# Some Effects of Wind on the Growth of White Clover ( *Trifolium repens L.* ) Seedlings.

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Summary.

The effects of wind velocity on Trifolium repens L. cv Grasslands Huia white clover seedlings were examined in a wind tunnel. Three experiments were conducted, each at a different wind velocity, in which the wind was applied to the seedlings at three distinct stages of growth ( cotyledons, unifoliate leaf, and trifoliate leaf ) for three periods of time ( 2, 4, and 6 days ). The wind velocities were 5.0, 7.5, and 10.0 m/sec. In all three experiments total plant, shoot and root dry weights and root/shoot ratios were determined after 28 days. Relative growth rates both during and after the application of wind were determined for the three stages of growth and the three wind durations. In one experiment, leaf area, leaf area ratio, net assimilation rate, relative water content, transpiration rate and stomatal aperture determinations were made. Response surfaces were derived where possible to facilitate the identification of significant trends which formed the basis of discussion rather than significant values. All three wind velocities had a marked effect on total plant, shoot, and root dry weights and root/shoot ratios. Relative growth rates during the application of wind were generally higher at 5.0 m/sec than at 10.0 m/sec. They were also higher at the unifoliate stage of growth than at either the cotyledon or trifoliate stages of growth during wind application. After the application of wind, the trends of response were reversed. Wind duration generally had little effect. In the one experiment where net assimilation rates were measured, the pattern of response both during and after the application of wind was similar to that of the relative growth rates. The relative water content determinations indicated the existence of water stress which was alleviated when the wind ceased. Wind generally had no effect on the rate of transpiration but closed the stomata of the most prominent leaves. The relevance of the results to the field situation is discussed.

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# Chapter 1. Review of the Literature.

## 1 : 1 Introduction.

In a study such as the one described in this thesis, a review of the literature entails a commentary on a wide range of subjects. Accordingly, only the aspects that are directly applicable are dis - cussed.

## 1 : 2 Effects of Wind on Plants.

Whitehead ( 1957 ) proposed a classification of plant res - ponse to wind based on field studies with artificial shelter and lab - oratory wind tunnel studies. 'Exposure evasive ' plants ( e.g. rosette plants ) were unaffected by continuous high wind velocities whereas ' exposure tolerant ' ( e.g. Hordeum vulgare ) and 'exposure sensitive ' ( e.g. Senecio nebrodenis ) plants exhibited slight and marked height reductions respectively.

Plant response to wind has generally been studied by measur - ing the response due to either shelter ( natural or artificial ) or to artificial winds. Tanaka ( 1968 ) , however, attempted to determine the response of plants to wind by determining the relationship between turbulence and the linear response of a plant using spectral analysis.

The effects of shelter on plants and the microclimate sur - rounding them have been described by Jensen ( 1954 ), Marshall ( 1967 ), and Rosenberg ( 1967 ).

Reduction of wind velocity on the leeward side of a windbreak is a function of the windbreak dimensions, position and permeability ( Marshall 1967 ). Sturrock ( 1973 ) states that the primary effects of shelter are an improvement in the water balance, reduced potential evapotranspiration, and better use of the available water by plants. Shah ( 1962 ) concluded that the major effects of wind reduction were higher temperatures, reduced transpiration, better conservation of soil moisture, and less mechanical injury. In bean and maize plants, these effects resulted in larger leaf areas, smaller root/shoot ratios, and increased crop yield. Sturrock ( 1973 ) reported higher root weights

often associated with increases in leaf area, in sheltered soybean plants and suggested that a bigger root system could mean an improved ability to extract water from the soil. Marshall ( 1967 ) observed that a major problem encountered in interpreting the results of shelter belt studies is that soil moisture is often confounded with wind velocity. In the few studies in which the effects of soil moisture had been virt - ually eliminated, contradictory results had been obtained.

Brown & Rosenberg ( 1971, 1972 ) in a series of experiments, attempted to define microclimate changes in response to shelter using energy budget techniques. They concluded that a windbreak traps water vapour in the air and excludes $CO_2$ from the air immediately above a pro - tected crop. The depletion of $CO_2$ is , however, insufficiant to affect photosynthesis. They also reported that shelter has a maximum effect on crop yields when they are generally low and a negilible effect when they are generally high. In the light of this work and that mentioned earlier, it would appear that the major effect of shelter on crops is to reduce the degree of water stress that would otherwise be induced.

Artificial winds have been used to study the effects of wind on transpiration ( Martin & Clements 1935, Jensen 1954, Shah 1962, Whitehead 1962, Whitehead & Luti 1962, Macklon & Weatherley 1965, Kalma & Kuiper 1966, Tinklin & Weatherley 1968 ) ; heat transfer ( Gates 1968, Drake et al 1970, Gates & Papian 1971, Parlange et al 1971, ) ; photosynthesis ( Denke 1931, Heinke & Hoffman 1935, both cited by Warren Wilson & Wadsworth 1958, Wadsworth 1959, 1960, Huht et al 1967 , ) ; respiration ( Todd et al 1972 ) ; plant anatomy and morphology ( Whitehead 1957, 1962, 1963a, 1963b, 1963c, 1965a, 1965b, Whitehead & Luti 1962 ).

Kalma & Kuiper ( 1966 ) cited Stalfelt ( 1932 ) who in short term experiments, observed a linear relationship between transpiration and wind speed up to 0.5 m/sec. Martin & Clements ( 1935 ) in short term studies of 24 hours found that for wind velocities up to 0.9 m/sec, transpiration was increased and maintained at a level 20 to 30 % above control in Helianthus annuus plants. At higher wind speeds, they report - ed an initial rapid rise in transpiration followed by a decrease which they attributed to stomatal closure. Yamaoka ( cited by Kalma & Kuiper 1966 ) found that an increase in wind speed from 0 to 1.0 m/sec

decreased transpiration but at higher wind speeds, transpiration remained constant. Whitehead ( 1962 ) and Whitehead & Luti ( 1962 ) observed decreases in the transpiration rates of H.annuus and Zea mays plants grown under conditions of continuous wind over a five week period. Kalma & Kuiper ( 1966 ) in an experiment of three weeks duration found that the total water use of Phaseolus vulgaris plants decreased with wind speeds up to 1.6 m/sec. Macklon & Weatherley ( 1965 ) and Tinklin & Weatherley ( 1968 ) found that low wind speeds ( 1 - 2 m/sec ) had no effect on the transpiration rate of Ricinus communis plants grown in water culture. In the short term, in sand or soil culture, it would appear that transpiration will increase in response to wind speeds up to 1.0 m/sec but thereafter will decrease, while in the long term, transpiration is likely to decrease or at least remain constant.

The effect of wind on the heat transfer processes of plants is complex. Idso & Baker ( 1967 ) reported that while reradiation was overwhelmingly the dominant mode of heat transfer in a soybean crop, transpiration transfer of heat was much more important than convection transfer. Drake et al ( 1970 ) found that for Xanthium strumarium leaves, wind affected the partioning of energy transfer between transpiration and convection. When leaf temperature was above the air temperature, an increase in wind velocity caused an increase in convective heat loss and decreased transpiration, whereas when leaf temperature was below air temperature , an increase in wind velocity caused convective energy addition to the leaf and also increased heat loss by transpiration. Gates ( 1968 ) and Gates & Papian ( 1971 ) have demonstrated quite conclusively the importance of transpiration in heat transfer processes. They used a wind tunnel to study the effects of leaf dimensions and wind velocity on boundary layer resistance to both transpiration and convection heat transfer. They derived constants of best fit so the the complete energy budget of a leaf could be solved. By varying two factors of the equation at a time they found that, leaf dimensions largely determined external diffusion resistance because the larger the leaf, the thicker the boundary layer. Gates ( 1968 ) was able to demonstrate that plants with small leaves would be better adapted to dry hot conditions than plants with large leaves which would be better adapted to hot humid conditions. He also demonstrated that wind velocities less than 0.5 m/sec had a big influence on transpiration and

leaf temperature by reducing the thickness of the boundary layer. At wind velocities greater than 0.9 m/sec, boundary layer thickness had no effect on the heat transfer processes because the resistance of the layer was negilible.

Prior to 1958 , eight groups of workers had examined the effects of artificial wind on the dry weight of whole plants ( Wadsworth 1959 ). Of these, six reported that an increase in wind velocity resulted in decreased growth. The remaining two groups had reported an increase in $CO_2$ uptake and assimilation rate with increased wind velocity. Warren Wilson & Wadsworth ( 1958 ) considered that these apparently contrad - ictory results could be reconciled. The first group of workers used wind speeds of between 2.2 and 27 m/sec while the second group used wind speeds between 0.0005 and 0.9 m/sec. They considered that there was an optimum wind speed for plant growth, i.e. the first group of workers used wind speeds above this optimum while the second used wind speeds below it. Wadsworth ( 1959 ) using a growth analysis approach and wind speeds between 1.2 and 12.0 m/sec found by extrapolation that the wind speed for optimum growth of Brassica napus grown in sand cul - ture was 0.3 m/sec. When the plants were less than 1 cm tall, relative growth rate and net assimilation rate increased with wind speed, plants 1 - 4 cm tall exhibited an optimum wind speed for growth, and plants 4 - 7 cm tall exhibited a decrease in relative growth rate and net assimilation rate as wind speed increased. Wadsworth ( 1960 ) extended his work to include Hordeum vulgare and Pisum sativum but used a water culture technique instead of sand culture and wind speeds between 0.3 and 4.0 m/sec. He found no significantly different relative growth rates or net assimilation rates between wind speeds and concluded that the reductions reported in his previous experiment were due to partial dry - ing out of the plants.

Todd et al ( 1972 ) reported increases in the rate of res - piration ( 20 to 40 % ) of several plant species in response to wind speeds of 7.2 m/sec under temperature controlled conditions with the rate of respiration returning to the initial rate within a short time of the wind being stopped. They suggested that elevated respiration rates such as they had measured might interfere with net assimilation and could be responsible for lower plant yields in windy regions.

Whitehead ( 1965a ) reviewed his previous work ( Whitehead 1957, 1962, 1963a, 1963b, 1963c, Whitehead & Luti 1962 ) and sug - gested that exposure to wind resulted in phenotypic changes ( anatomical and morpholgical ) enabling a plant to withstand its environment better. He summarised these changes as ;

1. reduced leaf area,
2. shorter internodes,
3. increased root/shoot ratio,
4. increased amount of vascular tissue,
5. increased number of stomata per unit area but decreased size,
6. reduced water loss per unit area, and
7. general development of xeromorphic characters.

In the series of experiments listed above, Whitehead found that Z.mays and H.annuus yields were reduced by continuous winds of 14.8 m/sec for 40 and 30 days respectively. He then grew H.annuus plants under different soil water potential regimes and found that at low soil water potentials, the plants had similar anatomical and morph - ological characteristics to those exhibited by plants exposed to a continuous wind for a period of time. Plants grown at low soil water potentials were better able to withstand lethal winds ( 17.9 m/sec ) than plants grown at high soil water potentials. Humphries & Roberts ( 1965 ) challenged Whitehead's conclusion that wind and soil moisture induced similar anatomical changes and that these changes led to re - duced water loss from the plant. They contended that Whitehead's data could be satisfactorily explained in terms of induced changes in root distribution and leaf area. They suggested that Whitehead's supposed technique of watering could have led to root concentration in the tops of the pots. Whitehead ( 1965b), however, refuted their hypothesis convincingly, pointing out that his technique of watering involved the injection of water at several points in the root zone and that as such, this would not lead to a redistribution of the roots.

To simulate field conditions in a wind tunnel is a virtual impossibility but it is possible to model turbulent boundary layer flow to a limited extent ( Wooding 1968 ) and it is probaly better to do this than to use laminar flow. Water vapour, $CO_2$, and energy exchange processes in the field are turbulent diffusion exchanges and hence the necessity to model turbuent flow as well as possible. High mean wind

velocities for extended periods of time do not occur in the field. Finnell ( 1928 ) used a mean wind velocity of 7.0 m/sec for sixty 24 hour days and Whitehead & Luti ( 1962 ) used a 18.0 m/sec wind for forty 24 hour days.

In regions where surface winds are a dominant part of the environment, calm periods frequently occur at night. During such periods, plants can replenish the water deficits that must occur under such windy conditions. However, in all eight studies where the effects of artificial wind on plants has been examined, no cognisance of this effect has been indicated. Hence it is probaly reasonable to suggest that the effects of artificial wind on plants reported to date must be interpreted in terms of the techniques used ( i.e. sand culture, water culture etc. ) and considered as extreme effects. It would seem neces - sary to attempt some simulation of the number of hours per day that wind actually blows before the effects of wind created in wind tunnels can be accurately established.

## 1 : 3 Wind Tunnels.

Bain et al ( 1971 ) described two basic types of wind tunnels used in the investigation of engineering problems ; open circuit and closed circuit tunnels. In many instances, however, the specifications and requirements of wind tunnels used for the investigation of agri - cultural problems are different to those required in engineering invest - igations. Wooding ( 1968 ) described some possible applications of low wind speeds tunnels in agriculture ;

1. investigation of turbulent boundary layers,
2. investigation of turbulent diffusion,
3. investigation of wind erosion,
4. investigation of shelter effects,
5. investigation of evaporation and plant transpiration, and
6. investigation of dynamic wind effects on plants.

Wind tunnels have also been used to study the flight patterns of insects, fungal spore and pollen grain distribution by wind.

Wooding ( 1968 ) classified wind tunnels as follows ;

1. the closed circuit blower tunnel driven by a single axial fan,
2. the open circuit suction tunnel with the fan (s) downstream of the

the working section, and
3. the open circuit blower tunnel which often has a centrifugal fan upstream of a settling chamber.

Weatherley & Barrs ( 1959 ) described a climatological tunnel of the same basic type as Wooding's class 1. It has subsequently been used in the investigation of plant transpiration e.g. Macklon & Weatherley ( 1965 ). Open circuit tunnels ( Wooding's class 2 ) have been used to investigate the effects of shelter ( Jensen 1954, Shah 1962 ) on growth and also plant physiological processes ( references cited in section 1 : 2 ). Wadsworth ( 1959 ) used a tunnel of this type except that it had a variable area which enabled him to study the growth of plants under identical conditions with the exception of wind speed. Tunnels of Wooding's class 3 are relatively few in number because of the large cost involved in their construction. Tunnels of this type have been used primarily in the study of microclimate and turbulent diffusion processes.

## 1 : 4 Effects of Water Stress on Plants.

Over the last decade or so, numerous reviews of the effects of water stress on plant growth, physiological and metabolic processes have been published ( Kramer 1959, Stocker 1960, Vaadia et al 1961, May & Milthorpe 1962, Kramer 1963, Henckel 1964, Gates 1964, Fischer & Hagan 1965, Slavik 1965, Shaw & Laing 1966, Peters & Runkles 1967, Salter & Goode 1967, Slatyer 1967, Vaadia & Waisel 1967, Crafts 1968, Gates 1968, Kramer 1969, Slatyer 1969, Laude 1972, Levitt 1972, and Hsiao 1973 ). The effects of water stress on plant growth and physiological processes only will be discussed.

Stocker ( 1960 ) considered the effects of soil dryness and air dryness on plants to be similar with both producing xeromorphic characters ;
1. smaller but thicker leaves,
2. shorter internodes,
3. increased root/shoot ratios,
4. increased amount of vascular tissue, and
5. increased number of stomata per unit area.
It is interesting to note that these features are similar to those reported by Whitehead as wind effects and lends credence to his hypothesis that wind effects are primarily moisture stress effects.

Stocker ( 1960 ) cited Simonis ( 1947 ) who grew Trifolium incarnatum in sand cultures which were watered to 80 % and 40 % of field capacity. He found that the total dry weight yield of the plant was reduced; the root/shoot ratio, the root/leaf ratio and the root/stem ratios were increased and the stem/leaf ratio decreased when the clover was grown at 40 % of field capacity. Salter & Goode ( 1967 ) in their review of the literature on crop responses to water comment that legumes such as Trifolium repens, Trifolium pratense and Medicargo sativa are most productive with respect to vegetative growth, under continuously moist conditions, provided that prolonged periods when the soil is wetter than field capacity do not occur. Davidson ( 1969 ) and Engin & Sprent ( 1973 ) have reported that T.repens plants subjected to water stress in the vegetative phase of growth have increased root/shoot ratios. Salter & Goode ( 1967 ) also found that for the above legumes , moisture conditions suitable for maximum growth up to flowering provide the greatest potential for seed production, but that during flowering a reduction in water supply could assist setting of the seed. In the final stages of development, dry conditions could prevent loss of seeds due to in situ germination.

The stage of ontogeny at which a plant is subjected to water stress can influence both its vegetative and reproductive yield. Slatyer ( 1969 ) states that both initiation and differentiation of the vegetative and reproductive primordia are very sensitive to water stress. Gates ( 1968 ) found that initiation of foliar ( vegetative ) primordia in lupin plants was very sensitive to water stress and that initiation ceased even at slight water stress. However, if the stress was neither too long nor too protracted, initiation resumed on relief of the stress. Slatyer ( 1969 ) considered that the effects of water stress on primordia are in some ways analagous to bud dormancy. Nicholls & May ( 1963 ) found that floral initiation in water stressed barley plants progressively slowed. If the water stress was mild, then upon relief of the stress, initiation occurred at a slightly higher rate than in the control plants. If the stress was severe, total spikelet number was permanently reduced. In grain sorghum, however, a similar process is not evident for the imposition of a severe water stress during floral initiation merely suspends development which is resumed on relief of the stress with no significant differences from the control plants apparent ( Slatyer 1969 ).

Water stress during anthesis can markedly reduce fertilisation and grain set in most cereals ( Slatyer 1969 ). He cites corn as being a very sensitive plant at this time and that germination of the pollen or the growth of the pollen tube may be impaired.

Hsiao ( 1973 ) states that in many species, cell expansion is one of the plant processes most sensitive to water stress and pos - sibly the most sensitive of all. He notes that reduction in cell size has been correlated with reductions in the water potential of the sur - rounding media. For example, the steady state enlargement of maize leaves was slowed by reducing the leaf water potential to - 2 bar and completely halted when the potential was reduced to - 7 bar ( Hsiao 1973 ). The range of turgor over which cell expansion occurs can be very narrow although the range can apparently be extended by osmotic compensation in some tissues ( Boyer pers. comm. ), e.g. soybean hypo - cotyls ( Meyer & Boyer 1972 ) and pea roots ( Greacen & Oh 1972 ). Gates ( 1968 ) states that physiologically young tissue exhibits greater tolerance of water stress than older tissue upon which the effects of water resemble hastened senescence. Osmotic compensation could possibly explain in part the high degree of tolerance to water stress exhibited by young tissue. While Hsiao ( 1973 ) concedes that the above reported studies indicated reasonably conclusively some osmoregulation , he contests that this is a general mechanism. He cites changes in cell wall extensibility and the threshold turgor as also allowing cell ex - pansion to continue under water stress.

Kramer ( 1969 ) considered that cell division is affected by water stress but much less so than cell expansion. Hsiao ( 1973 ) observed that the effect of water stress on cell division may not be direct but could possibly be indirect through suppressed cell expansion and also growth hormone effects.

Hsiao ( 1973 ) noted that stomatal closure is the main cause of transpiration decline as water stress develops. He also observed that an increase in stomatal resistance through closure of the stomata need not necessarily cause a proportional decrease in transpiration because leaf temperature could rise concurrently with a consequent increase in the water vapour concentration inside the leaf. Heat trans - fer processes and the role of transpiration were discussed in section 1 : 2. Some threshold values of leaf water potential above which stom -

atal opening is constant are - 7 to - 9 bar for tomato, - 10 to - 12 bar for soybean, and - 12 to - 16 bar for grape ( Hsiao 1973 ). A steady decline in stomatal aperture at leaf water potentials below the threshold values is observed. Cuticular transpiration can be a significant contributor to total transpiration ( 10 to 90 % ) accord - ing to Crafts ( 1968 ). Levitt ( 1972 ) considered that low cuticular transpiration could account for the superior drought resistance of some plants e.g. Pinus halepenis over Pinus pirea. Unique relationships between leaf water potentials, leaf water contents and transpiration rate have not been reported. This is understandable when the complex of factors that control transpiration are considered.

When the reproductive structures of a plant are fully formed, seed filling is entirely dependent upon photosynthetic activity and translocation of the assimilates to the seed. Slatyer ( 1969 ) observes that water stress at this time can have a marked effect on yield. Water stress is generally reported in the literature as causing a reduction in net photosynthesis ( e.g. Vaadia et al 1961, Kramer 1963, Crafts 1968, Wardlaw 1967, 1969, 1971 ). Hsiao ( 1973 ) maintains that there is almost unanimity of opinion that much of the reduction in $CO_2$ as - similation in light during water stress is due to stomatal closure. Slatyer ( 1969 ) maintains that net photosynthesis is progressively reduced by water stress and that both the photosynthetic apparatus and gross photosynthesis are relatively insensitive to water stress, at least until a severe stress exists. In cotton plants, net photosyn - thesis reduction could be completely attributed to stomatal closure until a severe water stress existed ( Troughton 1969 ). Hsiao ( 1973 ) considered that non-stomatal effects on net photosynthesis brought about by mild or moderate water stress were established in some plants. Boyer ( 1973 ) in soybean plants was unable to attribute directly to either the chloroplast membrane system or the cytoplasmic enzyme system the responses that occur when the system is dessicated. He considered that the responses to water stress were more likely to be indirect re - sults of other cellular responses to dessication. The accumulation of abcissic acid in Brussel sprout and tomato plants ( Wright 1972 ) during a wilting cycle suggests the involvement of growth hormones. Wright ( 1972 )has also reported a close correlation between abcissic acid levels and stomatal closure in Brussels sprout and dwarf bean but direct effects on the photosynthetic apparatus etc. have yet to be es - tablished. The effects of stomatal closure on transpiration and photo -

synthesis have already been mentioned.

Reduced sink size has been cited as a possible reason for reduced net photosynthesis under water stress conditions ( Slatyer 1969 ). In wheat and Lolium temulentum according to Wardlaw ( 1967, 1969 ) this is not so. He was unable to demonstrate a direct sink size effect on the rate of photosynthesis but the rate of assimilate translocation out of the leaf was reduced. Removal of competing sources of assimilate for the reduced sink size due to slowed growth offset this reduction. Wardlaw ( 1969 ) also found that water stress had little effect on phloem transport of assimilate. The photosynthetic activity of potato and sugar beet leaves has been directly related to root and tuber size ( Whittingham 1972 ) and Wardlaw himself conceded that lack of suitable sinks could retard photosynthesis.

The effect of water stress on respiration is rather obscure because dark and photorespiration have rarely been distinguished ( Slatyer 1969 ). Dark respiration appears to be relatively unaffected by moder - ate water stress whereas photorespiration appears to increase under comparable stresses ( Slatyer 1969 ). However, the linear increase of photorespiration with temperature ( Troughton & Slatyer 1969 ), is probaly of more importance than water stress per se , in view of the fact that during water stress, transpiration is inhibited to a greater or lesser extent with a consequent rise in leaf temperature.

## 1 : 5 Measurement of Water Stress.

Recent reviews of techniques of measuring water stress include Kramer & Brix ( 1965 ), Slatyer ( 1967 ), Slatyer & Shmueli ( 1967 ), Barrs ( 1968 ), Boyer ( 1968 ), Kramer ( 1969 ) and Sullivan ( 1972 ).

Plant water deficits are generally described by either one or both of the following parameters, water content and water potential. Only the most common techniques will be discussed.

The water content of a leaf can be expressed on dry weight, fresh weight, full turgor weight and area bases but full turgor weight is the only satisfactory base because dry weight fluctuates diurnally, fresh weight minimises large changes in water content and is affected by dry weight changes, and area decreases when water stress is high

( Barrs 1968 ). Water content at full turgor can be expressed as a function of either the amount of water taken up ( equation 1 : 1 ) or the initial water content ( equation 1 : 2 ) ( Barrs 1968 ).

$$\text{Water deficit} = \frac{(\text{fully turgid weight} - \text{fresh weight})}{(\text{fully turgid weight} - \text{dry weight})} \times \frac{100}{1} \quad (1:1)$$

$$\text{Relative water content} = \frac{(\text{fresh weight} - \text{dry weight})}{(\text{fully turgid weight} - \text{dry weight})} \times \frac{100}{1} \quad (1:2)$$

Relative water content is the expression most commonly used and the technique involves the floating of whole leaves or leaf discs on water until the tissue is fully turgid. The use of leaf discs can introduce errors from infiltration along the cut edges ( Kramer 1969 ) which Barrs ( 1968 ) suggests can be minimised by maintaining sharp edges on the leaf punch and using a disc diameter no greater than 0.8cm. Hewlett & Kramer ( 1963 ) found whole leaves more satisfactory than discs for some species although the usual arguement cited against the use of whole leaves is the time necessary for equilibration. A further limitation of the technique is that leaves of different species, of different physiological age, or from different environment may have similar relative water contents but different water potentials ( Kramer 1969 ) Beta guage determinations of water content have also been used in the laboratory.

Water potential can be measured by liquid exchange, vapour equilibrium, thermocouple psychrometry, pressure chamber, and freezing point depression techniques ( Sullivan 1972 ). Corrective measures for errors that could arise in liquid exchange techniques ( Gaff & Carr 1964 ) have been applied by Sullivan ( 1972 ) to sorghum plants under water stress. Sullivan considered them to be advantageous. Some workers using the vapour equilibrium technique have found it necessary to correct for respiration loss in weight ( Sullivan 1972 ). Thermocouple pyschrometry is currently considered to be the most accurate method of measuring plant water potential ( Cary & Fisher 1971 , Sullivan 1972 ) but the technique is limited to laboratory operation. Some of the errors and operating problems associated with thermocouple pyschrometers are discussed by Barrs ( 1968 ) . Results from pressure chamber determinations do not always agree closely with thermocouple pyschrometer values ( Cary & Fisher 1971, Sullivan 1972 ) and Sullivan comments

that while it appears a useful field technique it does not seem to be applicable to all plant species. Cary & Fisher ( 1969 ) found that potential measurements made with a thermocouple pyschrometer and a freezing point meter had a random average difference of 2.6 bar over the range - 5 to - 30 bar. They also reported a correlation coefficient between the two techniques of 0.8 for nine species of plants. Cary & Fisher ( 1971 ) reported discrepancies between pressure chamber and freezing point measurements and suggested that pressure chambers tend to measure the water potential in the xylem elements while the freezing point meter and the pyschrometer measure the potential of water in cell walls and intracellular spaces.

Other techniques which can be used for the measurement of water stress are osmotic potential, stomatal closure and leaf diffusive resistance ( Sullivan 1972 ),

Barrs ( 1968 ) concluded that both water content and water potential measurements were useful criteria while Kramer ( 1969 ) considered that water potential is the better parameter because it is apparently more closely related to the physiological and biochemical processes which control growth. Sullivan ( 1972 ) on the other hand observed that some workers considered relative water content more sig - nificant to plant growth and development, and water potential ( water activity ) more important in enzymatic reactions and directions of water movement.

## 1 : 6 Measurement of Transpiration.

Recent reviews on the measurement of single plant transpiration include those of Franco & Magalhares ( 1965 ), Slatyer ( 1967 ), Slatyer & Shmueli ( 1967 ) and Kramer ( 1969 ).

The four methods of measuring transpiration which are commonly used are ( Kramer 1969 ) :

1. phytometer ( potted plant ) method,
2. water vapour loss ( gaseometric ) method,
3. cut shoot ( rapid weighing ) method, and
4. diffusion porometry.

The phytometer method is the most widely used ( Franco &

Magalhares 1965 ) despite the limitations of confining the root system to a small space and that sealing the container can affect water ab - sorption by the roots through a soil aeration affect. Temperatures of sealed containers can rise to a point where plant growth is inhibited ( Franco & Magalhares 1965 ). The cut shoot method has received con - siderable critism and is not recommended as a good technique ( Slatyer 1967 ). Increases in stomatal aperture and a concurrent surge in trans - piration following the removal of a twig or leaf from a plant have been reported ( Slatyer 1967 ). Changes in energy load and wind structure could also result in changes in transpiration when using this technique. However, this technique can probaly give useful indications in the field. Water vapour loss techniques are generally regarded as very useful in basic studies carried out in the laboratory ( Franco & Magalhares 1965, Slatyer 1967, Kramer 1969 ) and extrapolation to the field is consider - ed dangerous where accurate estimates are more likely to be obtained from micro-lysimeter studies ( Slatyer 1967 ) or energy balance studies under special conditions ( van Bavel et al 1963 ). Diffusion porometers such as the gaseous diffusion porometer ( Slatyer & Jarvis 1966 ), the differential transpiration porometer ( Meidner & Spanner 1959 ), and the sensor element diffusion porometer proposed by Walligan ( 1964 ) will measure transpiration. The gaseous and differential transpiration diffusion porometers are laboratory instruments. The former can only be used with amphistomatous leaves whereas the latter can also be used with hypostomatous leaves. The sensor element diffusion porometer has been modified and developed into a portable instrument suitable for field use ( e.g. Kanemasu et al 1969, Beardsell 1973 ). Morrow & Slatyer ( 1971 ) state that the calibration of all diffusion poro - meters depends upon the assumption of isothermality. In the field, however, leaf - air temperature differences can be considerable and they suggested that shading a leaf for 30 to 60 seconds prior to attachment of the porometer cup and also during operation would over - come this difficulty. Ehrler & van Bavel ( 1968 ) found good agree - ment between rates of transpiration measured by a sensor element dif - fusion porometer and weighing for cotton and sunflower plants.

## 1 : 7 Measurement of Stomatal Aperture.

Four techniques for estimating stomatal aperture are ( Barrs 1968 ) ;

1. Lloyd's epidermis technique,

2. Sampson's surface impression technique,
3. infiltration techniques, and
4. porometric techniques.

Lloyd's technique is generally considered slow and laborious giving good results with a limited number of species only ( Barrs 1968 ). Sampson's surface impression technique on the other hand has been used with success by many workers with highly significant linear correlations between porometer readings and stomatal aperture ( silicone rubber impression ) recorded ( Barrs 1968 ). A good correlation with the infiltration technique has also been established ( Macklon & Weatherly 1965 ). Apertures of less than 1 $\mu$ are difficult to determine . Some difficulty can also be experimenced obtaining impressions from some plant species . However, repeated sampling can be carried out on the same leaf without causing injury ( Barrs 1968 ). Brown & Rosenberg ( 1970 ) described an adaptation in which a rapid drying acrylic resin is sprayed onto the leaf, removed with cellotape after drying and then mounted directly on a microscope slide. The necessity of making a positive impression is removed by this technique.

Infiltration techniques have been used primarily in the field to indicate when water deficits are large enough to warrant irrigation ( Barrs 1968 ). Shmueli ( 1964, cited by Barrs 1968 ) considered that even for irrigation purposes, infiltration techniques were limited because skilled operators were necessary to obtain satisfactory results.

Viscous flow porometers measure changes in stomatal conductance and hence stomatal aperture. However, stomatal conductance or aperture measurements are not as meaningful as diffusion resistance measurements in most investigations concerned with stomatal control of transpiration, photosynthesis, and plant water status ( Meidner & Mansfield 1968 ). Hence, direct measurements of stomatal aperture have limited application except as general indicators. Direct measurements of transpiration and internal diffusive resistance using diffusion porometers are probaly of more value.