf water potential, stomatal resistance, and yield of winter wheat exposed to normally strong north and south winds of central Oklahoma. The results showed that wheat plants oriented in NS rows grew taller, had a larger leaf area, and a higher leaf water potential than wheat oriented in EW, NE-SW, or NW-SE rows. These results suggested that wheat in Oklahoma, where prevailing winds come from the north and south, should be oriented in NS rows for maximum growth.

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