

Comparative Ecophysiology of Green Foxtail
(Setaria viridis (L.) Beauv.) and Spring Wheat

by

Brian John Douglas

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in
Plant Science

Winnipeg, Manitoba

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COMPARATIVE ECOPHYSIOLOGY OF GREEN FOXTAIL
(SETARIA VIRIDIS (L.) BEAUV.) AND SPRING WHEAT

BY

BRIAN JOHN DOUGLAS

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

DOCTOR OF PHILOSOPHY

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" pluralitas non est ponenda sine necessitate "

(" multiplicity ought not to be posited without necessity ")

" Ockham's razor " - William of Ockham 1280-1349

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ABSTRACT

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Comparative ecophysiology of green foxtail (*Setaria viridis* (L.) Beauv.)
and spring wheat. Major Professor; Ian N. Morrison.

The growth and development of green foxtail and spring wheat (cv. Benito) were studied in outdoor rain-out shelters filled with clay loam soil, in 1984 and 1985. Foxtail and wheat were established at 400 and 200 plants m^{-2} , respectively, in late May, and approximately 21 days after emergence two irrigation schemes were imposed (25 and 5 mm $week^{-1}$) to represent wet and dry situations. Plant development was assessed at weekly intervals. In both years, at all harvests, wheat was taller, and had a greater leaf area, leaf weight and total biomass than foxtail. Water stress significantly reduced the growth of both species. The leaf area ratio and specific leaf area of foxtail increased in response to shading by the wheat canopy. Water stress caused a significant reduction in seed yield of both species. In both years wheat was more competitive than foxtail as a result of environmental conditions favoring the growth of wheat over that of foxtail.

Controlled environment studies were conducted to elucidate the relative importance of temperature and water stress on the growth and competitive ability of the two species. Foxtail and wheat were grown singly and in combination at 30/25 C and 20/15 C in both water stressed and unstressed conditions. Foxtail had higher relative growth rates based on total biomass, leaf area, leaf weight and stem weight and a

greater extent of development in these parameters than did wheat. At 20/15 C wheat was superior to foxtail in these same attributes. Within a given temperature regime water deficit had a significant effect, but the effect was small compared to that of temperature. Foxtail effectively suppressed wheat at 30/25 C, while wheat suppressed the foxtail at 20/15 C.

The water relations of foxtail and wheat seedlings were studied, in a controlled environment at 25/20 C, in drying soil, to assess the physiological responses to soil water deficit. Foxtail maintained a higher water potential than did wheat, but this was attained at a lower relative water content.

However there was no evidence to support the contention that the C₄ photosynthetic pathway is an adaptation to dry environments, or that it is of competitive advantage in such environments. When foxtail and wheat were examined in their respective ecological niches there was no evidence for a superior competitive ability for foxtail in water limited environments.

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INTRODUCTION

Green foxtail (Setaria viridis (L.) Beauv) is an annual grassy weed with the C₄ photosynthetic carbon reduction cycle (PCRC). The C₄ system has often been proposed to confer a competitive advantage to weed species particularly under hot, arid climatic conditions (Chen et al. 1970; Black 1971) . On a worldwide basis 32 of the 76 worst weeds are C₄ species (Holm et al. 1977). However the superiority of C₄ over C₃ plants decreases as the level of organization progresses from cellular events to whole plant growth. The PCRC of a plant is but a single component of an integrated system and the advantages of the C₄ system in terms of weed-crop competition have been more closely examined in recent years (Cohen 1970 ; Baskin and Baskin 1978 ; Patterson 1985).

Green foxtail is currently one of the most abundant and widespread weed species in western Canada (Thomas and Wise 1984) where plant growth is limited primarily by a lack of precipitation (Oosterveld and Nicholaichuk 1983). Many C₄ weeds are proposed to be adapted to, and competitive in semiarid to arid environments (Black 1971 ; Jordan and Shaner 1979) and as green foxtail is most prevalent in western Canada (Alex et al. 1972), the C₄ PCRC may be advantageous in competitive situations. Field studies have shown that the competitive effects of green foxtail in cereals (Sturko 1978 ; Blackshaw et al. 1981b), corn (Nieto and Staniforth 1961 ; Sibuga Bandeen 1980a,b), and soybeans (Staniforth 1965) varies with environmental conditions, particularly temperature and precipitation. Also, Sturko (1978) reported that green

foxtail was more competitive in a semidwarf wheat than in a standard height wheat, which indicates that shading is very important in the interaction between the two species.

Computer simulation models have demonstrated that temperature, water potential, radiation, and dry weight accumulation are determining factors in the growth of Setaria spp. and their subsequent competitive ability at any given growth stage (Orwick et al. 1978). The sensitivity of foxtail growth to environmental factors is evident from the inconsistency in results of field studies (Blackshaw et al. 1981b). Although several studies have examined the comparative growth of foxtails in isolation, there are few detailed reports of the comparative crop-foxtail growth in a competitive situation. A summary of the biology and ecology of green foxtail is presented in Douglas et al. (1985).

Studies on the variability in deleterious effects of weeds, as determined by environmental conditions are important in that they aid in refining the concept of an economic threshold, above which weed control practices could be profitable. The potential effects of weeds such as wild oats (Avena fatua L.) on crop yield can be more accurately predicted, than for green foxtail, on the basis of density and time of emergence (Dew 1972), as they have a greater degree of niche overlap with cereals than does green foxtail (Barrett 1983). In contrast the growth and competitive ability of green foxtail is more environmentally sensitive than the growth of wild oats, and this, coupled with a potentially large degree of temporal niche separation, necessitates that environmental conditions must be taken into account in attempting to assess the competitive effects of green foxtail in cereals.

The purpose of this study was to examine the primary environmental factors which influence the growth and competitive ability of green foxtail in spring wheat in relation to the intrinsic differences in ecophysiology of the two species.

LITERATURE REVIEW

INTRODUCTION

In studying the comparative ecophysiology of green foxtail and wheat a distinction must be made between plant characters which are beneficial to survival and reproduction, and those which determine the relative competitive ability of the two species. "It is important to recognize that the ability to survive stress and the ability to outcompete a neighbor or control a resource within a distinct area are not necessarily the same phenomena" (Radosevich and Holt 1984). While not mutually exclusive, a species which is competitive in a seral situation may utilize a different strategy than one that is competitive in a climax plant community (Barbour et al. 1980).

Green foxtail is primarily a weed of cultivated fields, which represent seral communities, and from an agricultural viewpoint we are most interested in the detrimental effects of weeds on crop yield. The following literature review will thus concentrate on the comparative physiology of green foxtail and wheat in relation to competition, rather than to survival and reproduction.

The field of soil-plant-atmosphere water relations has been extensively studied and interested readers are referred the books by Kramer (1983a), Turner and Jones (1980), and Taylor (1983); the series of volumes edited by Kozlowski entitled "Water Deficits and Plant Growth"; and review articles by Boyer and McPherson (1975), Begg and Turner

(1976), Hsiao (1973) , Hanson and Hitz (1982) and Boyer (1985). In the present review the relevant features of plant water relations as they relate to crop-weed competition and plant ecology will be considered but a detailed and comprehensive review of the literature on plant water relations is not attempted. " The field is wide and to cover it is not only beyond my capacity but would provide a thin and insipid spread " (Weatherley 1970).

A list of abbreviations, symbols and dimensions, where appropriate, for parameters mentioned in the text, is included in Appendix Table 1.

GENERAL ECOPHYSIOLOGY OF C₃ AND C₄ SPECIES

As green foxtail is a C₄ species and wheat is a C₃ species a general understanding of the comparative physiology and ecology of these groups is necessary before their competitive abilities in a given environment can be assessed.

Carbon fixation

The C₄ PCRC acts primarily as a mechanism to concentrate CO₂ within the vascular bundle of the leaf. This effectively favors the carboxylase function of RuBP carboxylase:oxygenase (RuBP-C:O) over the oxygenase function and eliminates any effect due to the photosynthetic carbon oxidation cycle (PCOC). C₃ species lack this CO₂ concentrating mechanism and thus under atmospheric oxygen levels (21%) have reduced photosynthetic efficiency due to the PCOC (Leopold and Kriedemann 1975). This reduction can be 12 to 20% at 10 C and 45 to 60% at 40 C (Long 1983). The enzyme responsible for the initial CO₂ fixation step in C₄

species, PEP carboxylase, also has a higher affinity (lower K_m) for CO_2 , than does RuBP-C:O, so that net photosynthesis in C_4 species becomes CO_2 saturated at a much lower intercellular CO_2 concentration (c_i). At a given atmospheric CO_2 concentration (c_a) the gradient in CO_2 levels between the air surrounding the leaf and the internal leaf surface (ΔCO_2) will be greater for C_4 species than C_3 species. As CO_2 uptake is a diffusion process driven by ΔCO_2 , C_4 species will have a higher CO_2 uptake rate than C_3 species at the same atmospheric CO_2 level, because ΔCO_2 is greater. As a result of this CO_2 concentrating mechanism, photosynthesis by C_4 species is independent of O_2 concentration over the range of 2 to 21% (Leopold and Kriedemann 1975).

C_3 and C_4 species exhibit large differences within a group and between groups in their photosynthetic response to temperature (Pearcy and Ehleringer 1984) and in their growth rates (Monteith 1978). Similar differences exist both within C_3 species and between C_3 and C_4 species adapted to growing in different parts of the season. In C_3 species photosynthesis is often almost independent of temperature. The response depends on the photosynthetic photon flux density (PPFD) and CO_2 concentration to which the plants are exposed (Milthorpe and Moorby 1979). The lack of temperature response in C_3 species occurs because the ratio of oxygenase to carboxylase function of RuBP-C:O increases with temperature. C_4 species, because they either lack the PCOC or because it isn't expressed, exhibit a large increase in photosynthesis over the temperature range of 20 to 40 C (Pearcy and Ehleringer 1984). Thus the C_4 pathway can potentially exhibit high photosynthetic rates and this has often been interpreted to be an adaptation to high temperatures (Black 1971). However other factors such as

thermostability of the electron transport system (Pearcy et al. 1977) and the ability to regulate leaf temperature within the optimum range while maximizing photosynthesis may be more important (Leopold and Kriedemann 1975 ; Berry and Bjorkman 1980 ; Gates 1980). These characters are obviously not directly associated with the type of PCRC. C_4 species are native to such diverse habitats as coastal swamps, deserts and tropical forests and these species have widely divergent temperature optima for CO_2 fixation (Ludlow 1976 ; Pearcy and Ehleringer 1984).

Transpiration, water use efficiency, and stomatal regulation

Both water loss and CO_2 uptake by a plant are regulated by stomata which are influenced by both plant and environmental factors. Stomata function primarily to regulate the intercellular CO_2 concentration (c_i) while minimizing water loss, and as the PCRC in C_3 and C_4 species operate at different c_i (Nobel 1983), stomata in these two types behave differently (Farquhar and Sharkey 1982). In C_4 species stomata adjust the leaf conductance to water vapor (g) (which is related to stomatal aperture) relative to CO_2 uptake so that c_i is maintained at 100 to 150 $cm^3\ m^{-3}$ (Pearcy and Ehleringer 1984). Photosynthesis in C_4 species becomes CO_2 saturated at these levels so that any increase in g would result in a higher transpiration rate (assuming that the atmospheric water potential (ψ_a) and leaf water potential (ψ_l) remain constant) but no increase in CO_2 uptake (Farquhar and Sharkey 1982). In C_3 species, because of the PCOC, photosynthesis does not become CO_2 saturated until c_i is 220 to 260 $cm^3\ m^{-3}$, at atmospheric O_2 levels. In order to reach

this higher c_i , a greater g is required, as ΔCO_2 is less. At a given photosynthetic rate, g is higher in C_3 than in C_4 species and subsequently water loss or transpiration is greater at equal ψ_a and ψ_l (Farquhar and Sharkey 1982). Therefore C_4 species have a higher potential water use efficiency ($WUE = \text{assimilation/transpiration}$) than C_3 species. At a given g , stomata have a greater effect on water loss than on CO_2 uptake (Farquhar and Sharkey 1982) as the diffusivity of water vapor in air is about 1.56 times that of CO_2 (Nobel 1983). The difference arises from the fact that the speed of diffusion is inversely proportional to the square root of the molecular weight of the gas (Nobel 1983). As a result of these differences in c_i and g the potential WUE of C_4 species is always higher than C_3 species. WUE also depends on ψ_a , so that a C_3 species active during the cool, humid part of the season (wheat) may have a higher WUE than a C_4 species active during hot, dry weather (foxtail). In addition high WUE does not relate to greater tolerance of low ψ_l or low soil water potential (ψ_s). The ability to tolerate atmospheric drought and low ψ_s depends on factors such as osmotic adjustment and leaf morphology which are not obviously correlated with the type of PCRC (Bjorkman 1975 ; Pearcy and Ehleringer 1984).

Nitrogen use efficiency

In both C_3 and C_4 species the photosynthetic capacity is closely correlated with leaf nitrogen (N) content (Percy and Ehleringer 1984). RuBP-C:O is the major enzyme in leaves of C_3 species and can account for up to 50% of the total protein levels (Brown 1978). In C_4 species RuBP-

C:O is present in lower amounts and PEP carboxylase is in low amounts relative to RuBP-C:O. Thus for a given unit of CO₂ fixation, C₄ species have much lower N levels and a higher nitrogen use efficiency (NUE=moles CO₂ fixed per mol N present). This efficient use of nitrogen is due to the compartmentation of enzymes in the bundle sheath and mesophyll cells (Black 1985). Nitrate assimilation in the leaf is restricted to these two cell types. In C₄ species NO₃⁻ and NO₂⁻ reduction to NH₃ only occurs in leaf mesophyll cells, i.e there is no reductase activity in the bundle sheath cells, but both cell types can assimilate NH₃ (Black 1985). This selective compartmentation of key enzymes is proposed to be responsible for the high NUE (Black 1985). Brown (1978) suggested that in areas where soil nitrogen is low, C₄ species would have an advantage but there is no evidence to date that C₄ species are preferentially distributed in low soil nitrogen areas (Pearcy and Ehleringer 1984) or that a higher NUE is of ecological advantage (Christie and Detling 1982). However valid comparisons of the NUE of C₃ and C₄ species are difficult to conduct unless ecologically similar species are compared under the same environmental conditions (Nobel 1983).

Quantum yield

C₃ and C₄ species differ not only in their pathway of CO₂ fixation but also in the energy cost or quantum yield (Φ) associated with this CO₂ fixation. The quantum yield is defined as the moles of CO₂ fixed per mole of photons absorbed (Nobel 1983). It is important to consider Φ as a function of photons absorbed rather than incident radiation because pigments in leaves absorb radiation of different wavelengths and

because the energy content of photons varies with wavelength (Milthorpe and Moorby 1979). C_3 species require three ATP and two $NADPH_2$ per mole of CO_2 fixed and for RuBP-C:O regeneration. The PCRC in C_4 species requires two additional ATP to regenerate PEP, so energy costs in terms of ATP are higher than in C_3 species (Salisbury and Ross 1978). In C_3 species Φ is dependent on CO_2 and O_2 concentration, and temperature (Ehleringer and Bjorkman 1977 ; Monson et al. 1982). In C_3 species PCO increases relative to PCR, so Φ decreases, but there is no significant temperature effect in C_4 species (Pearcy and Ehleringer 1984). The decrease can be from 0.069 at 14 C to 0.042 at 38 C (Ehleringer and Bjorkman 1977). However there is wide variation in Φ among C_4 species and this may be associated with the subtype pathway (Ehleringer and Pearcy 1983). NADP-ME types, such as green foxtail, have the highest Φ among the C_4 species. The lower Φ in C_4 species results in greater energy costs and is the only known disadvantage of the C_4 PCRC (Ehleringer 1978), but this disadvantage only occurs at temperatures less than 18 to 23 C (Ehleringer and Pearcy 1983). Within this leaf temperature range Φ is greater for C_3 than for C_4 species. For single leaves the C_4 pathway is possibly most advantageous under high PPFD, high temperature and limited water supply but at the canopy level the lower Φ can be a disadvantage due to shading (Ehleringer 1978).

Geographic distribution and ecological diversity

Geographical studies have shown that there is generally a greater abundance of C_4 species in warmer environments, but the distinction must

be made between presence and performance with respect to specific environmental parameters (soil nitrogen, soil water, light, temperature) (Doliner and Jolliffe 1979). Ehleringer (1978) studied the distribution and productivity of C_3 and C_4 species on the prairies of North America in relation to temperature and solar radiation. He concluded that C_4 canopies had higher rates of photosynthesis at latitudes south of 45° N whereas further north, C_3 species were superior. The productivity of C_4 canopies in shaded conditions was dependent on temperature. At 10% of full sunlight ($0.2 \text{ mmol m}^{-2} \text{ s}^{-1}$), C_3 species were more productive below 32°C, while C_4 species were more productive above 32°C. The C_4 and C_3 canopies had the greatest canopy production at 40/20°C (day/night) and 10/5°C, respectively. Recent studies have demonstrated that C_4 species are native to cool, coastal environments; cold, high elevation savanna and hot, humid, tropical forests, as well as hot, high PPFD, arid conditions (Ludlow 1976 ; Pearcy and Ehleringer 1984). Thus differences in temperature and PPFD responses for C_3 and C_4 species are not solely a function of PCRC but also due to variations in niche characteristics.

There is a wide variation in C_3 and C_4 species in photosynthetic rates and productivity related to the habitat in which they have evolved and the type of community in which they exist (seral vs. climax). When similar ecological forms from the same habitat are compared, the advantage of the C_4 PCRC as a component of the integrated plant system becomes less profound (Percy and Ehleringer 1984).

STOMATAL PHYSIOLOGY, GAS EXCHANGE AND WATER DEFICIT

To what signals do stomata respond ?

Radiation

Stomata exhibit both a direct and an indirect response to radiation and these combined responses permit a sensitive adjustment of stomatal conductance to the CO_2 requirement for photosynthesis (Sharkey and Raschke 1981). Stomatal conductance is primarily determined by radiation absorbed in the guard cells. The indirect effect of radiation on stomatal conductance is via the PCRC and c_i , while there is a direct "blue light" response due to wavelength dependent (425 to 490 nm) activation of a photosystem in the guard cells (Zeiger 1983).

CO_2

Stomata respond to c_i rather than the atmospheric CO_2 concentration (Farquhar and Wong 1984). As c_i decreases, g is adjusted through guard cell action to satisfy the CO_2 deficit. Morison and Gifford (1983) found little difference in the sensitivity of g to CO_2 at a given atmospheric water vapor pressure deficit (VPD) between C_3 and C_4 species, but these responses vary with growing conditions.

Water vapor pressure deficit

Stomatal guard cell behavior and thus stomatal conductance is controlled directly by epidermal evaporation in response to VPD (Bunce 1985). Stomatal closure at high VPD is known to be a function of the evaporation rate from the outer surface of the epidermis rather than through the stomata. Epidermal evaporation is largely due to cuticular transpiration (Sheriff 1984). As the permeability of the cuticle changes with VPD and temperature, and as temperature gradients exist within a leaf there is a large spatial variation in ψ of guard cells and thus g . The ψ of the epidermis can also change independently of ψ_l in response to VPD and thus may be largely insensitive to ψ_l (Sheriff 1984). Bates and Hall (1981) observed decreases in g which were not related to ψ_l . This could explain the inability of many researchers to find a unique relationship between ψ_l and photosynthesis, transpiration, or g , in general (Jones and Rawson 1979 ; Jones 1983).

Leaf conductance is also affected by temperature and radiation (Bunce 1981) and exhibits ontogenetic drift (Jones 1977a). Stomata of species grown in low PPFD ($500 \mu\text{mol m}^{-2} \text{s}^{-1}$) are more sensitive to changes in VPD than are those of species grown in high PPFD ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Bunce 1981). Therefore any response of g to VPD depends considerably on the growing environment of the plant (Townley-Smith and Hurd 1977).

Photosynthesis

There is no doubt that leaf water deficit causes stomatal closure and reduction in photosynthesis, but many experimenters have measured the bulk ψ_l , which is probably not related to g (Sheriff 1984 ; Boyer 1985). There is also increasing evidence that the nonstomatal inhibition of photosynthesis can be as, or more, important than stomatal inhibition and that the stomatal limitation to photosynthesis can either increase or decrease with water deficit (Begg and Turner 1976 ; Woolhouse 1983 ; Jones 1985). The relative contributions of stomatal and nonstomatal effects vary with species, VPD, ψ_l , and the growth environment (Kriedemann and Downton 1981 ; Hanson and Hitz 1982). Furthermore the photosynthetic response to water deficit and subsequent recovery is also a function of the rate of development, duration, and intensity of the deficit (Kriedemann and Barrs 1983 ; Jones 1985). This makes it exceedingly difficult to correctly compare experiments, even within a given species.

Water deficit reduces chlorophyll formation (Virgin 1965) and also alters the pattern of assimilate partitioning (Radin 1983). Reduced translocation under water stress is usually the result of a reduction in photosynthesis of the source, or growth of the sink, rather than any direct effect on the conducting system. Matthews and Boyer (1984) reported acclimation of photosynthesis to low ψ_l in sunflower. The decreases in chloroplast activity contributed more than closure of the stomata to both reductions in photosynthesis with the onset of water deficit, and the acclimation of photosynthesis to low ψ_l . The importance of nonstomatal effects are emphasized in a study by

Kriedemann and Downton (1981) in which a low photosynthetic rate, induced by low ψ_l , persisted even following the restoration of g and leaf water content to pre-stress levels. This type of after effect may be more significant in reducing photosynthesis than stomatal effects. Water deficit is often accompanied by elevated leaf temperatures as latent heat exchange is reduced, and a lack of thermal stability of the photosynthetic apparatus may account for this after effect.

The ψ_l at which photosynthesis is zero varies as much among C_3 and C_4 species as between the groups (Ludlow 1976 ; Lawlor 1977). In general the variation among species in the photosynthetic response to water deficit is more closely related to their ecological niche and to previous growing conditions, than to the type of PCRC (Kriedemann and Barrs 1983).

Wheat

There is intraspecific variation in wheat stomatal response to ψ_l (Jones 1977a ; Clarke and McCaig 1982 ; Nicolas et al. 1985), however this does not necessarily correlate with increased drought resistance or higher yield under water stress conditions (Blum 1985).

Stomatal closure in field grown wheat leaves occurred at about the same pressure potential but ψ_l differed because of differences in the osmotic potential (π) of the leaves within the canopy (Yang and deJong 1972), and therefore the ψ_l vs photosynthesis relationship varied with height (Millar and Denmead 1976). Stomatal closure was induced at $P = 0.8$ MPa in leaves at all positions on the stem, but because of the different relationships between P and ψ_l for each leaf, the critical ψ_l

for stomatal closure were -0.7, -1.4, and -1.9 MPa for the bottom, middle, and top leaves of the canopy. However Frank et al. (1973) reported that stomatal density decreased with decreasing leaf position on the plant and this may confound these results. Furthermore bulk ψ_l was measured rather than epidermal ψ_l , and it may not be valid to determine a total leaf conductance as the upper surface of wheat leaves has a higher conductance than the lower surface (Kirkham and Kanemasu 1983). Lawlor (1976) reported a change in the CO_2 compensation point in wheat leaves with water stress from 60 ppm at $\psi_l = -0.5$ MPa to 80 ppm at -1.6 MPa to 320 ppm at -2.2 MPa. Clearly the photosynthetic response is very complex and there is no unique ψ_l vs photosynthesis relationship (Sionit et al. 1981).

Green foxtail

There are no data available for the ψ_l - photosynthesis response in green foxtail, but in giant foxtail (Setaria faberii Herm.) the minimum P for stomatal closure was altered by CO_2 level and PPFD (Sionit and Patterson 1984, 1985). However there is a wide variation among C_4 grasses in their ψ_l - photosynthesis relationship which is related primarily to their ecological niche (Ludlow 1976).

Transpiration

Transpiration and leaf temperature are mutually dependent and they are determined by at least seven other independent variables, all operating simultaneously - air temperature, radiation level, windspeed, VPD, leaf dimensions, and stomatal conductance (Leopold and Kriedemann 1975).

Latent heat loss through transpiration is crucial in reducing leaf temperature and under water deficit conditions small leaf size is advantageous in increasing sensible heat loss (Gates 1968 ; Barthakur 1975; Campbell 1977). For a given species there is no unique relationship between ψ_l and transpiration. There is both diurnal variation and hysteresis in the relationship (Jones 1978). Water absorbed in the leaf is utilized in both transpiration and expansive growth and the relative proportions used for each function can affect the ψ_l vs transpiration relationship and alter the transpiration rate at any given time (Boyer 1974 ; Fiscus et al. 1983 ; Boyer 1985). This partitioning of water between the two demands varies with time depending on the extensibility of the cell wall and osmotic adjustment phenomena (Fiscus et al. 1983).

Daily water use by a plant is determined by the transpiration rate and the leaf area (Morison and Gifford 1984a,b). In a field situation canopy transpiration per unit of land area is generally considered to be more important, in terms of water use, than is the transpiration rate of individual leaves (Teare et al. 1973 ; Monteith and Elston 1983). Leaf area is usually as important as g in determining evaporation from a crop especially when the leaf area index (LAI) is low as is common early in the season during seedling growth. Downes (1969) reported that temperate grasses from several genera had higher transpiration rates than did tropical grasses.

Wheat

In field grown wheat there is no evidence for strong stomatal control of water use even when the plant is under severe water deficit (Fischer and Kohn 1966a ; Seaton et al. 1977 ; Meyer and Green 1980). Almost all the transpiration from dryland wheat occurs from the top leaf and spike, while in irrigated wheat the water loss is more evenly distributed throughout the canopy (Denmead and Shaw 1962 ; Denmead and Millar 1976a,b). Jones (1977b) reported that 44.4% of the total transpiration occurred from the flag leaf, while 35% was from the spike, stem, and leaf sheaths. In a study of different cultivars the minimum flag leaf transpiration varied from 226 to 1076 $\text{mg dm}^{-2} \text{h}^{-1}$ (Blum 1985). Mean transpiration rates were lower in the spike than in the flag leaf by 74 to 89% and mean total transpiration was lower by 23 to 70%. As the plant water deficit increased transpiration from the flag leaf decreased and the spike became the major site for water loss (Blum 1985). Transpiration per unit area is lower in the spike than in the flag leaf due to the lower stomatal density in the spike (Blum 1985).

Cyclic oscillations

All of the studies in the preceeding discussion relating stomatal aperture and plant functioning should be considered with some skepticism in view of the increasing evidence for cyclic oscillations in stomatal conductance (Barrs and Klepper 1968 ; Barrs 1971). Kaufmann (1979) cautioned researchers in plant water relations to consider these oscillations in interpreting results.

Oscillations have been detected in stomatal aperture and related variables such as transpiration, CO₂ fixation, leaf water content and potential, leaf temperature (Cowan 1972,1977) and chlorophyll content (Hillman 1976). These oscillations are primarily water based and are due to instability in the negative feedback loop which controls stomatal aperture via the epidermal water status (Farquhar and Cowan 1974).

Ehrler et al. (1965) reported that oscillations in leaf temperature, transpiration, and leaf conductance occurred in a steady environment with respect to PPFD, VPD, CO₂ concentration, and air and root temperature. These self-sustained oscillations occur in light and dark and may be favored by the development of a moderate water deficit (Barrs 1971) or in environments which promote transpiration (Cowan 1972).

Stomata on opposite sides of a leaf may cycle out of phase or only one side may cycle. This cycling can occur but may not be detectable using overall gas exchange measurements since the out of phase cycles may cancel each other (Barrs 1971). These cycles have been detected in wheat (Nordin 1976) and can occur in both controlled environment and field grown plants (Kaufmann 1979). There is little effect of O₂ or CO₂ concentration on these oscillations (Klockare and Falk 1981) but the irradiance level affects the period of the oscillations in oat seedlings (Klockare et al. 1978). Both the amplitude and the phase of the oscillations can be altered by changes of the ψ of the root medium (Brogardh et al. 1974). The oscillations usually have a period of 10-50 min but they can be as short as 2 min (Barrs 1971). Klockare et al. (1978) reported transpiration oscillations with three different periods - one of 30 to 40 min, one of 100 to 110 min, and an overall circadian rhythm.

It appears that most experimenters do not search for or consider these oscillations and this may account for the failure to detect significant treatment or species differences in physiological function mediated by stomatal conductance.

Water use efficiency

WUE at the leaf level is a function of the environment and subsequent effects on stomatal regulation of water loss and CO₂ fixation (Nobel 1983). However at the whole plant level WUE is also influenced by canopy architecture, radiation penetration, leaf exposure (Patterson and Flint 1983), and rate of stress development (Jones and Rawson 1979).

WUE and drought resistance are often unrelated as tolerance of low ψ s may depend more on the ability to maintain turgor through osmotic adjustment (Begg and Turner 1976). In a weed-crop situation high WUE is a poor competitive strategy as the soil water will simply be exploited by less efficient species (Cohen 1970 ; Patterson 1985). Thus the less efficient species will usurp the water supply to the detriment of the more efficient species (Radosevich and Holt 1984). The high WUE of some C₄ species may therefore actually be disadvantageous in competition with less efficient C₃ species in seral communities. It is important to realize that the WUE of C₃ species is not necessarily less than that of C₄ species, particularly when ecologically similar species are compared (Pearcy and Ehleringer 1984).

Wheat

Aggarwal and Sinha (1983) reported that the WUE of wheat cultivars varied from 0.5 to 13.8 g dry matter kg^{-1} water used depending on the growth stage, cultivar, water stress, and temperature. Rawson et al. (1977b) reported that WUE was greater when water was applied sparingly during the vegetative phase of wheat, and Morgan and Willis (1983) reported higher WUE for more frequently irrigated wheat plots. The timing and frequency of irrigations would have influenced leaf area development, the subsequent balance between evaporation and transpiration, and the WUE in the two experiments.

Green foxtail

The WUE of green foxtail in a greenhouse experiment was 2.2 g dry matter kg^{-1} water used (Anderson and Best 1965).

ROOT GROWTH

Several studies have shown that the depth, extension and rate of root growth and subsequent water extraction profiles vary among plant species including both crops and weeds (Davis et al. 1965 ; 1967). Root growth is affected by many environmental parameters which are interdependent (Kramer 1983a). Soil physical and chemical properties, temperature, structure and aeration have direct effects on root growth and indirect effects through the modification of ψ s (Newman 1974 ; Taylor 1983). However roots are not autonomous organs and the importance of root:shoot relationships in seedling growth are often

neglected. Kramer (1983a) listed root:shoot ratios for 11 species but indicated that these ratios should be interpreted with caution because the completeness of root recovery is variable among different studies. In annual species, carbohydrates are primarily directed into the formation of new leaves, while root growth is minimal and dependent on further leaf growth (Schulze 1983).

In competitive situations two types of rooting strategies may exist: 1) deep rooted species which are able to survive periods of low precipitation due to their extensive root system and ability to grow on stored water deep in the soil profile, and 2) shallow rooted species with extensive lateral root spread near the soil surface which effectively exploit precipitation during the growing season (Berendse 1979). These two rooting types are not mutually exclusive as some species may have root systems with both types of distributions. The distribution of roots in the soil profile does not necessarily relate to root function, and the ability of a root system of either type to respond to increased soil water content (θ) following precipitation may be more important. Rhodes (1968) reported that the competitive ability of five different grass species was associated with the rate and extent of nodal root production.

Water uptake by roots in a soil layer is a function of: 1) the total root length in the layer, 2) the rate of water uptake per unit length of root per megapascal (MPa), 3) the potential difference ($\Delta \psi$) from bulk soil into the root system (Gardner 1964 ; Molz 1975 ; Taylor and Klepper 1978) , and 4) the relative importance of plant and soil resistances to water flow (Kramer 1983a). The root system is usually considered to be the major plant resistance to water flow in actively

transpiring plants (Kramer 1983a), until ψ_s decreases. With decreasing ψ_s soil hydraulic conductivity dominates the resistance network at about -0.1 MPa and -0.8 MPa in sands and clays, respectively (Meyer et al. 1978). In general roots extending into soils at ψ_s below -0.5 MPa usually intercept insignificant amounts of water (Taylor 1983) although most crop plants can extract water down to ψ_s of -1.5 to -2.0 MPa (Passioura 1983).

Root resistance is primarily due to radial (lateral) resistance to water flow in wet soils while in dry soils axial (longitudinal) resistance to water flow in the xylem elements is the dominant plant resistance (Taylor and Klepper 1978). Axial resistance is a result of frictional forces between the water column and the xylem vessel walls. Axial resistance varies 1) among plant species, 2) among soil depths in one species, 3) between seminal and nodal roots and among different nodal roots of cereals, and 4) when the number of adventitious roots increases (Taylor and Klepper 1978). However the rooting density of plants constantly changes during the growing season and these changes alter the axial resistance by altering the water uptake patterns. For example, an increase in the density, number and water uptake of nodal roots will decrease axial resistance because the total cross sectional area available for water flow is increased (Taylor and Klepper 1978). The primary effect of axial resistance is to decrease the rate of water uptake deep in the soil profile (Taylor 1983) and this may be an effective strategy for rationing water use over the season (Passioura 1983).

Wheat

Wheat cultivars differ in their extent, pattern and distribution of rooting due to both genetic factors (Hurd 1974) and soil conditions (Tennant 1976) so that comparisons between studies should be carefully interpreted. These difference may only be expressed under conditions of low ψ_s (Kirkham and Kanemasu 1983).

The depth of wheat root penetration is usually 1 to 2 m, with the greatest penetration occurring in sandy soils and the least in clay soils (Tennant 1976). In a three year study in Australia the depth of rooting also appeared to be independent of the depth of soil water penetration (Tennant 1976). The extension rate of wheat roots ranges from 0.5 to 3.0 cm day⁻¹ but this depends on the growth stage of the plant and soil characteristics. Much of the rapid root depth penetration in field studies occurred during stem elongation (Tennant 1976) or from inflorescence initiation to heading (Kirkham and Kanemasu 1983). The rapid elongation of a particular root segment depends on adequate supplies of growth regulators and photosynthate from shoots and on the soil conditions around the root, particularly soil water content. The extent of rooting can also be determined by the plant density. At anthesis, wheat plants had an average of five seminal roots per plant and 55, 30, and 15 nodal roots per plant at seeding rates of 27, 137, and 595 plants m⁻², respectively (Kirkham and Kanemasu 1983). Increasing the density also decreased the depth of penetration of both seminal and nodal roots. Field grown wheat plants typically have 3 to 4 seminal roots that penetrate deeply to the subsoil but the nodal roots are often restricted to the top 30 cm of the soil profile, and in prolonged early atmospheric droughts they may not develop at all (Passioura 1983).

Water uptake by wheat roots depends on the root distribution and ψ_s (Evans et al. 1975). Wheat roots absorb water from the top part of the soil profile first even if deep roots are in wet soil. When precipitation occurs, water uptake from the surface layers increases and uptake from lower layers decreases, but soil texture is important in the relative amounts of water extracted from different parts of the profile. Herkelrath et al. (1977) studied water uptake by wheat using a split root system in which a soil column was stratified vertically into five layers. The layer at the top of the column was designated as layer one and the sequence ascended to layer five at the bottom of the column (56 cm). The highest rate of water extraction per unit volume of soil was initially in section one, but as the soil dried the zone of maximum extraction rate shifted downward. The authors reported that when sections two, three, and four (representing 45% of the root zone) were irrigated subsequent to a drying cycle there was no recovery of ψ_l . However the ψ_l recovered to pre-stress levels only when the top layer of the column was irrigated. This preferential absorption from the surface region of a uniformly wet soil column was attributed to a high rooting density near the surface. However the ability to absorb water from previously dry soil will depend on the capacity of the plant to reactivate root functioning (Kramer 1983a).

The relative importance of radial and axial resistances in the ability of wheat to tolerate atmospheric drought, and the modification of axial resistances is a subject of controversy. The total resistance to water flow in wheat is the sum of the radial and axial resistances (Kramer 1983a). Radial and axial resistances are approximately equal in wheat plants with the normal complement of seminal and nodal roots

(Meyer et al. 1978) but the relative magnitude of the two resistances varies with the proportion of seminal and nodal roots. For wheat plants growing on a single seminal root, axial resistance is greater than radial (Meyer et al. 1978). Water flow in seminal roots is primarily in one large metaxylem element whose diameter determines the hydraulic resistance and subsequent flow characteristics (Taylor 1983). The diameter of these xylem vessels changes with depth in the wheat root, so resistances and flow rates also change (Kirkham and Kanemasu 1983). Passioura (1983) argues that by decreasing the number of seminal and nodal roots in wheat plants the axial resistance is increased. This results in a lower flow rate and thus forces the wheat plant to ration water use, leaving more water available for later growth. Water stress at the boot to anthesis stage results in the greatest reduction in wheat yield so a high water content (θ) at this time would be beneficial (Kirkham and Kanemasu 1983). However Taylor (1983) has proposed that the total available water can be increased by decreasing the axial resistance to water flow in the xylem by increasing xylem diameter. This decrease in resistance allows more of the daily decrease in ψ_l to be transmitted to the xylem of roots located deep in the soil profile. This effectively increases the $\Delta \psi$ gradient between soil and root and thus a larger flow rate. Therefore more water would be available for the aerial portions of the plant for use in transpiration or turgor maintenance. Wheat cultivars differ in their axial resistance therefore, due to variation in numbers of seminal roots and root xylem diameter and these factors are apparently genetically determined (Taylor and Klepper 1978).

However the ability of wheat to ration its' water supply over the duration of the season and survive under atmospheric drought does not necessarily relate to effective competition with weeds (Passioura 1983). Wheat plants with high axial resistances would be expected to have small or non-existent nodal roots (Meyer et al. 1978) but there may be an advantage to numerous nodal roots in the surface layers (Passioura 1983). A large rooting density in wheat in the upper 30 cm (depending on soil texture) would allow for rapid uptake of precipitation before it evaporates and the ability to compete with weeds for water (Passioura 1983). Perhaps different rooting strategies are required for competition and survival under low ψ_s .

Green foxtail

Orwick and Schreiber (1975) studied the root growth in Setaria spp. in 4 and 7 day old seedlings. The experiments were conducted using a silt loam soil in a growth room at 22.5 C. They found the mean extension rates ranging from 0.61 to 0.71 cm .root member⁻¹ day⁻¹. All the foxtail species developed only one seminal root and the extension rate increased as the length of the photoperiod increased from 8/16 to 16/8 (light/dark) at a PPFD of 0.5 mmol m⁻² s⁻¹. However this photoperiod effect would be of minor importance compared to temperature effects on root growth (Kramer 1983a). Green foxtail was reported to have a slower rate of root growth than Sorghum halepense (L.) Pers. and Sorghum bicolor L. in a loamy soil when grown in a greenhouse at 18 to 38 C (Evetts and Burnside 1973). In a controlled environment study (sandy loam soil) at 24/16 C the nodal root growth of green

foxtail was decreased with limited water supply (Nadeau and Morrison 1983). With restricted water supply 55% of the total root length consisted of seminal roots while under the wettest conditions seminal roots only comprised 5% of the total root length. The growth rate of roots was also reduced due to limited water supply. In outdoor studies (clay loam soil) the roots of green foxtail in large soil boxes penetrated to at least 58.5 cm (Nadeau and Morrison 1986) with the greatest root length occurring at the 15 to 35 cm depth irrespective of the irrigation regime of 0.3, 0.6 or 2.5 cm wk⁻¹. However plants in the 0.3 and 0.6 cm treatment would have utilized water stored in the soil profile for growth as these small irrigations had little effect on soil water potential.

Kutschera (1960) described the main roots of green foxtail as having approximately 12 laterals, each of which had branches up to the fourth order. However the extent and pattern of rooting depended on edaphic conditions. The root system in flowering plants consisted of 12 main roots and 3360 secondary roots (Dittmer 1948). In soil boxes 150 cm deep by 104 cm wide by 12 cm thick, filled with silt loam soil, the roots of giant foxtail (Setaria faberii Hermm.) were distributed throughout the profile (Parrish and Bazzaz 1976). The competitive effects of five associated annual species had no effect on the rooting pattern of giant foxtail in these boxes. Furthermore, the overriding effect of environmental conditions was evident in the fact that giant foxtail produced 40% of its' total root growth during one week in July. In field studies, Wieland and Bazzaz (1975) reported that the roots of giant foxtail were restricted to the upper 15 cm of the soil profile.

LEAF AND CANOPY GROWTH

Cell and tissue water relations

The water potential (ψ) of a cell is a function of three components:

$$\psi = P + \pi + \tau$$

where

P = pressure potential (+ve)

π = osmotic potential (-ve)

τ = matric potential (-ve)

assuming that gravitational effects on ψ are negligible in most agricultural crops (Kramer 1983b). Thus ψ is determined by the relative proportion of the three components. P represents the effect of pressure on the energy status of water resulting from protoplasmal water uptake and constraints imposed by the cell wall (Philip 1966 ; Preston 1974). P is a function of the protoplast volume and the elasticity of the cell wall or bulk elastic modulus (ϵ). ϵ is a measure of the reversible or elastic expansive properties. τ makes an insignificant contribution to the total water potential of a cell and thus is often excluded from the equation (Tyree and Karamanos 1981 ; Tyree and Jarvis 1982). π represents the effects of dissolved solutes on ψ (Dainty 1963):

$$\pi = - (RTn_s / V_w)$$

where

R = universal gas constant

T = Kelvin temperature

n_s = number of moles of solute

V_w = volume of solvent water

These parameters differ from cell to cell with differences in solute concentrations, ϵ , and cellular volumes, so that in tissues, weight or volume averaged values are determined. The values are averaged over vacuoles, cytoplasm and cell wall (Tyree and Jarvis 1982) although measurements of individual cell properties have been made (Steudle et al. 1977).

The expansive growth of a tissue (irreversible cell enlargement) results from the mechanical forces of P on the cell wall within the individual cells (Zimmerman and Steudle 1978). The driving force for growth is a difference in P (ΔP) between the inside and outside of the cell. As ψ is a function of P and π , ψ in a cell can be maintained constant by altering the relative contributions of P and π (Kramer 1983b). In a non-expanding cell in equilibrium with its' surroundings ($\Delta \psi = 0$), π is exactly balanced by P , therefore when $\Delta \psi = 0$ there is no water influx (Dainty 1963). Expansion of a cell is initiated by a relaxation or loosening of the cell wall (Hsiao and Bradford 1983). This immediately reduces P , ψ (inside) becomes less than ψ (outside), $\Delta \psi \neq 0$ and water flows into the cell. The cell then expands due to water uptake and the force of P until cell wall resistance causes P to rise to the point where $\Delta \psi = 0$. After equilibrium is reestablished, wall relaxation occurs and the process is repeated. During continuous growth these processes of wall relaxation, water flux, expansion and cell wall synthesis occur simultaneously (Hsiao and Bradford 1983). In order for

this growth to occur ψ (inside) must be less than ψ (outside). As growth occurs more water is taken into the cell which effectively dilutes the solute concentration within the cell. Thus the $\Delta \psi$ for growth must be maintained by increasing the solute concentration within the cell. These solutes must be accumulated in the cell or generated internally (Weatherley 1970). Therefore P, wall relaxation, and solute accumulation are mutually dependent components of growth. A minimum turgor pressure or threshold value must be exceeded before growth occurs and this commonly ranges from 0.1 to 0.65 MPa (Tyree and Jarvis 1982 ; Hsiao and Bradford 1983). However this threshold turgor for expansion varies with growth conditions and the degree and extent of water deficit (Tyree and Jarvis 1982; Nobel 1983). It is important to note that the growth rate of an organ such as a leaf, is only sensitive to the increment of P that exceeds Y, so small decreases in P can reduce or stop growth even though P may still be considerable. Cell enlargement may cease when P in leaves is as large as 0.6 to 0.8 MPa (Terry et al. 1983).

As growth is directly determined by ψ , it is the most sensitive parameter to decreasing ψ (Boyer 1968,1970,1985 ; Hsiao 1973). The ability to maintain P and leaf expansion at low ψ is accomplished by decreasing π within the cell (Turner and Jones 1980). This decrease in π , termed osmotic adjustment, may occur by the passive accumulation of solutes or active generation in the cell (Jones and Turner 1978 ; Radin 1983 ; Morgan 1984). Most reports of osmotic adjustment indicate a 0.5 to 0.7 MPa decrease in π (Radin 1983). Although osmotic adjustment results in P maintenance at low ψ , turgor maintenance may occur for other reasons. For example, cells with high elasticity show larger

changes in volume per unit change in turgor, so cell shrinkage maintains turgor (Radin 1983). Osmotic adjustment does not occur in all plant species and may not be present in pot grown plants as it usually results from repeated slow cycles of low ψ s (Jones and Rawson 1979 ; Jones 1983 ; Morgan 1984). At low ψ s, the $\Delta \psi$ between plant and soil is greater in species which exhibit osmotic adjustment, but ecologically this may be of greater benefit in clay soils than in sands, as the water content of clays is greater than sands at ψ below about -0.1 MPa (Tyree and Karamanos 1981).

Leaf expansion

Osmotic adjustment in leaves permits leaf expansion at lower ψ s which results in greater radiation interception. Leaves typically show a diurnal reduction in ψ and even with osmotic adjustment leaf growth may be insignificant during the daylight period (Ehrler et al. 1978). In sunflower (Helianthus annuus L.) Boyer (1968) reported 5 to 6 times more growth at night than during the day. Leaf enlargement was maximum at ψ of -0.15 MPa but negligible at -0.35 MPa, so that a 0.20 MPa change in ψ spanned the entire range of growth rates from maximum to zero. Under conditions where ψ is severely depressed during the day, growth over the long term occurs as a series of nightly pulses (Boyer 1968,1970). Growth at night under field conditions is usually limited more by temperature than by turgor (Jones 1983). As the soil dries with the onset of water stress, the nocturnal recovery from water deficits induced during the day decreases, ψ decreases, and eventually leaf enlargement ceases (Begg and Turner 1976). In the leaf expansion

process cell enlargement and ultimate leaf size are particularly sensitive to temperature and water deficit (Hughes et al. 1970).

The expansion of the leaf surface depends on rates of leaf production and senescence, rate and duration of leaf expansion, and tillering (Terry et al. 1983). With adequate soil water content or nightly recovery from low ψ_l , the temperature of the leaf base controls the leaf growth rate in grasses. Prior to lamina emergence, assimilate and hormones from more mature leaves are also important but following lamina emergence, light and temperature are overriding factors (Humphries and Wheeler 1963). In general temperature seems to have the largest effect on the duration of growth, while water and nitrogen have their largest effects on the mean rate of expansion (Monteith and Elston 1983).

Leaf display

Leaves of plants under water deficit commonly show changes in foliage display but there is little quantitative data in the resultant effect on light interception, water vapor and CO₂ transport (Gardner et al. 1985). Many species display leaf wilting and rolling but the effect in reducing water loss may be insignificant as stomata are usually closed at ψ_l above these values (O'Toole et al. 1979 ; O'Toole and Cruz 1980 ; Jordan 1983). It is also unlikely that photosynthesis would be reduced by these responses but they may protect against thermal damage by reducing the amount of direct radiation intercepted by the leaf and by altering leaf boundary layer characteristics (Zangerl 1978 ; Gates 1980).

In a grass canopy leaves may be at all angles, influenced by genotype, stage of growth, density and nutrient status (Donald 1963). More vertical leaves reduce the heat load and also generally make more efficient use of diffuse radiation (Gardner et al. 1985).

Leaf number

If ψ_l is reduced for an extended period of time there can be a reduction in leaf initiation rates (Humphries and Wheeler 1963 ; Jordan 1983). However the subsequent effects of water deficit on leaf enlargement and persistence are probably more important than any reduction in primordia number (Jordan 1983).

Leaf senescence

Complex ψ_l profiles exist within crop canopies because in addition to the variation in leaf age and length of the water transport pathway, environmental factors such as incident radiation, ψ_a , windspeed and temperature change rapidly within a canopy (Wilson 1977 ; Etchevers et al. 1982 ; Barlow 1983 ; Monteith and Elston 1983). Gradients in pressure potential and osmotic potential can also exist within the canopy (Barlow 1983).

The effect of water deficit in decreasing leaf area is especially important in the early vegetative stages of growth when there is incomplete light interception (Blackman 1961 ; Begg and Turner 1976 ; Green 1984). Water stress prior to anthesis in grasses reduces the area of the developing leaves, whereas stress after anthesis increases lower leaf senescence (Monteith and Elston 1983). Reduced leaf area directly

affects soil water-radiation-soil temperature relations which indirectly determines meristem temperature and leaf growth rates. The imposition of water stress in grasses increases leaf senescence at ψ_l values well above the level where photosynthesis is affected, so that radiation interception becomes more important to growth at high ψ_l (Jordan 1983). However this accelerated senescence of physiologically older leaves can also be considered an adaptive mechanism for reducing water usage. Reduced leaf area results in lowered transpiration and the release of carbohydrates and nitrogen from older leaves to support younger leaves (Boyer and McPherson 1975). It is important to realize that the reduction in leaf area is a permanent effect while photosynthesis can recover when the water deficit is relieved. Thus leaf senescence may be a poor competitive strategy in areas with intermittent drought.

Leaf area duration

The longevity of a leaf canopy, expressed as leaf area duration (LAD), in an annual crop depends on the rate at which complete ground cover is achieved, the maintenance of a maximum leaf area index (LAI) and the subsequent senescence of leaves (Monteith and Elston 1983). The environmental factors determining LAD are primarily water and temperature (Watson 1952). Most studies have demonstrated that LAD and the partitioning of dry matter into leaves is more important to plant growth than the photosynthetic rate of individual leaves (Watson 1952 ; Stoy 1965). In experiments with wheat conducted in a range of environments, about half of the variation in yield due to climate, agronomic practice, and cultivar was related to variation in LAD (Evans

et al. 1975). However in a competitive situation a high LAD may not be advantageous if the competitor is taller and able to intercept more energetic photons (Donald 1963). Shade radiation makes little contribution to photosynthesis because leaves have low absorption in the infrared portion of the spectrum (Nobel 1983). Thus leaf area, LAD and the spatial distribution of foliage of the competing species determines both the quantity and quality of radiation intercepted during the season (Spitters and Aerts 1983).

Wheat

Wheat cultivars vary in height, tiller production, leaf area, leaf arrangement (Evans et al. 1975), leaf angle (Donald 1963), and drought tolerance (Blum et al. 1983) so only general conclusions which relate to competitive ability can be discussed.

In the vegetative phase the competitive ability of wheat is associated with rapid development of a large leaf area (Zimdahl 1980). Leaf extension in wheat is linearly related to $1/\text{temperature}$ from 5 to 25 C and this is probably the dominant factor determining extension (Terry et al. 1983). As wheat cultivars differ in their capacity for osmotic adjustment (Morgan 1977), leaf expansion under conditions of low ψ_s is also variable. However the reduction in leaf area with water stress is not related to cultivar ranking in drought resistance or yield potential (Blum et al. 1983).

Several of the studies which have examined the effect of water stress on plant growth have to be interpreted with caution as osmotica such as mannitol and polyethylene glycol (PEG) have been used to induce

water deficits. There is ample evidence that such osmotica are absorbed by plants and exert direct effects on the ψ_l (Kramer 1983a). Water stress (PEG) had little effect on wheat seedlings from the onset of germination up to a coleoptile length of 3 to 4 mm in wheat (Barassi et al. 1980). Duysen and Freeman (1974), using PEG, reported that the growth of wheat seedlings was reduced 90% when ψ_l was between -0.9 and -1.4 MPa, but the components of ψ_l were not determined. Munns et al. (1979) reported that elongation in wheat leaves ceased at a P of 0.2 to 0.3 MPa, when measured on the lamina. Senescence of leaves begins when ψ_l reaches -2.0 MPa but plants can recover from a ψ_l of -4.0 MPa upon rewatering (Angus and Moncur 1977). However attempts to relate extension rates of grass leaves to P or ψ measured on the lamina have been less than successful as it is the cell water relations in the meristem which determines the rate of elongation (Chu and McPherson 1977). To date there are no reliable methods for measuring P or ψ at the enclosed meristem. While leaf elongation rates can be related to ψ_s , there is no unique relationship between ψ_s and plant ψ (Kramer 1983a).

The ability to survive water deficits appears to be greatest for young enclosed tissues in grasses as they are: 1) protected from rapid evaporative water loss by enclosure in older sheaths, and 2) able to adjust osmotically by maintaining their strength as a sink for translocated materials. There is evidence for osmotic adjustment in leaves, expanding hypocotyls, roots and meristems (Morgan 1980), so it may be a general phenomenon throughout the plant. However drought resistance in vegetative growth is not necessarily related to that in reproductive growth in wheat (Blum et al. 1983). Simmelsgaard (1976)

noted that if leaf enlargement is reduced as a result of water deficit (PEG), the cell volume remains small and the amount of solutes necessary to lower π is reduced. Thus there may be a combination of osmotic and structural adaptation to water deficit (Boyer et al. 1985). The severity of water deficit in the meristematic tissue determines the continuance of leaf production and yield potential. In general wheat apices are more tolerant of water deficit than expanded leaves, so that even if photosynthesis is reduced, the plant remains viable and can resume growth upon alleviation of the deficit (Angus and Moncur 1977). Barlow et al. (1977) studied the response of ψ in the apex, enclosed leaf (leaf 7), and fully expanded leaf (leaf 4) of wheat plants in drying soil. The apex maintained a higher ψ than did leaf 4 but leaf 7 had approximately the same ψ . The apex and enclosed leaves were able to survive, and recover from, ψ as low as -6.0 MPa, whereas the exposed leaf wilted at ψ between -0.8 and -1.0 MPa, and died at -4.0 MPa. In addition the stressed apex had a much higher water content (75%) than did the leaves (35%) at the same ψ (-3.5 MPa). The authors suggested that the higher water content was due to osmotic potential adjustment in the apex and this may be related to the ability to survive and recover from drought (Barlow et al. 1980a,b).

Green foxtail

Field and controlled environment studies have demonstrated that the leaf area and tillering of green foxtail are reduced by both shade (Lee and Cavers 1981 ; Bubar and Morrison 1984) and low soil water potential (Maurice 1985 ; Nadeau and Morrison 1986).

In field studies in Alberta green foxtail required an average of 5.7 days to advance from one leaf stage to the next (while wheat required 6.3), but no detailed climatic data are reported to relate development to environment (Dew 1980). Leaf area was not determined so variability may have existed in plant size between years, even though a given phenological stage had been attained.

C₃ - C₄ COMPETITION

There is a wide range in the niche characteristics of C₃ and C₄ species and any attempt to relate PCRC to a specific environment is erroneous (Ludlow 1976 ; Percy and Ehleringer 1984). Many previous investigators have considered that the competitive ability of a plant species is directly related to PCRC (Black et al. 1969) but success in a competitive situation is determined by many other factors, most of which are whole plant characteristics (Wiese and Vandiver 1970 ; Bull 1971 ; Baker 1974 ; Baskin and Baskin 1978).

The competitive success of a plant species in a seral community is associated with early and rapid establishment from large seeds, and rapid leaf area and root development (Barbour et al. 1980). In an agronomic situation successful weeds: 1) have efficient and rapid uptake of water and nutrients through rapid development of exploitive root systems, 2) allocate a large proportion of assimilate to leaf area production which effectively shades the crop , and 3) have high relative growth rates (Patterson 1982).

The outcome of competition between lamb's-quarters (Chenopodium album L.) (C₃) and redroot pigweed (Amaranthus retroflexus L.) (C₄)

was determined primarily by differences in the relative growth rates prior to canopy closure (Pearcy et al. 1981). The relative growth rate for the two species was temperature dependent - at 17/14 C lamb's-quarters was more competitive, at 34/28 C redroot pigweed was more competitive, while at 25/18 C there was little difference between the two species (Chu et al. 1978). However it is important to stress that these two species have different niche characteristics and that when ecologically similar species are compared many factors other than temperature will determine the result of competition (Allen 1982). Percy et al. (1981) found that in contrast to temperature, growth of the two species under limited water supply had no effect on the competitive interactions. The C₄ PCRC is not strictly an adaptation to water deficit and does not appear to confer a competitive advantage in water limited environments (Hofstra and Stienstra 1977 ; Barnes et al. 1983).

The competitive outcome between lamb's-quarters and redroot pigweed was determined by differences in growth, leaf area production, and whole plant photosynthesis prior to canopy closure (Percy et al. 1981). It appears that any photosynthetic differences after canopy closure, due to lower Φ in C₄ for example, have a minor effect on competition compared to factors which determine the relative position of each species within the canopy.

Wheat-foxtail competition

Various field studies of green foxtail competition in wheat (Sturko 1978 ; Blackshaw et al. 1981b), barley and flax (Rahman and Ashford

1972b), sugar beet (Brimhall et al. 1965) and peas (Nelson and Nylund 1965) have demonstrated increasing yield reductions due to increasing weed densities but the results over years are variable due to differences in weather conditions and the relative time of emergence of the competing species.

In cereal crops, weed competition occurs initially among the roots, although the foliage is important in supplying assimilate beyond the coleoptile stage (Milthorpe 1961). Pavlychenko and Harrington (1934) attributed the success of competitive weeds in cereals to: 1) the ability to develop a large leaf area in the early seedling stage, and 2) a large mass of fibrous roots close to the soil surface as well as deeply penetrating main roots. The rate and extent of seminal root growth and the subsequent effect on plant growth is important in competitive situations (Pavlychenko and Harrington 1935 ; Rhodes 1968). Blackman and Templeman (1938) reported that cereal crops and annual weeds competed for nitrogen and light but Welbank (1963) found that competition for nitrogen was not responsible for the detrimental effects of weeds in wheat.

Although there are numerous studies which have examined weed competition in cereal crops there are few wheat-green foxtail competition studies and the data which do exist are ambiguous and confounded with environmental variation (Sturko 1978 ; Zimdahl 1980 ; Blackshaw et al. 1981b).

Sturko (1978) conducted field experiments to examine the effect of green foxtail density and time of removal on wheat yield. The contrast in results between 1975 and 1976 clearly demonstrate the importance of temperature in green foxtail competition. Table 1 lists accumulated

degree-days (Σ DD) (base temperature=5 C), accumulated precipitation (Σ PPT), and the difference in degree-days between 1975 and 1976 (Δ DD) for 10 day intervals to 60 days after seeding. The plots were seeded June 18, 1975 and June 3, 1976. Canopy closure would have been complete by the end of this 60 day period which is the critical period for $C_3 - C_4$ competition (Pearcy et al. 1981). There was little difference in Σ PPT between the two years but a much greater Σ DD in 1975 than in 1976. Sturko (1978) reported a 67% yield reduction in 'Napayo' wheat by 1600 foxtail m^{-2} in 1975, but there was only a 14% reduction in 1976. The greater yield reduction due to foxtail in 1975 can be directly attributed to the greater Σ DD as a result of higher temperatures. Sturko (1978) also conducted time of removal studies in which green foxtail was established at 200, 400, and 800 plants m^{-2} in wheat and removed at the 1 to 3 leaf, 4 to 5 leaf, 6 to 7 leaf, and heading stages. In 1975 there was no yield reductions of Napayo wheat if the foxtail was removed in the 1 to 3 leaf stage, but if left until the 4 to 5 leaf stage or later significant (12 to 34% depending on density) yield reductions occurred. In 1976 there were no wheat yield reductions even if the foxtail was left for the entire season. Blackshaw et al. (1981b) obtained similar results over a 2 yr field study. In 1977 there were no significant yield reductions in 'Sinton' wheat at any given foxtail density from 0 to 1600 m^{-2} . However in 1978 wheat yields were decreased 43 and 54% at 800 and 1200 foxtail m^{-2} , respectively. Reductions in tiller number and leaf area with increasing foxtail density were also reported, but density and competitive effects are confounded in these additive experiments. Rahman and Ashford (1972a) reported that over a 2 yr period green foxtail infestations up to 1550 m^{-2} had no significant affect on wheat growth or yield.

TABLE 1
Environmental conditions at Winnipeg for 1975 and 1976.¹

Days from seeding	1975		1976		
	Σ DD	Σ PPT	Σ DD	Σ PPT	Δ DD
10	146.7	64.5	153.9	34.7	-7.2
20	312.7	69.3	254.2	67.2	58.5
30	464.8	77.5	378.5	81.6	86.3
40	625.2	93.5	529.3	86.7	95.9
50	788.0	101.8	676.9	105.8	111.1
60	915.8	131.3	809.1	112.1	106.7

Σ DD=summation of growing-degree days from time of seeding

Σ PPT=summation of precipitation from time of seeding

Δ DD=difference in accumulated growing degree days between 1975 and 1976

¹ from Sturko (1978).

Bubar and Morrison (1984) reported that the leaf area of green foxtail (at densities of 286 to 326 m^{-2}) after 4 weeks of growth in a wheat crop (180 m^{-2}) was 157,74 and 48 cm^2 in 1979, 1980 and 1981 respectively. The authors concluded that the differences in leaf area among the years was due to differences in water supply during the time of seedling establishment.

It is apparent from the studies by Sturko (1978) and Blackshaw et al. (1981a,b) that results of competition experiments between green foxtail and spring wheat are highly variable and this variability can be partially attributed to the prevailing temperature conditions.

MATERIALS AND METHODS

OUTDOOR STUDY

Experimental design, methodology, and sampling technique

During the summer of 1984 and 1985 experiments were conducted outdoors in four large wooden boxes. Each box was 5.5 m long by 1.8 m wide by 0.8 m deep and was subdivided into four compartments. The compartments were lined with plastic to prevent drainage from the soil and filled with Altona clay loam (39% sand, 32% silt, 29% clay, pH 7.7). Three of the boxes were filled in 1979 and one in 1980, and the soil was compacted to a bulk density of approximately 1.21 g cc^{-1} . Semi-circular hoops constructed of 3 m lengths of electrical conduit, were placed over the compartments of the boxes perpendicular to the long axis of the boxes to support sheets of polyethylene. The sheets were unrolled to cover the boxes during periods of precipitation and thus permitted accurate control of the water regime. Complete details of the dimensions, location, and construction of the boxes can be found in Maurice (1985), and Nadeau and Morrison (1986).

The soil was fertilized with 10 kg ha^{-1} phosphate (as triple superphosphate) as a broadcast application, following soil test recommendations for spring wheat (Soil Testing Laboratory, Province of Manitoba). The compartments of each box were divided into 10 by 10 cm squares using nylon line and seeded by hand with wheat (cv. Benito) and green foxtail on May 31 to June 3, 1984 and May 30 to June 5, 1985. In

1984 the wheat was seeded at 400 seeds m^{-2} , while in 1985 the wheat was seeded at 200 seeds m^{-2} . In both years the seeding depth for wheat was approximately 3 cm in east-west rows, 10 cm apart while green foxtail was broadcast on the soil surface and incorporated to a depth of approximately 1.0 cm. This planting arrangement on a square grid maximizes the competitive ability of the crop (Jensen and Federer 1965 ; Fischer and Miles 1973). In both years the two species emerged about 4 days after seeding. Following emergence the populations were reduced to the final densities of 200 wheat and 400 foxtail plants m^{-2} . The thinning procedures began June 18, 1984 and June 20, 1985. In 1984 thinning was hampered by extended periods of rainfall. At the initiation of thinning green foxtail and wheat were in the 3 to 4 lf stage. Subdividing the boxes into 10 by 10 cm squares permitted the establishment of precise densities.

A box was designated as a block and two compartments of a box constituted a plot. Two irrigation treatments were imposed on each plot beginning 2 weeks after emergence. The two treatments consisted of applying 0.5 or 2.5 cm of water $week^{-1}$ to the soil surface using a watering can following plant and soil sampling. Hereafter the 0.5 cm irrigation will be termed the "dry" treatment and the 2.5 cm irrigation the "wet" treatment. These irrigations were applied on a weekly basis following plant and soil sampling. The total amount of water applied to the wet and dry treatments amounted to 175 and 35 mm in 1984 , and 200 and 40 mm in 1985, respectively. A completely random sampling scheme was achieved by assigning a random number to each of the squares within a compartment. Each compartment in a box measured 180 by 130 cm. A 20 cm "buffer" zone was planted but not harvested around the perimeter of

each compartment. Thus an area of 160 by 110 cm, or 176 squares each 10 by 10 cm, was used for sampling. Adjacent squares were not sampled during the course of the experiments. At 7 day intervals from 22 days after emergence to wheat maturity, two random numbers were generated for each compartment and the corresponding squares were selected as samples. This amounted to a total of 32 samples at each harvest date. The plants from each square (two wheat and four foxtail) were harvested and evaluated individually.

Following plant sampling, soil samples were taken with a soil probe (2 cm diameter) from 5 to 10 cm, 15 to 20 cm, 25 to 30 cm, 45 to 50 cm, and 65 to 70 cm depths within each sample square. The gravimetric water content was determined by drying at 105 C for 48 h. Gravimetric water content was converted to soil water potential using a soil water release curve (Appendix Figure 1). The sample holes were filled with soil following core removal.

Daily maximum and minimum temperatures were recorded from plant emergence to harvest using a mercury thermometer in a standard Stevenson screen at a 1.5 m height. Precipitation was collected and recorded daily with a rain gauge. In 1985 four black Bellani plate atmometers (C & M Meteorological Supply, Riverside, CA) one in each box, equipped with mercury-in-wool valves were used for daily estimates of evapotranspiration (see Appendix Figure 3) (Livingston 1935 ; Carder 1968).

Parameters measured and data analysis

The height (to the highest node), leaf area (Model LI-3000 leaf area meter, LI-COR, INC., Lincoln, NE) and tiller number of each plant were determined. The plants were separated into leaves, culms, and inflorescences where appropriate and dried at 80 C for at least 48 h. Dry weights were determined to the nearest 1.0 mg.

The dry weight and leaf area data were analyzed by ANOVA in a split-split-split-split-plot design (Monlezun et al. 1984) using the Statistical Analysis System (SAS). Growth analysis techniques were used to examine the dynamics of plant growth with the formulae outlined in Table 2. More complete details of the theory and methodology of growth analysis can be found in Kvet et al. (1971), Evans (1972), Causton and Venus (1981), and Hunt (1978, 1982). Curve fitting was accomplished using the SAS General Linear Models (GLM) procedure (Berenson et al. 1983) and mean values for RGR, RLGR, and ULR were calculated using an author written SAS program. The seed yield of each species in the two treatments was determined by harvesting the plants from five sample squares on August 23, 1984 and September 2, 1985. The inflorescences were dried at 80 C and seed dry weights determined.

TABLE 2. A synopsis of derived quantities involved in growth analysis.

Quantity	Contraction	Symbol	Instantaneous Value	Mean Value	Dimensions	Reference
biomass duration	BMD	Z	$\int_{t_1}^{t_2} W dt$	-	weight time	Kvet et al. 1971
leaf area duration	LAD	D	$\int_{t_1}^{t_2} A dt$	-	area time	Hunt 1982
leaf area partition coefficient	LAP	-	$\frac{dA/dt}{dW/dt}$	-	$\frac{\text{area time}^{-1}}{\text{weight time}^{-1}}$	Potter and Jones 1977
leaf area ratio	LAR	F	A/W	$\frac{\int_{t_1}^{t_2} A dt}{\int_{t_1}^{t_2} W dt}$	area weight ⁻¹	Ondok 1971
leaf weight partition coefficient	LWP	-	$\frac{dLW/dt}{dW/dt}$	-	$\frac{\text{weight time}^{-1}}{\text{weight time}^{-1}}$	Potter and Jones 1977
leaf weight ratio	LWR	-	LW/W	-	-	Hunt 1982
relative growth rate _f	RGR	R	$\frac{1}{W} \frac{dW}{dt}$	$\frac{\ln W_2 - \ln W_1}{t_2 - t_1}$	time ⁻¹	Evans 1972
relative leaf growth rate	RLGR	R(L)	$\frac{1}{A} \frac{dA}{dt}$	$\frac{\ln A_2 - \ln A_1}{t_2 - t_1}$	time ⁻¹	Hunt 1982
specific leaf area	SLA	-	A/LW	-	area weight ⁻¹	Hunt 1982
stem weight partition coefficient	SWP	-	$\frac{dSW/dt}{dW/dt}$	-	$\frac{\text{weight time}^{-1}}{\text{weight time}^{-1}}$	Young et al. 1982
unit leaf rate	ULR(=NAR)	E	$\frac{1}{A} \frac{dW}{dt}$	$\frac{W_2 - W_1}{A_2 - A_1} \left(\frac{A_2 - A_1}{A_2 - A_1} \right)^{a-1}$	weight area ⁻¹	Whitehead and Myerscough 1962, Radford 1967
				$\frac{a}{a-1}$	time ⁻¹	

CONTROLLED ENVIRONMENT STUDIES

Temperature and soil water effects on growth

Results of the outdoor study of 1984 and the literature indicated that any differences in optimum growth temperature for two species must be determined before any investigation of competition for soil water can be reliably conducted (Christie and Detling 1982). The following experiment was conducted to assess the growth responses of green foxtail and wheat to temperature in an effort to more fully understand the potential effects of water deficit in a given environment.

One liter plastic food containers were filled with 1.0 kg of air dried Almassipi very fine sandy loam (79% sand, 12% clay, 9% silt, 4% OM, pH 7.8) amended with 200 ppm N, 50 ppm P, 160 ppm K, and 66 ppm S in the form of NH_4NO_3 , $\text{Ca}(\text{HPO}_4) \cdot \text{H}_2\text{O}$, and K_2SO_4 , respectively. Perlite was added to the soil surface to a depth of approximately 1.0 cm (10 g) to minimize evaporation from the soil surface (Rawson et al. 1977a). Each container was watered to 20% (w/w) and seeded with two wheat (cv. Benito) and/or four green foxtail seeds. Following emergence the pots were thinned to give one wheat, one foxtail or one plant of each species per pot. Pots in the stressed treatment were permitted to cycle between ψ s of 0 to -2.0 MPa (7% w/w) while the unstressed pots were maintained near a ψ s of 0 MPa (13% w/w). A water retention curve for the Almassipi soil is presented in Appendix Figure 2. Table 3 details the species and watering regime combinations. The pots were placed in a growth cabinet under a PPFD of 650 to 750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 30 cm from a lamp bank containing a 3:1 mixture of Sylvania GTE Cool White VHO : Sylvania GRO-LUX WS VHO. The experiment was conducted in the same cabinet in two different environments : 30/25 C (day/night) and a mean

TABLE 3

Watering regime and species combinations for the controlled environment experiment.

Treatment No.	Pot No.	Species	Watering Regime
1	1	foxtail	unstressed
2	2	foxtail	stressed
3	3	foxtail	unstressed
4	3	wheat	unstressed
5	4	foxtail	stressed
6	4	wheat	stressed
7	5	wheat	stressed
8	6	wheat	unstressed

water vapor pressure (WVP) of 3.362 kPa (measured with a sling psychrometer, Bacharach Instruments, Pittsburgh, PA), and 20/15 C and a WVP of 1.862 kPa. The photoperiod for both experiments was 16 h. The experiment was conducted in a randomized complete block design, each treatment being replicated four times. Within a block each treatment was repeated six times to allow for six harvest dates. At 7 day intervals from 5 to 40 days after emergence each treatment was harvested from each block, for a total of 24 pots per harvest. For pots 1, 2, 5, and 6 the soil was washed from the roots. In pots 3 and 4 it was not possible to separate the roots of the two species. The height (to the highest node), leaf number, leaf area, leaf weight, stem weight, root weight, and weight of dead plant material were determined for each individual plant. All weights were determined after drying for 48 h at 80 C.

The dry weight data were fitted to the following equations for the period from 5 to 33 days after emergence (McKinion et al. 1974 ; Potter and Jones 1977):

$$A = A_0 \exp(k_A t)$$

where A is the leaf area at time " t " , A₀ is the leaf area extrapolated to t=0, and k_A is the relative leaf area growth rate.

$$W = W_0 \exp(k_W t)$$

where W is the total biomass (excluding roots) and k_W is the relative growth rate.

$$LW = LW_0 \exp(k_{LW} t)$$

where LW is the leaf weight and kLW is the relative leaf weight growth rate.

$$SW = SW_0 \exp(k_{SW} t)$$

where SW is the stem weight and kLW is the relative stem weight growth rate (Young et al. 1982). The data for each treatment were fitted individually and LAP, LWP, and SWP were calculated as given in Table 2. The amount of water consumed during growth for each treatment was recorded and WUE for each harvest date were calculated for treatments 1, 2, 7 and 8 as listed in Table 3.

Dummy variable coding was used to fit linear models of the imposed treatments to the Napierian logarithms of the measured and derived parameters (Hicks 1973 ; Chew 1977 ; Berenson et al. 1983). A full model incorporating all variables and interactions was initially fitted and then subsequently reduced to incorporate only meaningful and easily interpreted coefficients .

Tissue water relations in green foxtail and wheat seedlings

One liter plastic food containers were filled with 1.0 kg of Almassipi very fine sandy loam. Each pot was watered to 20% (w/w) and seeded with four wheat (cv. Benito) and four foxtail. Following emergence the pots were thinned to two wheat and two foxtail per pot. The pots were placed in a growth room under a 1:1 mixture of Sylvania Cool White VHO : Sylvania GRO-LUX VHO lamps producing a PPFD of 250 to 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 30 cm from the source and a mean WVP of 2.440 kPa. The temperature regime was 25/20 C with a 16 h photoperiod. The pots

were maintained near a ψ_s of 0 MPa (13% w/w) until the third leaf was half emerged. Both species reached the same phenological stage at approximately the same time and pots for inclusion in the experiment were selected for uniformity of plants. When the third leaf was half emerged each pot was watered to 20% (w/w) (day 0) and sampling was initiated. The third leaf of one of the plants of each species in a pot was sampled. Each leaf was cut into four approximately equal segments and each segment was placed into a capped 10 ml glass vial. These were immediately weighed to the nearest tenth of a mg (fresh weight) and then transferred to 25 ml vials containing distilled water for 6 h under a PPFD of $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ from a 1:1 mixture of Sylvania Cool White VHO:Sylvania GRO-LUX VHO lamps at 25 C (Barrs and Weatherley 1962 ; Weatherley 1970 ; Molz et al. 1975). The leaf segments were then removed from the distilled water, surface dried, placed in dry 10 ml vials, and reweighed (turgid weight). The leaf segments were then dried at 105 C for 12 h and weighed again (dry weight). The relative water content (RWC) was determined by the following equation (Kramer 1983a):

$$\text{RWC} = (\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight})$$

The temperature of the third leaf of the other plant in a pot was determined using an infrared thermometer (IRT) (Everest Interscience Model 210, equipped with an optical sighting system to view an area 10 mm in diameter). The transpiration and photosynthetic rate were measured using a portable photosynthetic system (LI-6000, LI-COR, Inc., Lincoln, NE). Immediately after the measurements were complete the leaf was cut from the plant, placed in a plastic bag to minimize water loss, and the water potential was determined using a pressure chamber

(PMS Instrument Corp., Corvallis, OR). The technique and cautions in methodology are described in Boyer (1967), Tyree and Hammel (1972), Frank and Harris (1973), Millar and Hansen (1975), Ritchie and Hinckley (1975), Cheung et al. (1975), Turner (1981), and Turner and Long (1980). The pots were not watered for the following 6 day period. On each day of the 6 day period, eight pots were harvested and the appropriate measurements were made. Each pot was weighed prior to harvesting and the mean ψ s determined for the pot. The experiment was conducted as a randomized complete block design with eight blocks. The pots within a block were randomized every 2 days to minimize any effect of spatial variability in PPFD. The experiment was conducted three times in the same growth room. There were no significant differences between the experiments, so the data were pooled for analysis.

Additive experiments to examine wheat-foxtail competition

An additive experiment was conducted to examine the effect of temperature and soil water potential on green foxtail competition in wheat. Although density and competitive effects are confounded in these types of experiments they more closely resemble a typical weed-crop situation than do substitutive experiments (Harper 1977 ; Zimdahl 1980).

The experiment was conducted using double walled plastic pots (System Kick / Brauckmann, Gebruder Baumann GmbH & Co. , Amberg, West Germany) 28.5 cm in diameter and 25.5 cm deep. This double walled construction permitted watering from the bottom.

The pots were filled with 9 kg of Almassipi very fine sandy loam amended with 200 ppm N, 50 ppm P, 160 ppm K, and 66 ppm S in the form of

NH_4NO_3 , $\text{Ca}(\text{HPO}_4) \cdot \text{H}_2\text{O}$, and K_2SO_4 , respectively. The pots were watered to 20% (w/w) and seeded with 10 wheat, and 0, 10, 20, 30, 40, 50, 60, or 70 foxtail. Following emergence the pots were thinned to 8 wheat and 0, 8, 15, 23, 30, 38, 46, and 53 foxtail plants to represent a wheat density of 200 m^{-2} and foxtail densities of 0, 200, 400, 600, 800, 1000, 1200, and 1400 m^{-2} , respectively. The pots were placed in a growth cabinet under a PPFD of 650 to $750 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 30 cm from a lamp bank containing a 3:1 mixture of Sylvania GTE Cool White VHO: Sylvania GRO-LUX WS VHO and a 16-h photoperiod. The experiment was conducted in the same cabinet in two different environments ; 30/25 C and a mean WVP of 3.362 kPa, and 20/15 C and a mean WVP of 1.862 kPa. The experiment was conducted in a randomized complete block design with four replicates. The position of the pots within a block was changed every 3 days to minimize any effect due to spatial variability in PPFD. There were two watering treatments within each temperature regime ; stressed where the pots were cycled between ψ s of 0 to -2.0 MPa (7% w/w) and unstressed where the pots were maintained near 0 MPa (13% w/w). The pots were weighed daily and watered as required until the wheat was mature. The seed number, seed weight, and mean seed weight (seed weight/seed number) for each wheat plant in a pot were determined after drying for 48 h at 80 C. Each temperature/water combination was conducted separately in time as the physical size of the pots limited the number to 32 at a time in the growth cabinet. Due to space limitations, a repetition of the experiment was conducted in the same growth chamber at later date.

RESULTS AND DISCUSSION

OUTDOOR STUDY

The environmental data for the field studies are presented in Figure 1. Detailed weather data for the experimental site is listed in Appendix Tables 2 and 3. Long term normals (1951 to 1980) were obtained from Environment Canada for Winnipeg International Airport. The weather was wetter, but hotter than normal during the period of seedling growth (0 to 29 days after emergence) in 1984, and colder and slightly drier than normal in 1985. Although the accumulated degree days (ΣDD) were higher for 1984 than for 1985, the extreme rainfall during seedling growth in 1984 was accompanied by low radiation levels due to cloud cover.

The soil water potential decreased as the season progressed in both the wet and dry treatments in the two years (Figures 2 and 3) . However the decrease was greater in 1984 than in 1985, particularly towards the end of the harvest period and at the 5 to 30 cm depth in the dry treatment. There was little difference in ψ_s between the wet and dry treatments at the 45 to 70 cm depth. It appears that only small amounts of water were extracted at these lower depths and that most of the water was withdrawn from the 0 to 30 cm layer. The 0.5 cm irrigation wetted only the top 2 to 3 cm of the soil and the applied water quickly evaporated, particularly on days with high radiation levels and high windspeed. The only effect of this small irrigation

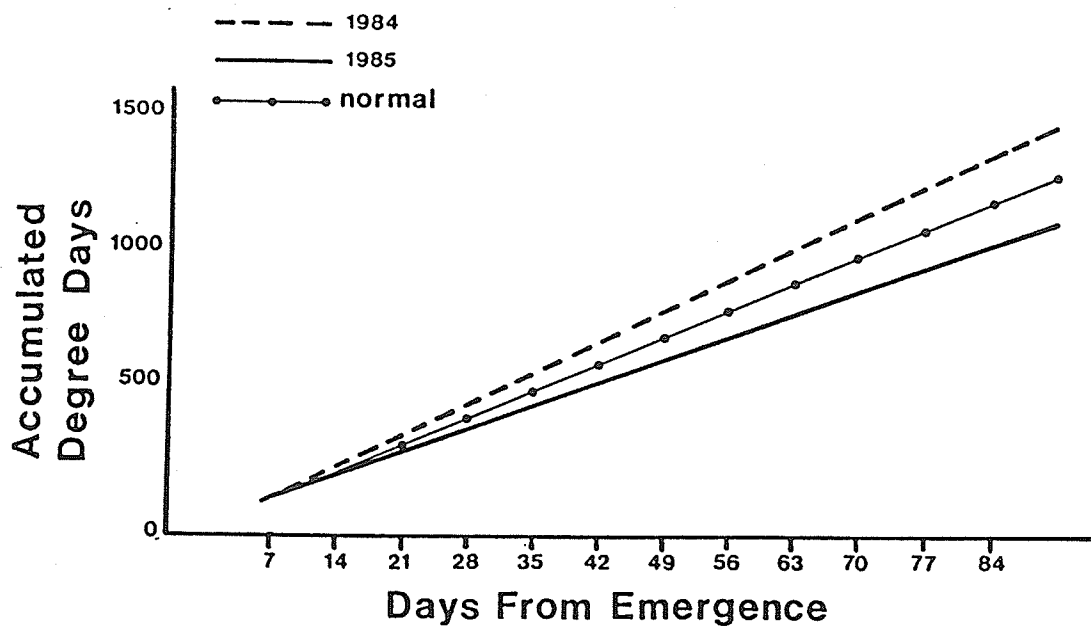
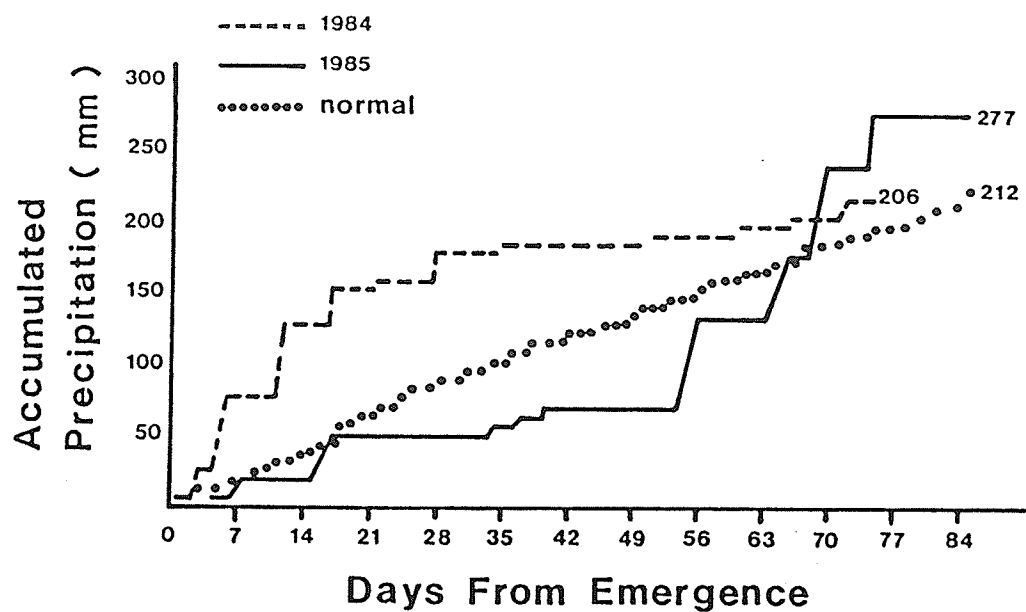


Figure 1: Accumulated precipitation and degree-days for the outdoor experiments in 1984 and 1985.

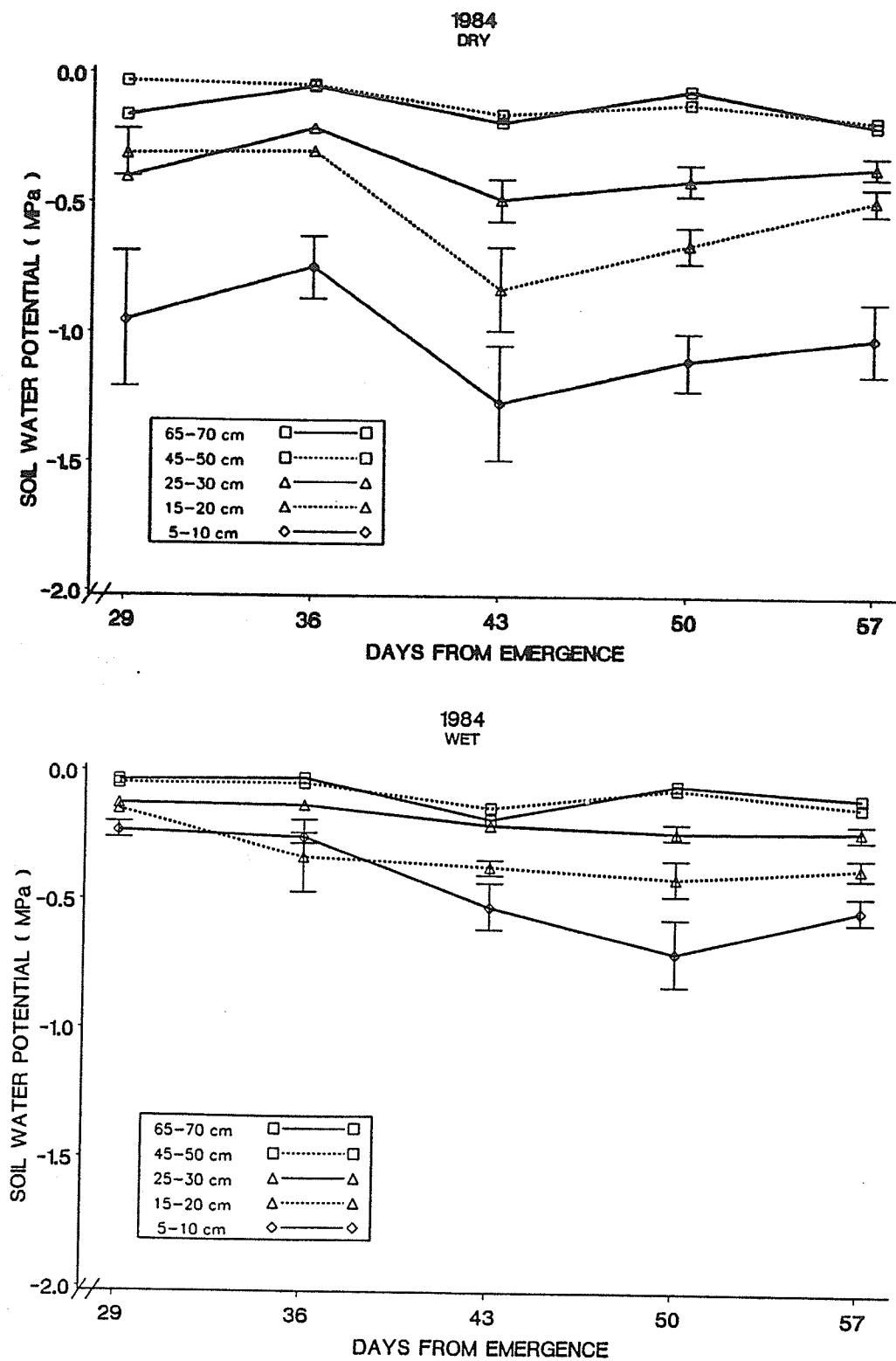


Figure 2: Soil water potentials under dry (5 mm) and wet (25 mm) irrigation regimes, 1984 (mean values \pm one standard error).

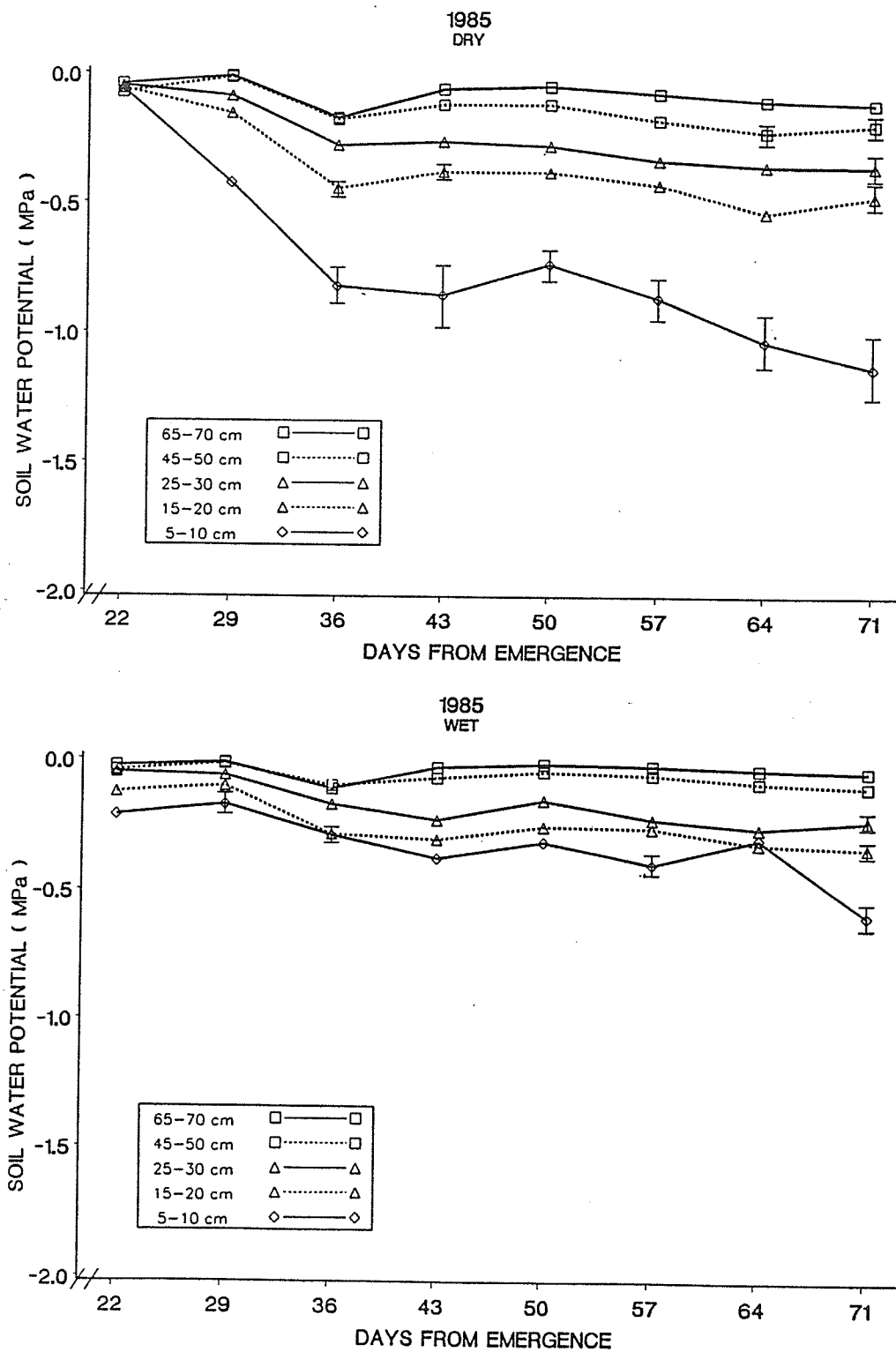


Figure 3: Soil water potentials under dry (5 mm) and wet (25 mm) irrigation regimes, 1985 (mean values \pm one standard error).

would have been a temporary modification of the microclimate within the canopy and a temporary reduction of soil surface temperature. Plants in the dry treatment therefore were dependent on water stored in the soil profile. In the wet treatment the top 15 to 20 cm of the profile was wetted by irrigation and the canopy primarily extracted water from the 0 to 30 cm depth. Thus water deficit had little effect on the extraction pattern of the mixed canopy.

Least-squares equations for leaf area, leaf weight and total biomass as a function of the time from emergence were produced using the SAS-GLM procedure (Table 4) with the coefficient of determination calculated as:

$$R^2 = \sum (\hat{y} - \bar{y})^2 / \sum (y(i) - \bar{y})^2$$

(see Kvalseth 1985 for details on the determination and interpretation of R^2 values).

The equation of "best fit" was determined by calculating the significance of each additional term in the polynomial by:

$$t = (\text{final coefficient}) / (\text{standard error of the final coefficient})$$

with $n-(m+1)$ degrees of freedom, where n is the number of points fitted and m is the degree of the polynomial (Elias and Causton 1976). The transformation of data before fitting is often proposed (using polynomial exponentials), but differentiation of the first order equation results in a constant RGR, which is highly unlikely under field conditions except for a short duration during vegetative growth (Hunt 1982 ; France and Thornley 1984). Derived functions of RGR and ULR at any time are also very dependent on the degree of polynomial fitted to

TABLE 4

Equations and coefficients of determination for leaf area (A), leaf weight (LW), and total biomass (W) for 1984 and 1985 as a function of the time (in days) from emergence (t).

Treatment	Equation	Coefficient of Determination
1984		
foxtail 5 mm	$A = -3.00 + 0.65t - 0.008t^2$	0.02
25 mm	$A = -3.45 + 0.70t - 0.007t^2$	0.05
wheat 5 mm	$A = 25.63 + 4.98t - 0.09t^2$	0.53
25 mm	$A = 4.04 + 6.44t - 0.1t^2$	0.47
1985		
foxtail 5 mm	$A = -10.17 + 0.99t - 0.01t^2$	0.04
25 mm	$A = -58.70 + 3.46t - 0.03t^2$	0.21
wheat 5 mm	$A = -64.55 + 8.94t - 0.11t^2$	0.36
25 mm	$A = -117.23 + 11.80t - 0.14t^2$	0.30
1984		
foxtail 5 mm	$LW = -57.38 + 4.68t - 0.05t^2$	0.07
25 mm	$LW = -45.89 + 3.57t - 0.03t^2$	0.17
wheat 5 mm	$LW = -435.86 + 51.18t - 0.71t^2$	0.55
25 mm	$LW = -526.56 + 56.06t - 0.75t^2$	0.47
1985		
foxtail 5 mm	$LW = -116.08 + 6.90t - 0.07t^2$	0.15
25 mm	$LW = -104.32 + 5.42t - 0.03t^2$	0.30
wheat 5 mm	$LW = -679.51 + 55.08t - 0.63t^2$	0.33
25 mm	$LW = -658.57 + 52.42t - 0.54t^2$	0.25
1984		
foxtail 5 mm	$W = 2.01 + 2.71t$	0.07
25 mm	$W = -94.83 + 5.45t$	0.25
wheat 5 mm	$W = -67.34 + 33.99t$	0.30
25 mm	$W = 387.13 + 46.80t$	0.38
1985		
foxtail 5 mm	$W = 4.07 + 1.94t$	0.06
25 mm	$W = -289.34 + 11.18t$	0.36
wheat 5 mm	$W = -627.34 + 48.09t$	0.37
25 mm	$W = -1498.24 + 77.40t$	0.61

the underlying data (Nicholls and Calder 1973). In addition the standard errors of derived functions tend to increase with the number of terms in the polynomial (Nicholls and Calder 1973 ; Hardwick 1984). Polynomials have been widely used to describe plant growth (Hunt 1982) and they have the advantage of being linear rather than non-linear models (Neter and Wasserman 1974). It is important to note the empirical nature of polynomials when applied to plant growth, i.e. the equation does no more than redescribe and summarize the data, and yet a balance is required in finding a statistically appropriate and biologically sound curve (Elias and Causton 1976 ; Erickson 1976 ; Landsberg 1977). The majority of plant growth studies, where the fitting of equations has been attempted, have been with single plants growing in isolation under non-limiting conditions (Hunt 1978,1982). There are few, if any, studies where equations have been fitted to species in competition under limiting conditions. The appropriateness of a model would certainly differ in these situations (Hurd 1977). In view of the ease of "over fitting" with computers, these models (Table 4) appear to represent adequate descriptions of the growth of the two species for the purposes intended.

A summary of the significance of the F-test in the ANOVA for the different parameters measured is provided for 1984 and 1985 in Appendix Table 4.

Leaf area (Figure 4) was greater for wheat than for foxtail in both years. There were significant treatment effects but no significant treatment by species interaction. Plants in the wet treatment had a greater leaf area than plants in the dry treatment. In both years the leaf area of foxtail in the wet treatment increased slightly as the

season progressed. This can be partially attributed to a decrease in leaf area of the wheat with an increase in phenological age and subsequent higher radiation levels reaching the foxtail. This advantage in leaf area for wheat was attained by the first harvest date and was due to weather conditions prior to this date favoring the wheat growth (Biscoe and Willington 1985). The leaf weight per plant was also greater for wheat than for foxtail except where the wheat had matured but leaf growth was continuing in the foxtail (Figure 5). Generally water stress also decreased leaf weight.

In 1984 the LAI peaked at about 29 days from emergence (DFE) in both the wet and dry treatments (Figure 6). However in 1985 the LAI did not reach a maximum until 36 DFE. This later maximum in 1985 was due to the cooler growing conditions following emergence in 1985 as compared to 1984. In both years the total LAI attained (wheat + foxtail) was greater for the wet treatment than for the dry treatment. In general grass canopies can be considered to be closed at LAI of 3 to 5 (Gardner et al. 1985), and a wheat canopy can be considered closed at an LAI of 3.0 (Porter 1985) but this may vary depending on leaf inclination and leaf size. In this study the LAI's achieved in the wet treatment would represent a closed canopy but in the dry treatments the LAI's of approximately 3.0 represent a more open canopy. Perhaps shading was of lesser importance in the competitive interaction in the dry treatment. The decline in LAI was more rapid in 1984 than in 1985 due to the greater degree of water deficit in the first year compared to the second, resulting in a more rapid leaf senescence.

As environmental conditions prior to canopy closure determine the relative position of each species in the canopy and thus the potential

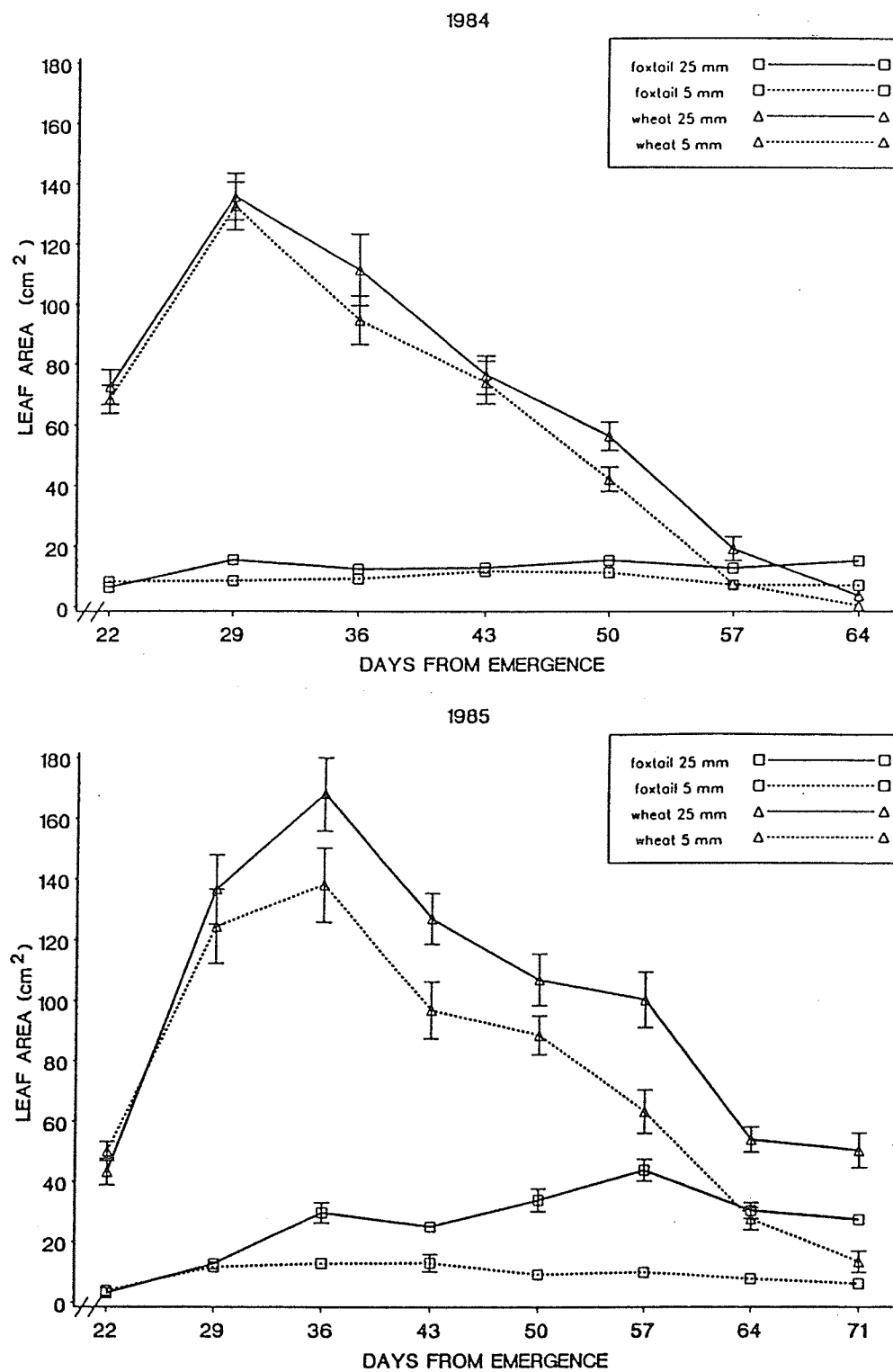


Figure 4: Leaf area per plant in the outdoor experiment under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

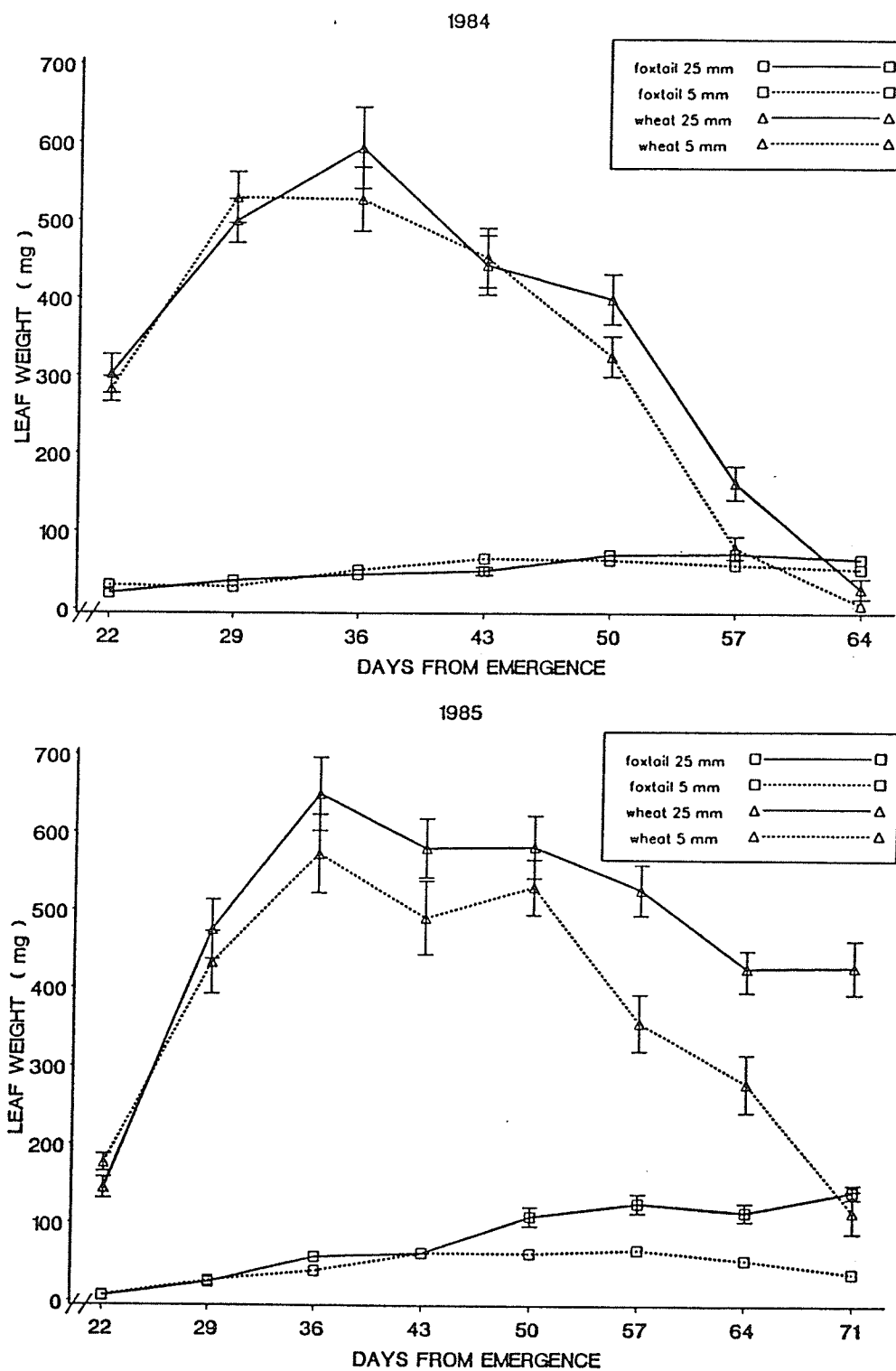


Figure 5: Total leaf weight per plant in the outdoor experiment under dry (5mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

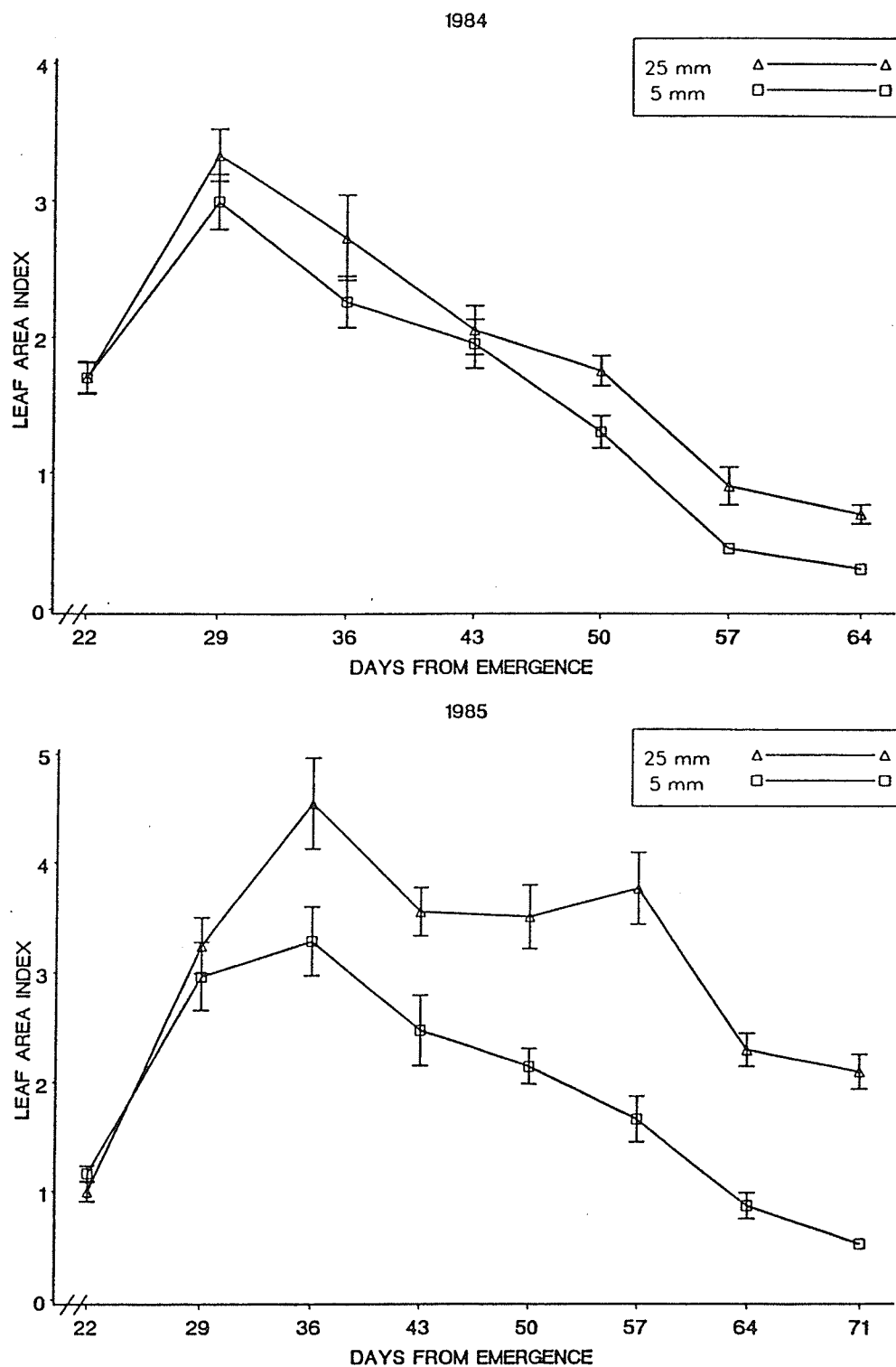


Figure 6: Leaf area index (LAI) of the total plant canopy (foxtail and wheat) in the outdoor experiment under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

radiation interception, environmental conditions in the period 0 to 29 DFE in 1984, and 0 to 36 DFE in 1985, influenced the competitive results. In both years the growth of wheat was favored over that of foxtail with a resultant superiority of wheat in the canopy. Although PPFD within the canopy was not measured, one can assume that radiation in the canopy decreases with depth as a negative exponential function as LAI increases (France and Thornley 1984). As wheat had a greater leaf area than foxtail (Figure 4) at a greater height within the canopy (Figure 7), wheat would have intercepted more radiation than did the foxtail. Environmental conditions following canopy closure are of less importance than those prior to canopy closure which determine the relative position of each species in the canopy (Spitters 1984) .

The effectiveness of one species shading another species is a result not only of a greater leaf area, but also the spatial distribution and longevity of the leaf area. Plant height was not determined in 1984, but in 1985 wheat was taller than green foxtail at all harvest dates (Figure 7) . There was also a significant treatment effect with plants in the wet treatment taller than plants in the dry treatment. In foxtail the effect of the wet treatment is confounded with shading by the wheat, but this represents a typical competitive situation so the additive effects are somewhat realistic. Bubar and Morrison (1984) reported that the height of green foxtail was reduced when grown in a wheat crop, but the methodology for height assessment was not reported, so comparisons are inappropriate. Patterson (1982), Spitters and Aerts (1983), and Weiner and Solbrig (1984) have emphasized the importance of height in plant competition. The taller species intercepts more radiation of greater energy than does the shorter species at equal leaf

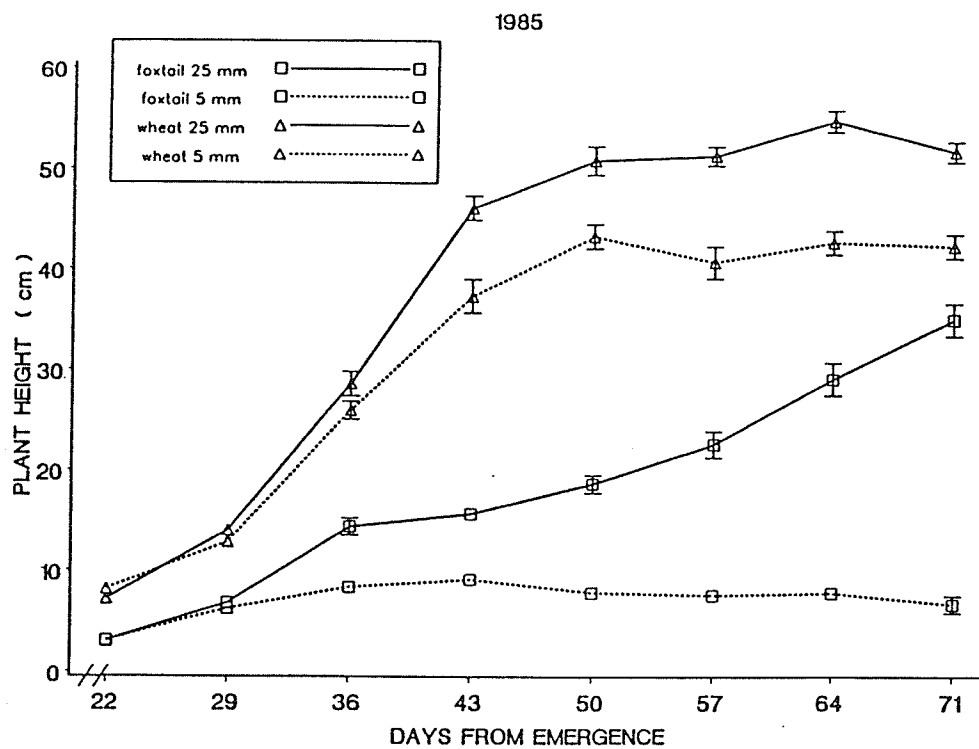


Figure 7: Plant height (to the highest node) in the outdoor experiment, 1985, under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

area. This advantage allows the taller species to effectively increase its presence in the canopy. A greater height is probably a greater advantage under unstressed conditions, with respect to water, because the total LAI is larger than under stressed conditions and thus the intensity of radiation received by the shorter species is lowered (Spitters and Aerts 1983). The distribution of leaf area and the leaf area density for a species varies with height, particularly in a grass canopy where leaf inclination can vary during the day and the leaves have substantial vertical spread compared to many broadleaved species. The spatial distribution of the leaf area over the soil surface also differed for wheat and foxtail. As the wheat was sown in rows and the foxtail was distributed randomly, there was a greater likelihood of self shading in the wheat.

The LAD (Table 5) was greater for wheat than for foxtail in both years and greater in the wet treatment than in the dry treatment. In 1984, wheat had an LAD about 6 times greater than foxtail in the wet treatment, and 7 times greater in the dry treatment. The reduction in LAD due to water stress (wet to dry) was 25% in wheat and 29% in foxtail, in 1984. In 1985 wheat had an LAD about 3 times greater than foxtail in the wet treatment and 7 times greater in the dry treatment. The reduction in LAD due to water stress was 9% in wheat and 64% in foxtail.

In terms of crop-weed interactions the LAD is of fundamental importance in determining the relative competitive ability of the species (Radosevich and Holt 1984). The ability of wheat to maintain a greater LAD, at a greater height than green foxtail and the shading of the weed resulted in a competitive advantage for wheat, even under water

TABLE 5

Leaf area duration (LAD) (cm^2 days) in the outdoor experiment, 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes.

Treatment		Harvest Interval (days)							
		22-29	29-36	36-43	43-50	50-57	57-64	64-71	Total
1984									
foxtail	5 mm	58.4	67.5	71.1	69.3	61.9	49.1	--	377.2
	25 mm	68.7	83.1	92.8	97.6	97.6	92.8	--	532.5
wheat	5 mm	656.1	644.4	570.9	435.6	238.6	15.7	--	2561.2
	25 mm	719.8	751.2	714.9	608.1	433.6	190.6	--	3417.1
1985									
foxtail	5 mm	57.9	77.5	90.3	96.2	95.2	87.3	72.6	577.1
	25 mm	69.3	153.6	217.3	260.4	365.0	284.9	266.3	1616.8
wheat	5 mm	640.1	765.5	815.5	790.0	689.1	512.7	260.8	4473.7
	25 mm	644.4	824.8	909.0	897.3	789.5	585.6	285.8	4936.4

deficit conditions. Flint and Patterson (1983) reported that the competitiveness of soybean (Glycine max L.) and C₃ and C₄ weeds was more closely related to LAD than to ULR, and that environmental effects on LAD have a major influence on the success of a species in competition.

In both 1984 and 1985 the total biomass was greater for wheat than for foxtail and greater for the wet treatment than for the dry treatment (Figure 8). Asymptotic functions are often utilized to describe dry weight increase over the season, especially where harvests are made closer to maturity than in this study. The first order polynomials appear to satisfactorily describe the data and the low coefficient of determination for foxtail in the dry treatment can be ascribed to a poor relationship with time (Table 4). The biomass duration (BMD) was greater for wheat than for foxtail in both years (Table 6). In 1984 wheat had approximately 12 times the BMD as foxtail in both the wet and dry treatments (Table 6). In 1985 wheat had about 9 and 17 times the BMD as foxtail in the wet and dry treatments, respectively. In addition the reduction in BMD due to water stress was 14.2% and 15% in 1984, and 23% and 59% in 1985 in wheat and foxtail, respectively. The differences in BMD reduction due to water stress between the 2 years could be a result of the wet weather near maturity of the wheat in 1985 and thus greater persistence of leaf area in 1985 than in 1984.

BMD summarizes in one quantity the change in time of the plant biomass and describes the integrated response of the entire organism to environmental change: in these studies water deficit and seasonal changes in radiation and temperature regimes (Kvet and Ondok 1971 ; Ondok and Kvet 1971). However the BMD also contains an ontogenetic

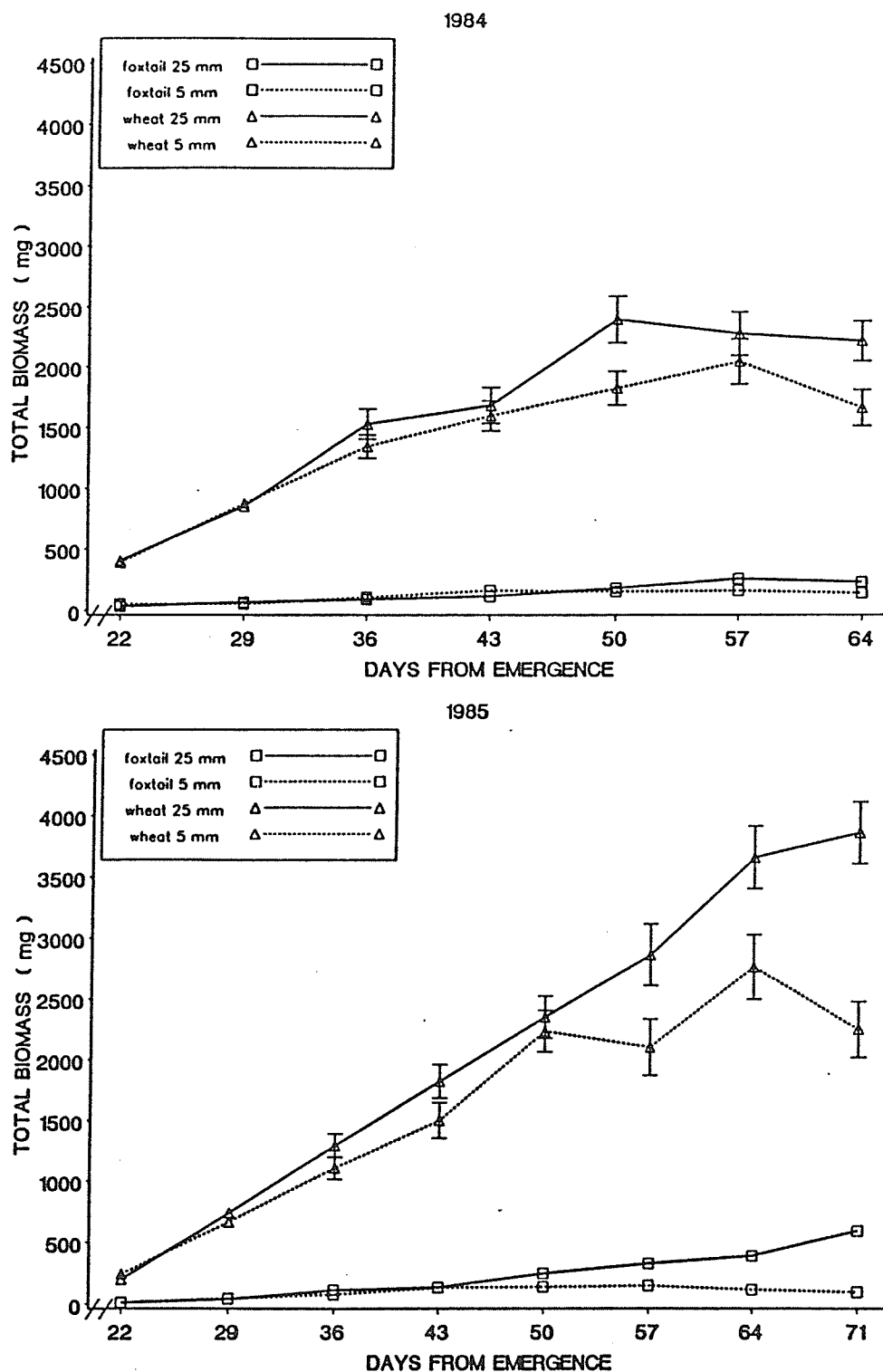


Figure 8: Total biomass for green foxtail and wheat in the outdoor experiment under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

TABLE 6

Biomass duration (BMD) (g days) in the outdoor experiment, 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes.

Treatment		Harvest Interval (days)							
		22-29	29-36	36-43	43-50	50-57	57-64	64-71	Total
1984									
foxtail	5 mm	0.497	0.631	0.763	0.896	1.029	1.162	--	4.98
	25 mm	0.309	0.576	0.843	1.110	1.377	1.644	--	5.86
wheat	5 mm	5.596	7.261	8.927	10.592	12.258	13.923	--	58.56
	25 mm	5.644	7.973	10.230	12.524	14.817	17.110	--	68.26
1985									
foxtail	5 mm	0.375	0.470	0.565	0.660	0.755	0.850	0.945	4.62
	25 mm	0.488	0.518	1.066	1.614	2.162	2.709	3.257	11.30
wheat	5 mm	4.193	6.549	8.906	11.262	13.618	15.975	18.331	78.83
	25 mm	3.328	7.121	10.913	14.706	18.499	22.291	26.084	102.94

component, as do most of the growth analysis parameters, and there can be a significant treatment interaction with ontogeny. In this study the soil water deficit caused increased and earlier leaf senescence and also hastened plant development, which reduced BMD through the time component. BMD, by definition, is determined by both the dry weight changes and the life span of the plant, thus environmental factors which alter the rate of development can have an indirect effect on the time component of BMD (Haber et al. 1964).

The harvest interval approach to determining RGR (Figures 9 and 10) demonstrated a general decrease in RGR with time for both years and treatments. There is no obvious or pronounced treatment effect on RGR. RGR is expected to change (in this case decrease) in the same direction and to a greater extent than LAR, unless the ULR can maintain or increase with less leaf area (Richards 1969).

However RGR also has a significant ontogenetic component (Leopold and Kriedemann 1975). Correlations between environmental factors and RGR are difficult to determine with long time intervals as the ontogenetic component becomes dominant (Kvet et al. 1971). In general foxtail maintained a higher RGR than wheat but this could be attributed to increased growth of the foxtail, with higher radiation levels, as the wheat canopy senesced. However wheat cultivars differ in RGR particularly after the seedling stage as a result of: 1) a different pattern of dry matter allocation within the plant, especially as a result of genetic diversity in the rate of development, and 2) different rates of senescence (Spitters and Kramer 1985, 1986).

The ULR for both 1984 and 1985 varied with the harvest interval (Figures 11 and 12). The primary factor affecting the determination of

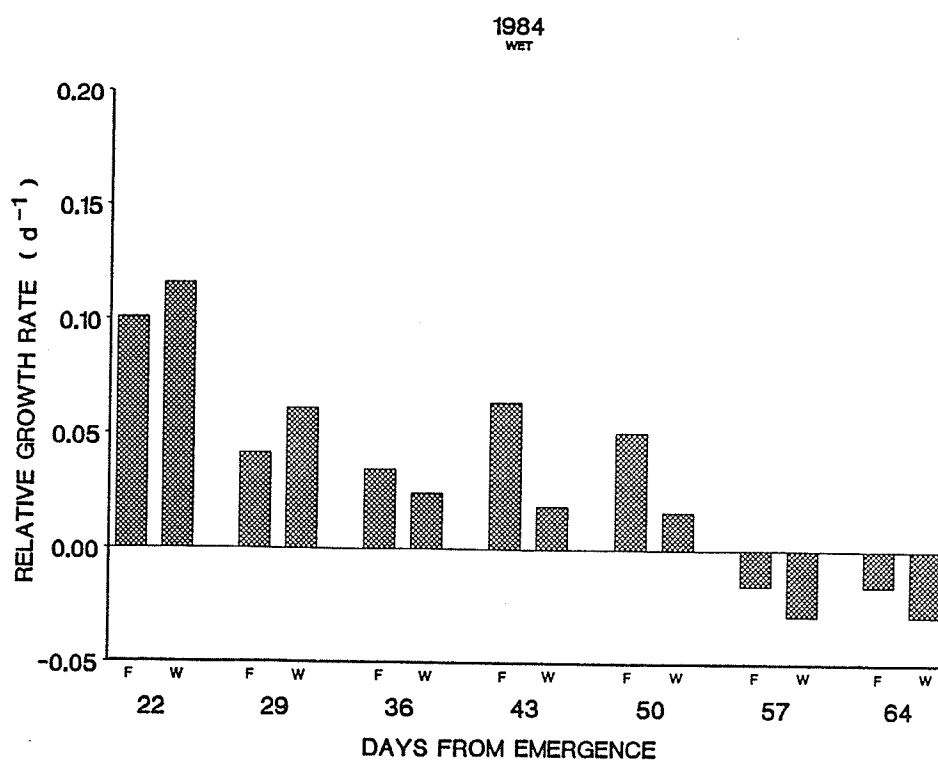
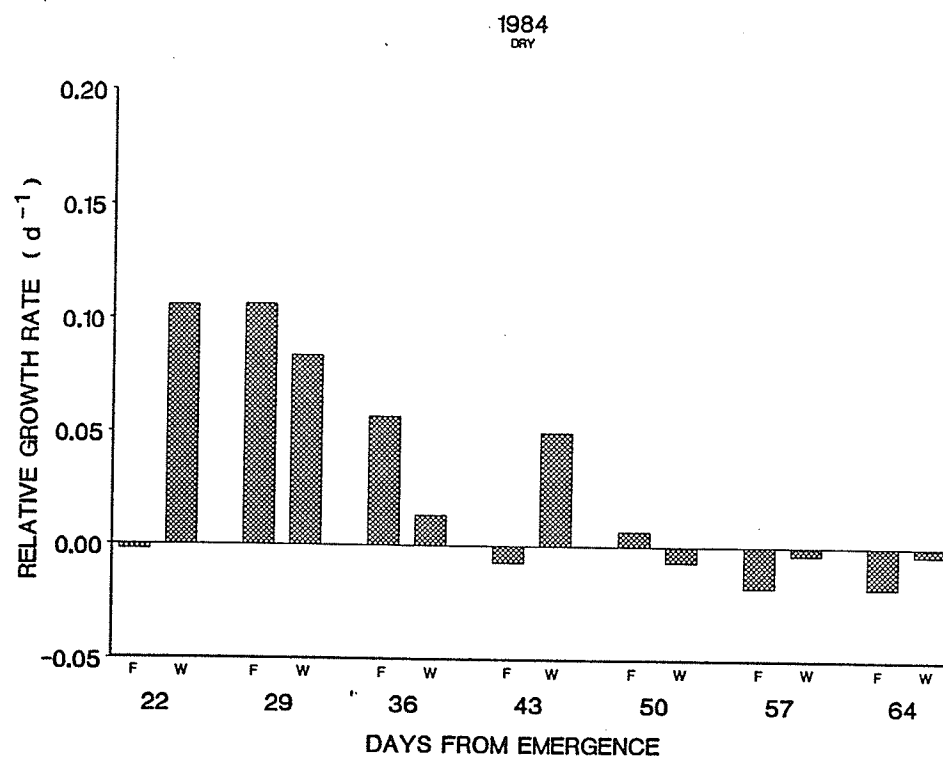


Figure 9: Mean relative growth rates for green foxtail (F) and wheat (W) for a harvest interval under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment, 1984.

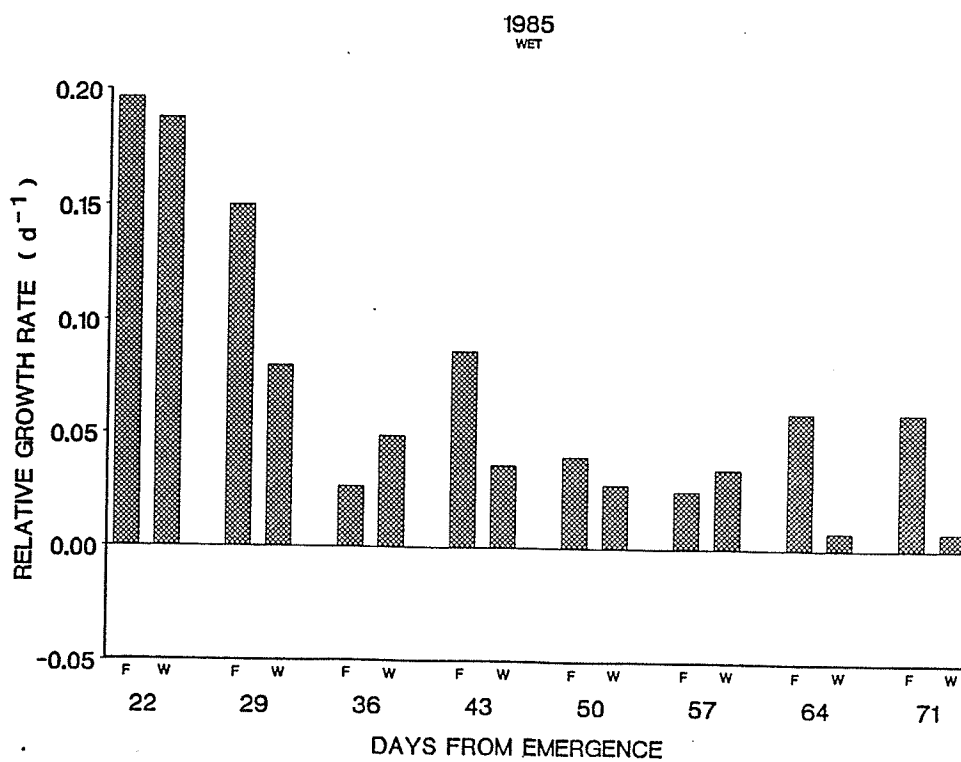
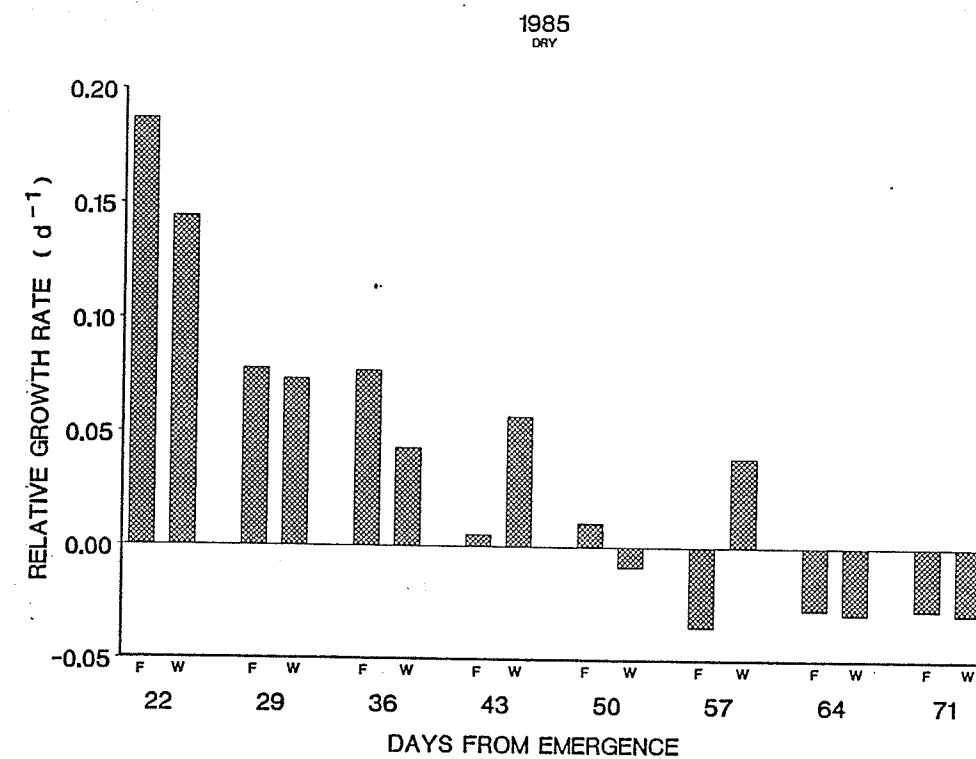


Figure 10: Mean relative growth rates for green foxtail (F) and wheat (W) for a harvest interval under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment, 1985.

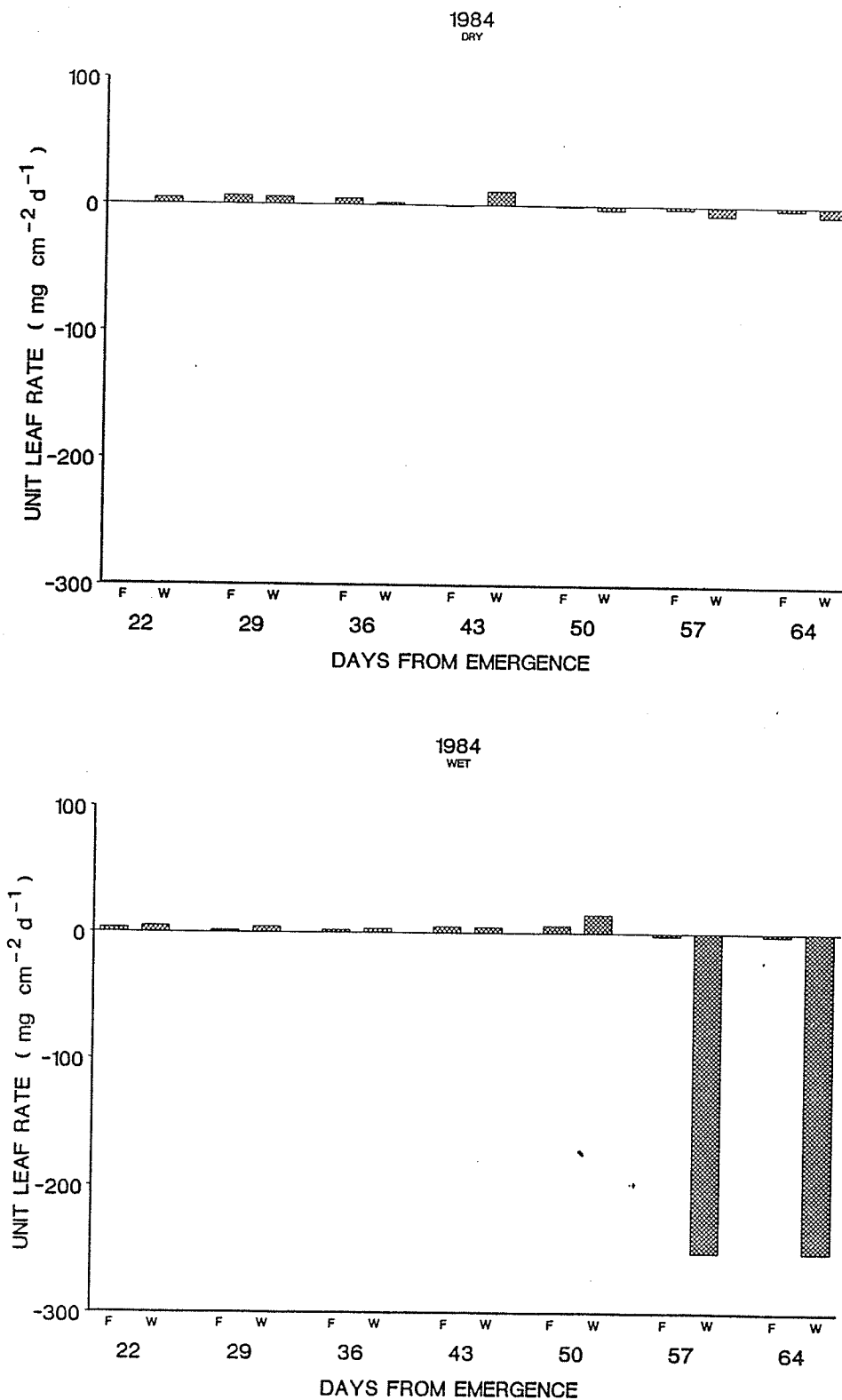


Figure 11: Mean unit leaf rates for green foxtail (F) and wheat (W) for a harvest interval under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment, 1984.

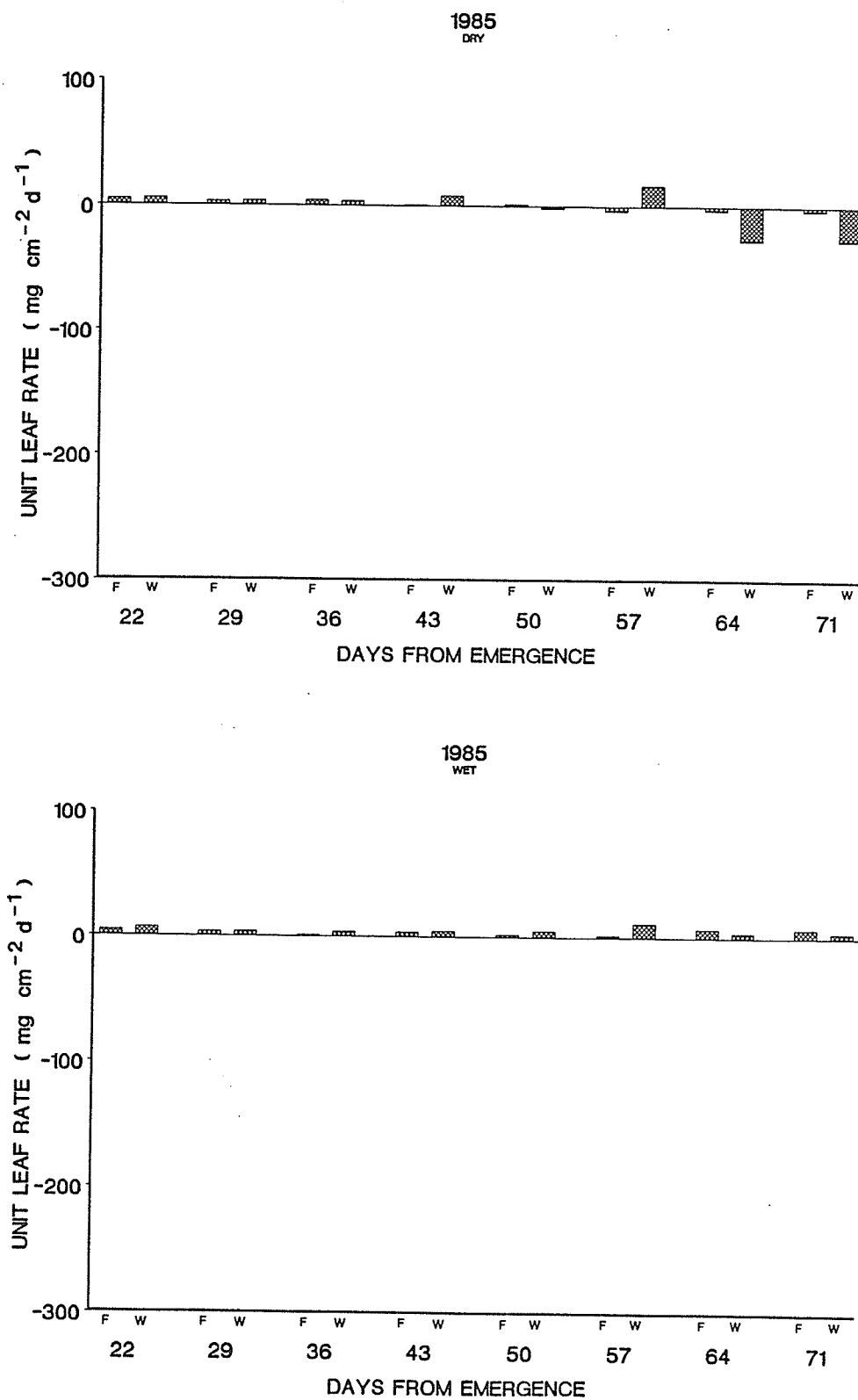


Figure 12: Mean unit leaf rates for green foxtail (F) and wheat (W) for a harvest interval under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment, 1985.

ULR was the difference between harvest intervals in the coefficient a used in the calculation ($a = \text{RGR}/\text{RLGR}$) (Table 7) (Evans and Hughes 1962 ; Whitehead and Myerscough 1962) and associated random fluctuations which are common to the harvest interval estimation method (Vernon and Allison 1963 ; Benjamin and Hardwick 1986). Clearly the common assumption that $a=1$ would be inappropriate in this case and would lead to erroneous results (Radford 1967). Whale et al. (1985) also reported a wide range in a values among the harvest intervals. The variation in ULR in this experiment is due to shading, temperature and ontogenetic effects. The ULR is used as a measure of the production of new biomass per unit leaf area and thus it is difficult to interpret or assess its' significance when the largest component of dry weight change is senescence due, for example, to water stress (Whale et al. 1985). ULR declines with plant age, with a denser canopy as mutual shading of leaves increases (Williams 1946) , and with water deficit as CO_2 uptake decreases (Leopold and Kriedemann 1975).

ULR has both a genetic and an environmental component; the genetic component determining the optimum temperature and the environment regulating the expression of potential ULR. The ULR is generally considered to be much less variable than is the LAR, and differences in RGR are usually attributed to changes in LAR rather than ULR (Richards 1969 ; Ondok 1970). The expectation is that the ULR of foxtail is greater than that of wheat at high temperatures, and vice versa, at low temperatures. However the ULR and response to the environment may be of less importance in plant growth and competitive interactions than the rate and extent of partitioning of assimilate into leaf area (Potter and Jones 1977).

TABLE 7

Alpha values for harvest intervals for the outdoor experiment in 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes.¹

Treatment		Harvest Interval						
		22-29	29-36	36-43	43-50	50-57	57-64	64-71
1984								
foxtail	5 mm	-0.479	9.022	1.646	-1.361	-0.103	6.495	--
	25 mm	0.789	-1.357	6.652	2.523	1.949	-0.635	--
wheat	5 mm	1.747	-2.969	-0.254	-1.154	0.046	0.016	--
	25 mm	1.224	-1.271	-0.701	-0.234	-0.068	0.074	--
1985								
foxtail	5 mm	1.199	5.528	39.711	-0.107	0.946	0.959	0.853
	25 mm	0.971	1.239	-1.112	2.034	1.096	-0.482	-4.076
wheat	5 mm	1.108	4.878	-0.857	-4.350	0.182	-0.331	0.284
	25 mm	1.141	2.682	-1.229	-1.472	-3.011	-0.396	-0.768

1. These alpha values were utilized in the calculation of mean unit leaf rates for a harvest interval as presented in Figures 11 and 12. The equation for this calculation is presented in Table 2.

It is important to recognize that the RGR is a product of ULR and LAR, so that a change in one component can be compensated by an equal and opposite change in the other component. For example, shading results in a decrease in ULR but an increase in LAR, so there may be little change in RGR. The LAR is the product of LWR and SLA so changes in LAR result from changes in one, or both of the components. The LAR, at a given harvest, was greater in foxtail than in wheat (Figure 13), as was the mean LAR over a harvest interval (Table 8) (Ondok 1971). The LAR was greater in foxtail than in wheat in both years and greater in the wet treatment than the dry treatment for foxtail. The greater LAR of foxtail resulted from shading of the foxtail by the wheat canopy and as the wheat matured, the wheat canopy senesced, and increased radiation levels were intercepted by the foxtail and the LAR declined. The effect of increased radiation level was also evident in the LAR for foxtail in the dry treatment, but as the LAI at any given date was lower in the dry treatment than in the wet treatment, radiation intercepted by the foxtail was of a higher intensity than that in the wet treatment and thus the LAR was lower. There is also an ontogenic component in LAR: the three factors radiation, water deficit, and plant age interacted to determine LAR. LAR decreases with water deficit as a result of decreased leaf initiation rates, decreased leaf size, and increased leaf senescence.

The LWR decreased at a greater rate in wheat than in foxtail, but there was little effect of treatment (Figure 14). As wheat had a greater increase in stem weight (Figure 15) than did foxtail and leaf weight had reached a maximum and was decreasing the decline in LWR is expected. However foxtail had little change in LWR with time but a

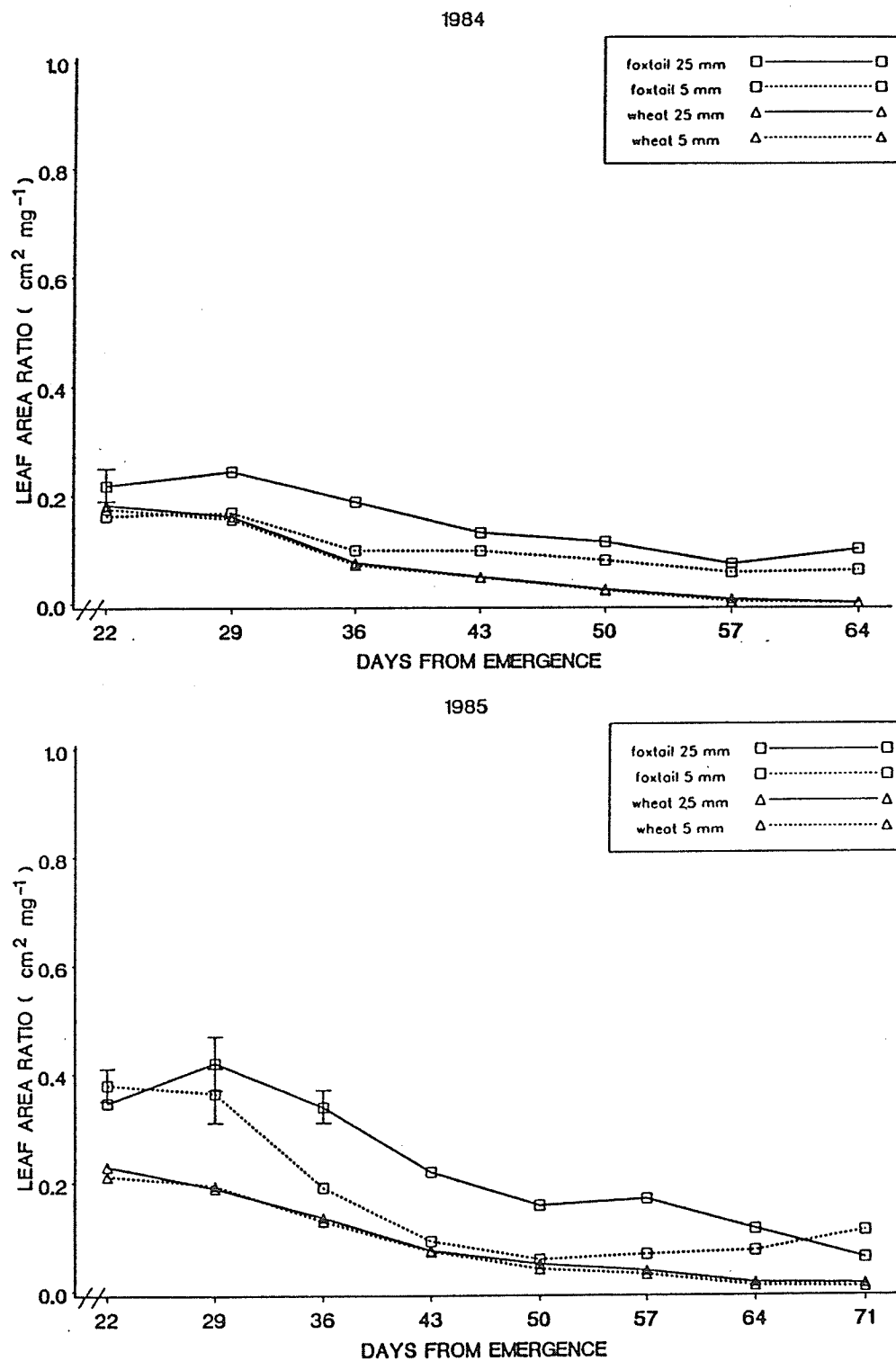


Figure 13: Leaf area ratios (LAR) in the outdoor experiment under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

TABLE 8

Mean leaf area ratios (LAR) ($\text{cm}^2 \text{ g}$) for a given harvest interval for the outdoor experiment in 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes.

Treatment	Harvest Interval (days)						
	22-29	29-36	36-43	43-50	50-57	57-64	64-71
1984							
foxtail 5 mm	117.3	107.1	93.2	77.3	60.2	42.2	--
25 mm	222.5	144.3	110.1	88.6	70.8	56.4	--
wheat 5 mm	117.3	88.7	63.9	41.1	19.5	1.1	--
25 mm	127.5	94.6	69.9	48.6	29.3	11.1	--
1985							
foxtail 5 mm	154.6	165.1	159.8	145.7	126.1	102.7	76.9
25 mm	141.9	296.5	203.9	161.4	168.9	105.2	81.7
wheat 5 mm	152.7	116.9	91.6	70.1	50.6	32.1	14.2
25 mm	114.2	103.9	88.9	71.7	53.3	34.2	14.7

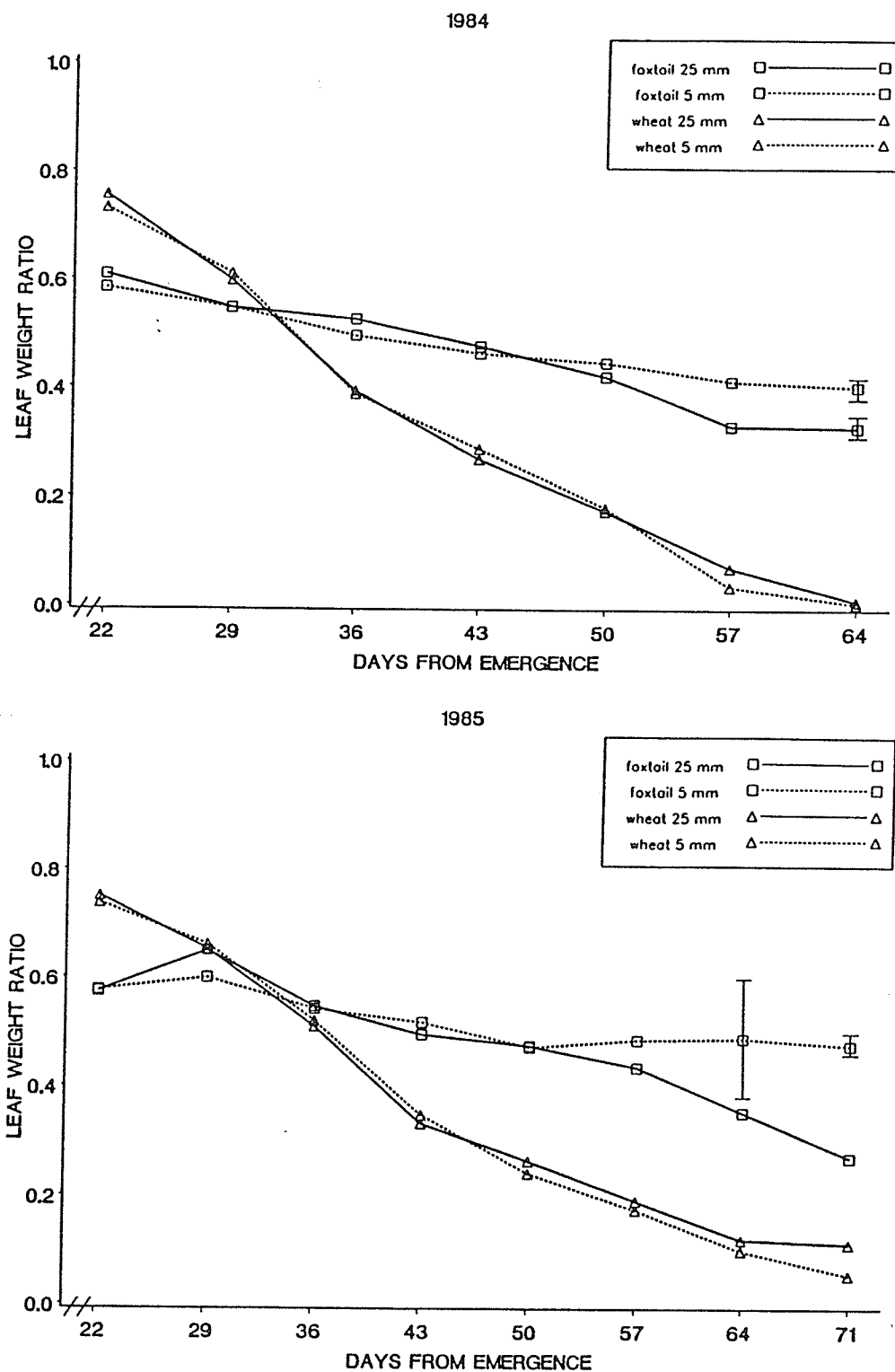


Figure 14: Leaf weight ratios (LWR) in the outdoor experiment, 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

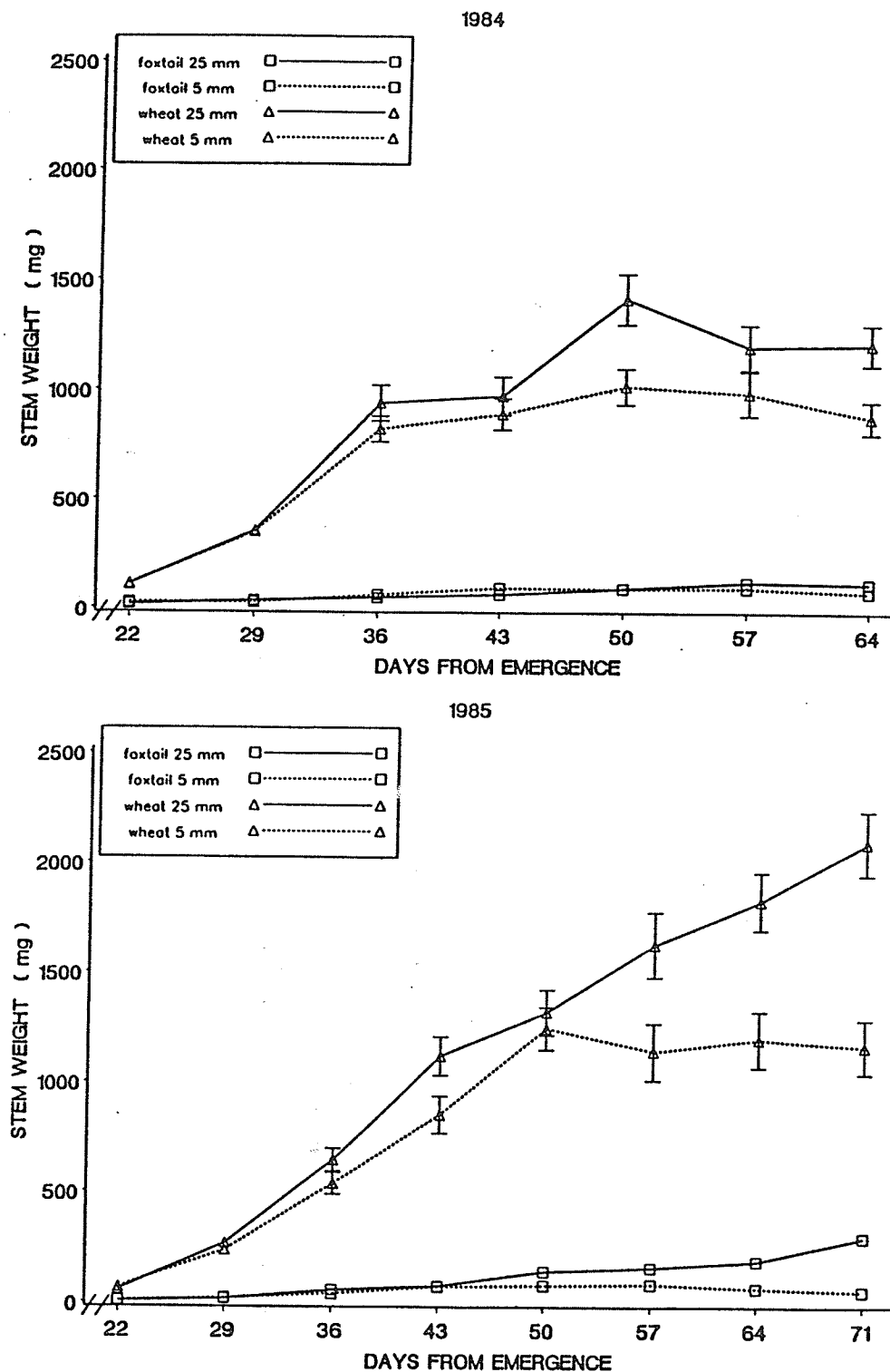


Figure 15: Stem weights in the outdoor experiment, 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

significant decrease in LAR. This decrease in LAR was due to a decrease in SLA (Figure 16). SLA is a function of the radiation regime (Nobel 1983). In a low radiation environment large, thin leaves are produced (high SLA) and this morphological adaptation results in a greater potential radiation interception and subsequently a higher photosynthetic rate. The SLA was greater in the wet treatment than in the dry treatment due to the greater LAI and more shading of the foxtail by wheat. The decrease in SLA with time in foxtail was due to interception of increased radiation levels as the leaf area of wheat decreased. The SLA values were greater in 1985 than in 1984 for foxtail in both treatments because of a more extensive wheat canopy in 1985. In both years there was little change in SLA in wheat, as the wheat canopy was taller than the foxtail canopy and experienced no significant changes in radiation levels beyond daily fluctuations. Although both species demonstrated a decrease in LAR, the mechanisms for the decrease were different. In wheat the decrease in LAR was due to a decrease in the amount of biomass allocated to the leaves (LWR), while in foxtail the decrease was primarily due to a change in leaf density. The decrease in LWR resulted from both water deficit and ontogenetic effects, while the decrease in SLA was due to increasing radiation levels.

Many studies have shown that leaf area is a more common determinant of plant growth than is the photosynthetic rate of individual leaves (Leopold and Kriedemann 1975 ; Potter and Jones 1977) and from a weed-crop competition standpoint, the rapid development and maintenance of a taller plant canopy has important consequences for shading by one species over another (Spitters and Aerts 1983). The RLGR (analogous for

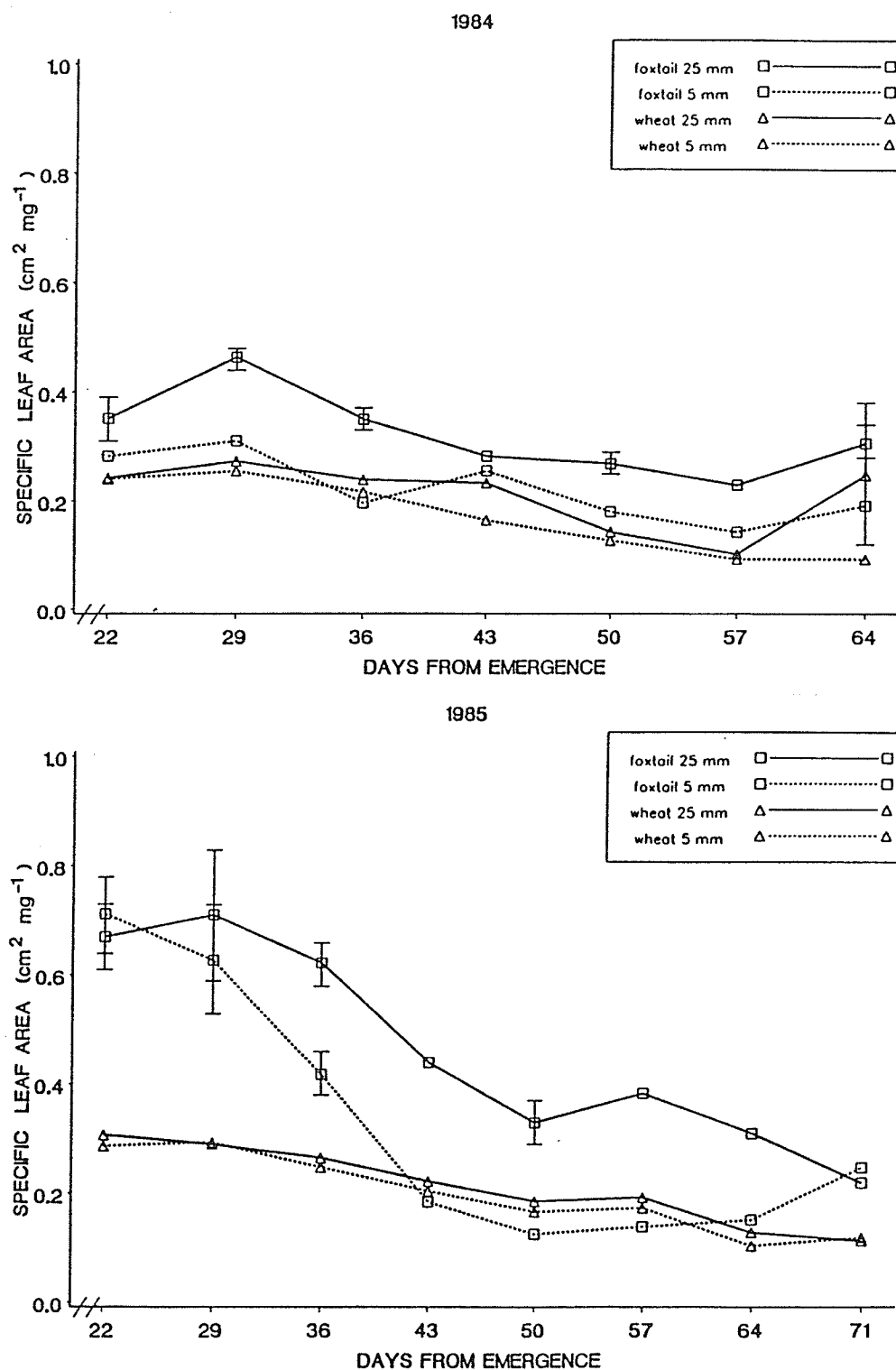


Figure 16: Specific leaf areas (SLA) in the outdoor experiment, 1984 and 1985, under dry (5 mm) and wet (25 mm) irrigation regimes (mean values \pm one standard error).

leaf area to RGR) declined in both years with time (Figures 17 and 18). The RLGR was positive, but declined early in the season and eventually became negative especially in wheat, as the plants matured. The larger decrease in RLGR in the wet treatment than in the dry treatment in 1984 was due to the greater leaf area in the wet treatment and thus the decrease was proportionally larger. The maintenance of RLGR in foxtail in 1984 resulted from increased growth of foxtail as the wheat canopy senesced, and higher radiation levels and a greater proportion of the soil water became available to the foxtail. The treatment and species effects in RLGR were not as evident in 1985 due to the cool, rainy conditions in late August.

The LAP coefficients for 1984 and 1985 (Figure 19) declined with time in both years. Potter and Jones (1977) considered LAP to be the daily change in LAR, but this is incorrect (Patterson et al. 1978). LAP is the product of $(RL(\text{area})GR/RGR)$ and LAR, so that LAP depends on the relative changes in leaf production (or senescence) and total biomass gain, and the partitioning of the biomass (Jackson 1963). The trend in all three components decreased with time and thus LAP also declined. The largest decrease and rate of decrease in LAP (slope) was in the wet treatment for foxtail in both years. Although there was no difference in the rate of LAP decline in the 2 years, the magnitude of the decrease was greater in 1984 than in 1985. There was no significant treatment effect on LAP in wheat in either year. The decrease in LAP can be attributed to the decline in LAR, which was due to changing radiation conditions within the canopy. The value of LAP is that it accounts for any differences in $RL(\text{area})GR$ and RGR due to treatment and/or species differences.

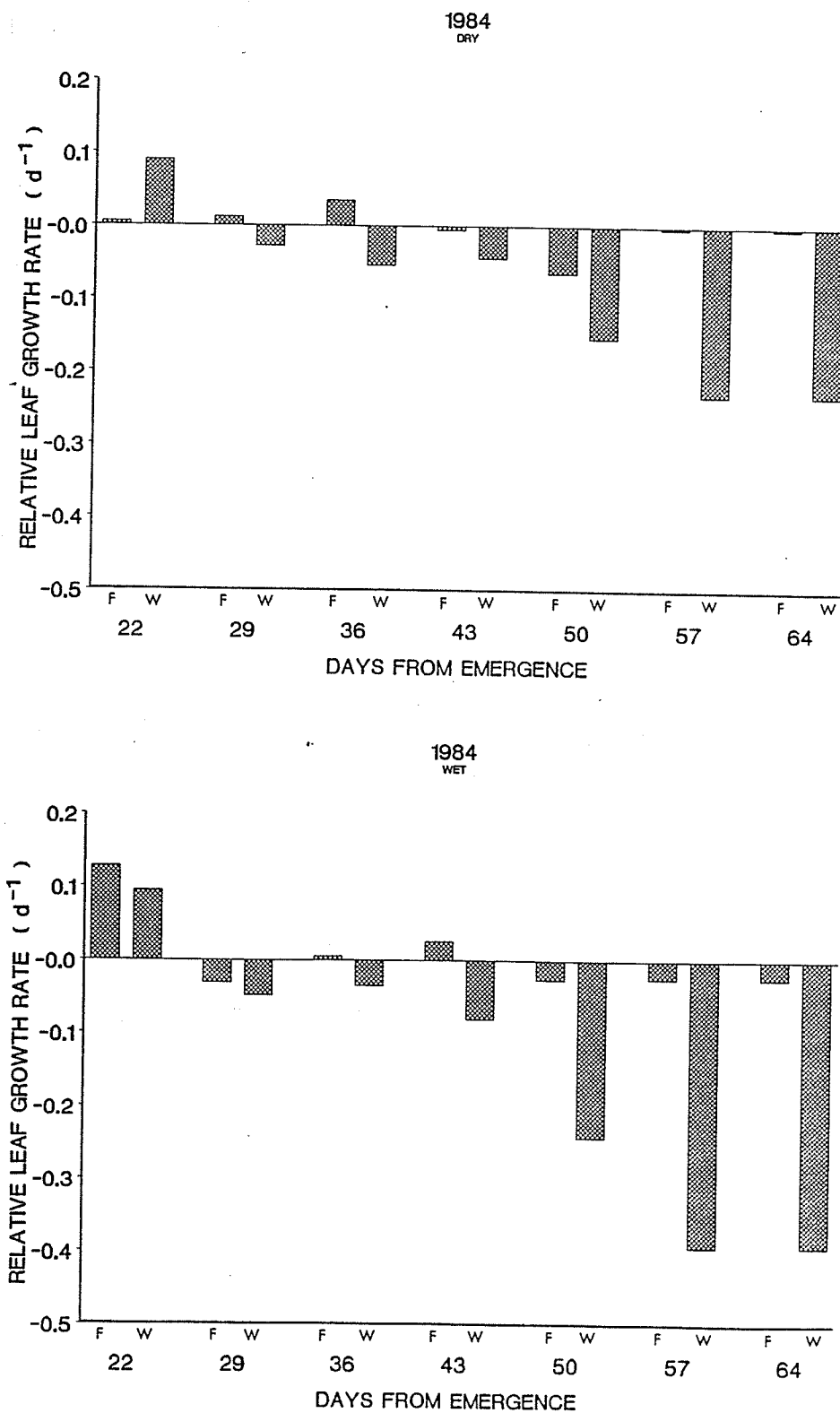


Figure 17: Mean relative leaf growth rates for green foxtail (F) and wheat (W) for a harvest interval under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment, 1984.

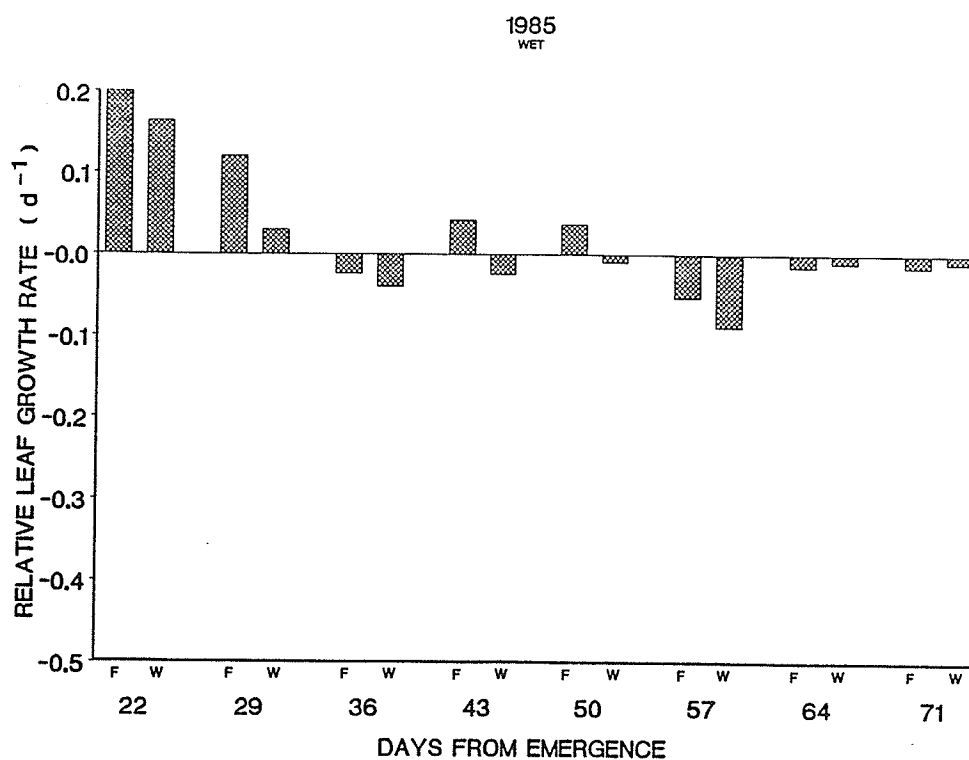
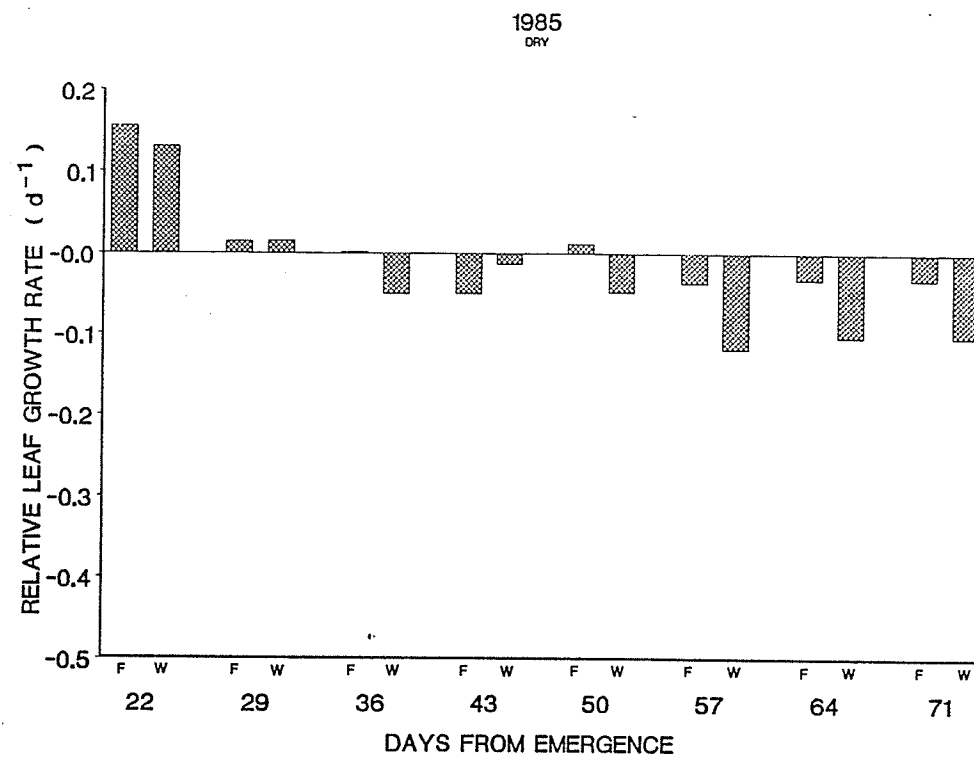


Figure 18: Mean relative leaf growth rates for green foxtail (F) and wheat (W) for a harvest interval under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment, 1985.

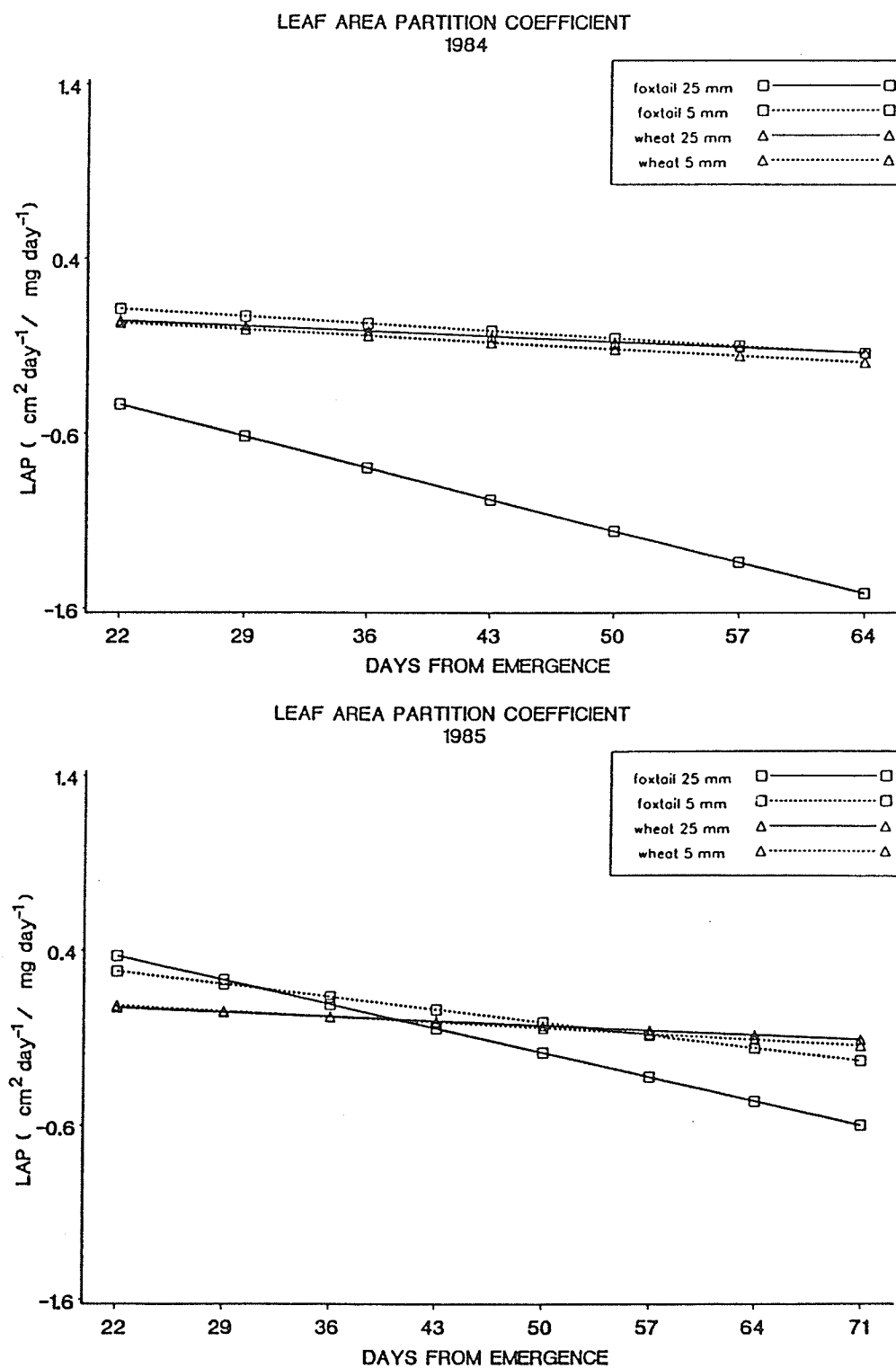


Figure 19: Mean values of leaf area partition coefficients under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment.

The LWP is analogous to LAP in that $LWP = (RL(\text{weight})GR/RGR) \times LWR$. Thus the LWP accounts for any differences in RGR and RLGR on a weight basis. This is important because although the LAP may increase or decrease, the LWP may have a different trend. For example, in response to decreases in irradiance, large thin leaves are produced, which could result in an increase in LAP, but the allocation to these leaves may decrease and thus LWP decreases (Kallis and Tooming 1974). Increased leaf area would result in a greater radiation interception but decreased weight may result in a lower mesophyll volume and thus lower photosynthetic rates (Nobel 1983 ; Spitters and Aerts 1983). Smaller, thicker leaves maintain photosynthesis at lower ψ_l and thereby contribute to drought tolerance (Kriedemann and Barrs 1983). Foxtail in the dry treatment had the greatest decrease and rate of decrease in LWP in 1985 (Figure 20). Both species in the dry treatment had greater decreases in LWP than in the wet treatment. Foxtail in the dry treatment in 1985 had a large decrease in LWP but very little change in LWR, indicating that $RL(\text{weight})GR/RGR$ declined substantially.

The final yield data for the two years (Table 9) show a significant year and treatment effect in seed number and weight, but less of an effect on mean seed weight. The seed number and seed weight per plant for foxtail were erratic for two reasons: 1) the foxtail seed matures unevenly in the panicle and readily falls from the panicle when mature, and 2) the foxtail plants recovered, at least partially, from the water stress as the wheat matured. Thus if the irrigation treatments had continued following maturity of the wheat, seed production by foxtail in the dry treatment would have increased (Milthorpe 1961). The absence of seed production by foxtail in the dry treatment in 1985 can be at least

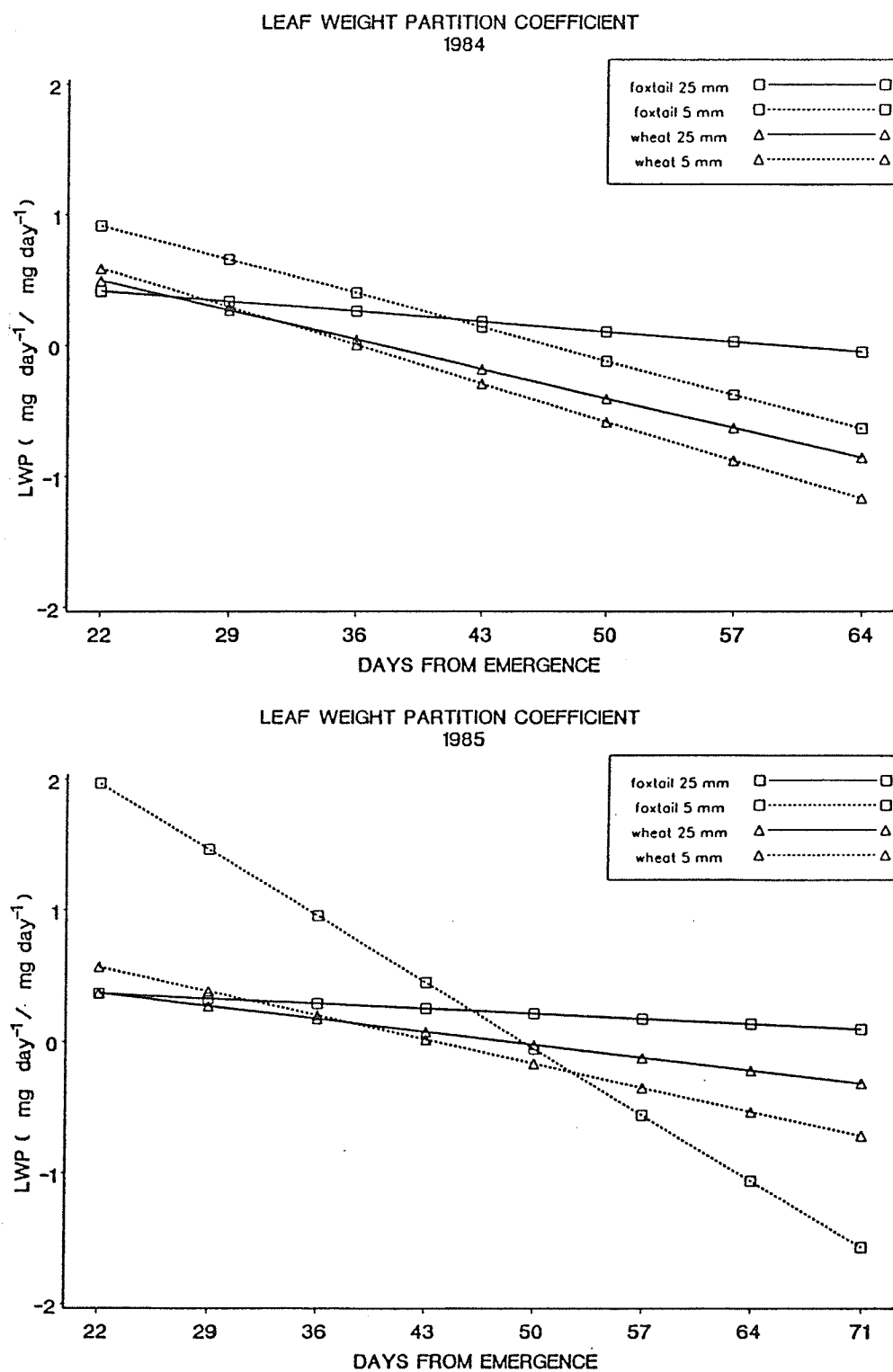


Figure 20: Mean values of leaf weight partition coefficients under dry (5 mm) and wet (25 mm) irrigation regimes in the outdoor experiment.

TABLE 9

Total seed number and total seed weight per plant, and mean seed weight for wheat and green foxtail grown outdoors under dry (5 mm) and wet (25 mm) irrigation regimes.¹

Treatment	Seed Number		Seed Weight (mg)		Mean Seed Weight (mg)	
	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error
1984						
foxtail 5 mm	33.07	4.85	37.68	5.90	1.14	0.05
25 mm	338.88	24.98	384.11	31.02	1.13	0.04
wheat 5 mm	73.09	4.03	1458.85	89.88	19.96	0.25
25 mm	79.01	4.34	1779.22	100.94	22.52	0.28
1985						
foxtail 5 mm	0	--	--	--	--	--
25 mm	924.15	32.06	1135.86	44.86	1.23	0.02
wheat 5 mm	10.47	1.09	223.35	26.12	21.33	0.78
25 mm	44.45	3.31	964.06	81.41	21.69	0.83

¹ harvest dates - August 23, 1984 and September 02, 1985

partially explained by the fact that the foxtail was harvested when the wheat was mature. If the irrigation treatments had continued beyond this time foxtail growth would have persisted and seed would likely have been produced. Wicks et al. (1986) reported a similar effect with winter wheat on foxtail seed production. In giant foxtail flowering was delayed by competition (Pickett and Bazzaz 1978). Kawano and Miyake (1983), and Vanden Born (1971) reported that seed production by green foxtail was very dependent on plant size. Kawano and Miyake (1983) reported that the seed number per panicle ranged from 24 to 1078, with a mean of 234.2, while individual seed weight ranged from 0.695 to 0.745 mg, with a mean of 0.709 mg. In both wheat and foxtail the total seed weight and seed number per plant were decreased by water stress, but there was little effect on mean seed weight. This is consistent with many other studies which have shown that seed weight is one of the most stable of plant properties (Bradshaw 1965 ; Harper 1977).

However the time of onset and the severity of the water deficit have a substantial effect on both potential and actual yield (Fischer and Kohn 1966c ; Desjardins and Ouellet 1980 ; Knight 1983). Blum et al. (1983) have emphasized that drought tolerance in the vegetative phase is not related to drought tolerance in the reproductive stage and that conditions during seed filling may be more important than previous environmental conditions.

CONTROLLED ENVIRONMENT STUDIES.

Temperature and soil water effects on growth.

The total biomass accumulated by foxtail at 30/25 C was greater than that for wheat in both stressed and unstressed conditions growing alone and in combination with wheat (Table 10). At 30/25 foxtail biomass was decreased by water stress. Wheat growing in combination with foxtail was severely reduced in growth and there was no effect of water deficit on the competitive relationship. There was also no effect of water stress on wheat growing alone. At 20/15 C wheat was superior to foxtail both in combination and alone. There was a significant effect of water stress on wheat grown in combination with foxtail.

Foxtail had greater leaf area than wheat at 30/25 C both alone and in combination. The leaf area of foxtail was reduced by water stress both alone and in combination, but there was no appreciable effect of water stress on leaf area production in wheat (Table 11). At 20/15 C wheat had a greater leaf area than foxtail in both stressed and unstressed conditions and there was a decrease in leaf area due to water stress. Even at this low temperature foxtail produced a small leaf area which was reduced by water stress, but foxtail was completely suppressed by wheat in the competitive situation.

An analogous situation to leaf area existed for leaf weight (Table 12). Foxtail was superior to wheat under the 30/25 C regime, while wheat was superior to foxtail at 20/15 C. There were also significant water stress effects on leaf weight in both species.

Foxtail had a greater stem weight than wheat at 30/25 C, while wheat had a greater weight at 20/15 C (Table 13). Foxtail was taller than wheat at 30/25 C, while the opposite was true at 20/15 C (Table 14).

TABLE 10

Mean (X) and standard errors (Sx) of total biomass per plant (mg) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
----- (mg) -----									
Stressed									
30/25 C	5	12.8	0.2	0.7	0.1	1.4	0.1	1.6	0.1
	12	40.6	10.6	165.6	15.4	33.4	3.6	65.9	29.4
	19	145.4	23.2	1434.6	112.1	142.8	22.1	860.1	116.1
	26	336.9	102.6	2236.7	186.9	216.7	53.2	2224.9	193.7
	33	322.9	119.6	4220.2	311.3	209.7	18.6	3974.0	131.8
	40	661.6	189.5	5881.7	74.9	183.3	15.9	5423.6	134.2
Unstressed									
30/25 C	5	11.1	0.3	1.2	0.1	9.8	0.1	12.6	0.4
	12	39.5	4.0	176.7	26.1	44.8	3.3	60.6	15.5
	19	134.3	37.2	1081.2	94.3	86.9	19.1	440.2	110.9
	26	315.9	52.6	2437.7	253.9	137.2	27.2	942.7	86.6
	33	696.9	187.3	5570.7	230.5	322.9	119.6	3840.6	446.2
	40	1171.8	475.7	7845.2	455.9	125.3	35.1	7683.3	322.8
Stressed									
20/15 C	5	26.9	6.8	1.1	0.2	43.2	9.7	2.3	0.7
	12	55.9	2.3	12.7	3.4	41.6	3.9	6.2	2.6
	19	212.5	31.6	79.9	25.8	206.9	58.1	36.7	15.2
	26	589.2	78.0	181.2	81.2	544.8	69.3	38.2	14.0
	33	1195.7	78.7	450.2	138.0	915.4	246.3	50.5	18.2
	40	3034.4	222.7	477.1	173.9	2361.9	496.3	63.4	16.6
Unstressed									
20/15 C	5	28.8	9.6	1.8	0.4	53.9	17.9	1.6	0.6
	12	43.6	8.4	9.3	3.5	50.0	7.2	6.3	1.5
	19	248.9	32.1	81.1	15.8	221.0	42.8	29.3	12.6
	26	775.7	151.8	128.7	28.9	464.9	143.6	29.1	10.5
	33	1842.5	58.3	242.6	53.5	1155.3	119.1	69.0	23.8
	40	4260.6	210.6	366.3	107.9	1698.5	430.1	42.4	14.4

¹ stressed pots cycled to ψ_s of -2.0 MPa
unstressed pots maintained near ψ_s of 0 MPa

TABLE 11

Mean (\bar{X}) and standard errors (S_x) of leaf area per plant (cm^2) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
----- (cm ²) -----									
Stressed									
30/25 C	5	1.66	0.22	0.34	0.01	0.50	0.03	0.55	0.02
	12	4.71	1.10	24.82	2.52	3.80	0.45	8.82	3.30
	19	13.78	1.67	131.01	8.71	12.30	1.57	93.89	9.79
	26	24.35	7.57	144.82	21.27	8.99	1.33	180.23	19.96
	33	12.27	3.42	213.62	15.82	1.84	0.48	241.50	31.85
	40	33.77	11.83	220.43	20.24	0.47	0.19	202.78	13.34
Unstressed									
30/25 C	5	1.86	0.19	0.20	0.01	1.40	0.09	1.77	0.13
	12	4.91	0.54	27.86	6.60	4.96	0.31	10.42	2.82
	19	15.09	3.69	102.80	11.88	8.82	1.72	55.15	7.55
	26	27.83	3.20	180.11	13.55	8.90	2.66	110.51	7.59
	33	39.23	8.40	303.97	18.24	8.17	3.78	359.93	43.55
	40	32.72	6.24	284.89	10.22	1.60	0.29	367.27	44.12
Stressed									
20/15 C	5	5.72	1.42	0.66	0.12	6.39	1.09	0.58	0.15
	12	7.88	0.70	1.58	0.38	6.20	0.68	1.05	0.54
	19	26.81	3.35	11.00	3.55	23.51	6.65	4.70	0.44
	26	54.23	7.04	18.12	7.19	44.23	5.71	2.09	0.64
	33	106.08	8.85	50.96	19.44	61.29	16.43	1.74	0.43
	40	110.75	32.27	40.71	11.85	125.29	26.68	2.04	0.16
Unstressed									
20/15 C	5	5.29	1.63	0.50	0.07	9.11	3.25	0.45	0.01
	12	5.75	1.26	1.90	1.00	7.14	1.04	1.00	0.34
	19	24.10	3.16	11.86	2.81	22.16	5.83	3.52	2.18
	26	73.79	12.25	13.44	3.85	40.11	11.35	3.64	1.34
	33	159.82	5.34	30.66	7.22	85.13	12.18	3.22	1.90
	40	186.20	14.32	23.87	5.07	52.31	11.39	1.63	0.45

¹ stressed pots cycled to ψ s of -2.0 MPa
unstressed pots maintained near ψ s of 0 MPa

TABLE 12

Mean (\bar{X}) and standard errors (S_x) of leaf weight per plant (mg) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
----- (mg) -----									
Stressed									
30/25 C	5	11.7	1.6	0.2	0.0	1.0	0.1	1.1	0.3
	12	27.6	8.2	94.2	11.7	22.1	1.9	35.5	14.8
	19	81.9	10.3	694.8	56.5	71.1	7.1	433.2	55.3
	26	141.4	39.6	822.9	125.0	49.8	6.8	900.8	94.4
	33	179.2	27.4	1389.2	98.3	31.3	4.7	1305.4	195.9
	40	230.9	82.4	1580.2	149.5	103.7	7.7	1564.3	50.6
Unstressed									
30/25 C	5	10.1	2.1	0.4	0.0	8.9	2.0	11.5	1.0
	12	26.6	2.0	95.1	22.5	31.1	2.5	37.8	10.2
	19	85.1	20.7	486.6	70.4	52.4	9.8	237.8	51.5
	26	160.7	16.3	922.7	93.5	48.5	13.3	422.9	34.8
	33	231.9	49.9	1793.3	40.8	45.0	21.9	1622.4	149.5
	40	255.8	65.3	2253.5	52.7	7.8	1.5	2490.4	291.0
Stressed									
20/15 C	5	17.3	4.8	0.5	0.0	29.7	5.9	1.3	0.4
	12	43.6	3.3	9.2	2.5	32.2	3.1	4.3	1.9
	19	146.9	22.6	51.9	16.9	144.1	41.3	25.4	11.4
	26	407.8	51.4	114.6	52.5	357.9	47.2	19.1	6.3
	33	599.7	57.8	232.9	72.9	414.8	121.4	13.7	4.3
	40	742.2	165.8	235.4	73.4	777.8	164.1	20.2	3.3
Unstressed									
20/15 C	5	18.7	7.2	1.1	0.3	38.3	15.5	1.0	0.2
	12	32.8	6.9	6.5	2.8	38.3	15.3	4.6	1.2
	19	173.7	22.2	54.9	10.9	160.2	33.7	21.0	4.6
	26	515.2	31.5	74.6	17.2	302.8	95.1	17.2	6.6
	33	964.5	38.5	135.2	29.8	558.3	53.7	22.9	11.3
	40	1189.9	67.5	171.9	41.5	340.4	75.7	10.6	2.8

¹ stressed pots cycled to ψ s of -2.0 MPa
unstressed pots maintained near ψ s of 0 MPa

TABLE 13

Mean (\bar{X}) and standard errors (S_x) of stem weight per plant (mg) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
----- (mg) -----									
Stressed									
30/25 C	5	1.1	0.1	0.5	0.1	0.5	0.1	0.5	0.1
	12	13.0	2.4	71.5	3.8	11.9	1.6	30.5	14.6
	19	60.2	11.1	706.7	65.6	64.5	11.5	411.9	65.5
	26	181.8	66.7	1202.7	105.3	116.7	37.1	1444.5	118.1
	33	163.0	70.6	2175.9	202.1	120.9	13.7	2042.5	80.9
	40	694.5	254.4	3084.5	108.8	103.7	7.7	2787.7	123.1
Unstressed									
30/25 C	5	1.0	0.1	0.4	0.1	0.9	0.1	1.1	0.2
	12	12.9	2.1	81.7	6.7	13.7	0.8	22.9	5.3
	19	49.3	16.7	559.0	32.6	34.5	9.3	197.1	57.5
	26	155.2	37.2	1351.3	163.9	73.8	15.3	459.3	55.1
	33	329.9	91.8	3051.0	174.4	107.9	44.3	1892.3	198.9
	40	505.3	229.4	4418.5	349.1	69.3	16.4	4251.3	102.1
Stressed									
20/15 C	5	9.6	2.1	0.6	0.2	13.5	3.8	1.1	0.4
	12	12.3	1.0	3.5	0.9	9.3	1.1	1.8	0.7
	19	65.3	9.1	27.9	9.0	62.8	16.9	11.4	3.9
	26	181.4	27.3	66.6	29.0	185.2	24.2	19.1	7.6
	33	552.2	30.4	196.2	66.5	443.2	123.9	24.3	8.9
	40	2016.8	135.1	200.0	77.5	1523.2	345.7	31.4	10.7
Unstressed									
20/15 C	5	10.1	2.4	0.8	0.3	15.7	2.5	0.6	0.3
	12	10.8	1.4	2.8	0.7	11.7	1.9	1.7	0.4
	19	75.2	11.3	26.1	5.2	60.8	16.7	8.3	4.6
	26	260.2	50.3	45.4	10.9	162.1	48.5	11.8	4.1
	33	863.8	20.9	91.8	22.8	553.5	74.9	31.1	11.8
	40	2814.4	222.5	163.8	61.2	1069.3	430.1	16.0	4.7

¹ stressed pots cycled to ψ s of -2.0 MPa
unstressed pots maintained near ψ s of 0 MPa

TABLE 14

Mean (\bar{X}) and standard errors (S_x) of plant height (cm) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
----- (cm) -----									
Stressed									
30/25 C	5	0.7	0.	1.0	0.1	1.3	0.1	0.8	0.1
	12	4.1	0.3	4.8	0.2	2.8	0.4	3.1	0.2
	19	6.6	0.5	15.5	2.1	8.2	0.9	11.4	1.0
	26	17.3	2.3	28.1	1.9	15.9	4.1	22.9	3.8
	33	16.3	3.2	32.7	2.4	18.5	2.5	32.5	1.2
	40	22.1	0.3	32.3	2.9	21.1	1.2	34.8	1.9
Unstressed									
30/25 C	5	1.0	0.1	0.9	0.1	0.5	0.1	0.8	0.1
	12	3.9	0.3	4.9	0.4	3.6	0.1	3.7	0.1
	19	5.9	0.3	11.7	1.8	5.8	0.7	9.2	1.6
	26	13.9	2.3	22.1	2.9	13.1	2.3	18.1	2.7
	33	19.4	4.0	34.3	1.5	16.2	3.3	24.1	4.4
	40	20.9	1.0	43.6	1.2	15.9	3.5	45.2	5.5
Stressed									
20/15 C	5	4.1	0.3	0.5	0.1	5.3	0.2	0.8	0.1
	12	3.8	0.3	1.1	0.1	2.6	0.1	0.8	0.2
	19	5.2	0.4	2.4	0.5	4.8	0.6	1.4	0.4
	26	6.9	0.5	3.7	0.8	7.1	0.2	2.2	0.3
	33	15.3	1.3	9.6	3.3	12.8	1.4	2.4	0.7
	40	31.6	0.8	7.4	1.6	28.4	1.5	3.3	0.5
Unstressed									
20/15 C	5	5.1	0.8	0.7	0.1	4.4	0.5	0.8	0.1
	12	4.2	1.0	1.2	0.3	3.2	0.5	0.9	0.1
	19	6.0	0.6	3.1	0.4	4.7	0.4	1.8	0.5
	26	8.8	0.4	3.7	0.4	6.8	0.6	2.0	0.5
	33	15.4	0.6	7.6	2.2	13.2	0.5	3.3	0.8
	40	33.8	2.5	7.3	1.1	25.8	4.5	2.6	0.5

¹ stressed pots cycled to ψ_s of -2.0 MPa
unstressed pots maintained near ψ_s of 0 MPa

The SAS-GLM procedure for dry weight of the entire plant, leaf area, leaf weight, and stem weight produced the coefficients listed in Table 15 . At 30/25 C the RGR, kW, for foxtail and wheat was reduced as a result of water stress. The RGR of wheat in competition with foxtail was reduced from the value when growing alone. Foxtail RGR was reduced by 0.008 and wheat by 0.010. At 20/15 C the RGR of wheat decreased from 0.156 to 0.140 as a result of water stress, while the RGR for foxtail actually increased. This is consistent with the greater biomass accumulation in foxtail in the stressed condition at 20/15 C. However the effect of water stress on the comparative growth of the two species in isolation was relatively minor compared to the temperature effect. The RGR of foxtail was reduced by 0.008 and 0.021 in the stressed and unstressed treatments, respectively, when the temperature regime was decreased from 30/25 C to 20/15 C. In comparison the RGR of wheat increased by 0.033 and 0.039 in the stressed and unstressed treatments, respectively, as the temperature was decreased. The high temperature regime clearly had an adverse effect on the growth of wheat, while comparatively foxtail was at less of a disadvantage under the low temperature regime. These differences may at first seem insignificant but during the period of growth examined W, A, LW, and SW are all exponential functions of their " k " values (Causton 1977). While the competitively superior species at each temperature regime suppressed the growth of the associated species, under field conditions the effect would be magnified as shading would be of greater importance than in the controlled environment (Patterson 1982,1983).

The kA was greater for foxtail than for wheat at 30/25 C and greater in the unstressed than in the stressed treatments for both

TABLE 15

Relative growth rates for wheat and foxtail in a controlled environment under two temperature regimes and a water stressed and unstressed condition.

Treatment	kW	kA (day ⁻¹)	kLW	kSW
30/25 C				
foxtail in combination unstressed	0.197	0.140	0.168	0.199
foxtail in combination stressed	0.183	0.120	0.151	0.181
foxtail alone unstressed	0.171	0.108	0.144	0.166
foxtail alone stressed	0.163	0.094	0.127	0.155
wheat in combination unstressed	0.052	-0.013	0.051	0.066
wheat in combination stressed	0.065	-0.036	-0.024	0.087
wheat alone unstressed	0.117	0.066	0.079	0.129
wheat alone stressed	0.107	0.051	0.058	0.128
20/15 C				
foxtail in combination unstressed	0.082	0.016	0.039	0.075
foxtail in combination stressed	0.087	0.014	0.052	0.079
foxtail alone unstressed	0.150	0.086	0.127	0.130
foxtail alone stressed	0.155	0.099	0.140	0.141
wheat in combination unstressed	0.114	0.090	0.111	0.158
wheat in combination stressed	0.125	0.087	0.099	0.151
wheat alone unstressed	0.156	0.114	0.133	0.172
wheat alone stressed	0.140	0.090	0.111	0.158

species. At 20/15 C, k_A decreased for foxtail in the unstressed treatment but increased for foxtail in the stressed treatment, compared to the 30/25 C values. This resulted from the fact that leaf area was greater in the stressed than in the unstressed regime. Thus even under this low temperature regime the higher WUE of foxtail may have been responsible for greater leaf area under stressed than under unstressed conditions. When grown in combination the k_A of wheat was severely depressed by the foxtail at 30/25 C in both stressed and unstressed conditions, and furthermore the k_A values were negative. At 20/15 C the k_A values were greater for wheat than for foxtail and foxtail was able to maintain positive k_A values. A similar pattern of foxtail superiority at 30/25 C and wheat superiority at 20/15 C existed for k_{LW} and k_{SW} . However, for foxtail in the stressed treatment, k_{LW} increased and k_{SW} decreased as the temperature decreased, indicating a greater biomass allocation to leaves than to stems.

This pattern is evident in the LAR (Table 16). Foxtail in the stressed treatment (alone) had a greater LAR than any of the other combinations. As the pots were well spaced, this increased LAR cannot be attributed to any shading effects. This increase in LAR may have contributed to the relatively lower decrease in k_W for foxtail in the stressed treatment than in the unstressed treatment with decreased temperature. Both the LAR and LWR (Table 17) for foxtail in the stressed treatment were greater at 20/15 C than at 30/25 C. From this one could infer that at low temperatures and under water deficit conditions, foxtail increases the rate of leaf production (k_A), and the biomass allocated to leaves (LAR and LWR) in an attempt to increase whole plant carbon fixation to compensate for lower unit fixation rates.

TABLE 16

Mean (\bar{X}) and standard errors (S_x) of leaf area ratio ($\text{cm}^2 \text{mg}^{-1}$) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
-----($\text{cm}^2 \text{mg}^{-1}$)-----									
Stressed									
30/25 C	5	0.13	0.01	0.49	0.03	0.36	0.04	0.34	0.06
	12	0.12	0.01	0.15	0.01	0.11	0.01	0.15	0.02
	19	0.10	0.01	0.09	0.01	0.09	0.01	0.11	0.01
	26	0.07	0.01	0.06	0.01	0.05	0.01	0.08	0.01
	33	0.06	0.01	0.05	0.00	0.01	0.00	0.06	0.01
	40	0.02	0.01	0.04	0.00	0.00	0.00	0.04	0.00
Unstressed									
30/25 C	5	0.17	0.02	0.17	0.01	0.14	0.01	0.14	0.01
	12	0.12	0.01	0.15	0.01	0.11	0.01	0.17	0.03
	19	0.12	0.01	0.09	0.01	0.10	0.01	0.14	0.01
	26	0.09	0.01	0.07	0.00	0.06	0.01	0.12	0.01
	33	0.07	0.01	0.05	0.00	0.04	0.00	0.10	0.01
	40	0.03	0.00	0.04	0.00	0.01	0.00	0.05	0.00
Stressed									
20/15 C	5	0.21	0.02	0.71	0.20	0.15	0.01	0.26	0.01
	12	0.14	0.01	0.13	0.01	0.15	0.01	0.15	0.02
	19	0.11	0.02	0.13	0.02	0.11	0.01	0.10	0.01
	26	0.09	0.00	0.11	0.01	0.08	0.01	0.06	0.01
	33	0.09	0.00	0.11	0.02	0.07	0.00	0.04	0.01
	40	0.03	0.00	0.11	0.01	0.05	0.00	0.04	0.01
Unstressed									
20/15 C	5	0.19	0.01	0.29	0.02	0.17	0.01	0.33	0.01
	12	0.13	0.01	0.18	0.03	0.14	0.01	0.15	0.01
	19	0.11	0.01	0.14	0.01	0.11	0.01	0.09	0.01
	26	0.10	0.00	0.10	0.01	0.09	0.00	0.12	0.00
	33	0.09	0.00	0.13	0.00	0.07	0.00	0.04	0.00
	40	0.04	0.00	0.07	0.00	0.03	0.00	0.06	0.00

¹ stressed pots cycled to ψ s of -2.0 MPa
unstressed pots maintained near ψ s of 0 MPa

This could result from lower enzyme functioning at the lower temperature (Long 1983).

The significance of variables in the linear models fit to Napierian logarithms of the data indicate that temperature was the dominant factor determining the expression of plant growth (Table 18). There was a significant species effect only for total biomass, leaf area, and leaf area ratio, but a very significant temperature interaction with species and no interaction between watering regime and species. Thus any of the measured or derived plant attributes can be adequately predicted solely on the basis of time from emergence, temperature and a species indicator.

The LAP coefficients (Figure 21) at 20/15 C for foxtail in the stress treatment were greater than for every other species and treatment combination, but the values rapidly declined with time. As k_W and k_A were constant during this period of growth the decline in LAP was due to a decline in LAR. This decrease in LAR can be attributed to low temperature effects on leaf expansion or initiation rates (Causton et al. 1978). At 30/25 C wheat in the unstressed treatment had the greatest LAP initially. As there was little difference in LAR between the two temperature regimes, the high LAP can be attributed to the higher rate of leaf area production relative to total biomass production. However the LAP rapidly declined with time, indicating a more adverse effect of high temperature on leaf area production, than on total biomass. At 30/25 C wheat in combination with foxtail in both the stressed and unstressed treatments increased the rate of both leaf area production and leaf weight production relative to total biomass (Figure 22). In the competitive situation, at adversely high temperatures,

TABLE 17

Mean (X) and standard errors of (Sx) of leaf weight ratio (mg mg^{-1}) in a controlled environment under stressed and unstressed conditions.¹

Temperature Regime	Days	Wheat		Foxtail		Wheat in Combination		Foxtail in Combination	
		X	Sx	X	Sx	X	Sx	X	Sx
-----(mg mg^{-1})-----									
Stressed									
30/25 C	5	0.91	0.13	0.29	0.08	0.64	0.21	0.69	0.14
	12	0.67	0.02	0.56	0.02	0.67	0.02	0.56	0.03
	19	0.57	0.03	0.48	0.02	0.51	0.04	0.51	0.01
	26	0.43	0.03	0.36	0.04	0.25	0.04	0.40	0.02
	33	0.27	0.02	0.32	0.03	0.15	0.02	0.33	0.02
	40	0.14	0.01	0.27	0.03	0.03	0.01	0.29	0.01
Unstressed									
30/25 C	5	0.87	0.21	0.33	0.05	0.91	0.08	0.91	0.11
	12	0.68	0.03	0.52	0.05	0.69	0.01	0.62	0.01
	19	0.65	0.01	0.44	0.03	0.61	0.02	0.56	0.02
	26	0.52	0.02	0.38	0.01	0.35	0.04	0.45	0.03
	33	0.38	0.02	0.32	0.02	0.18	0.03	0.43	0.03
	40	0.18	0.01	0.29	0.02	0.07	0.01	0.32	0.03
Stressed									
20/15 C	5	0.63	0.03	0.42	0.18	0.69	0.02	0.55	0.01
	12	0.78	0.03	0.73	0.02	0.78	0.01	0.69	0.05
	19	0.69	0.01	0.64	0.02	0.68	0.02	0.65	0.09
	26	0.69	0.02	0.64	0.03	0.66	0.01	0.51	0.01
	33	0.50	0.01	0.52	0.03	0.44	0.05	0.31	0.05
	40	0.23	0.04	0.53	0.05	0.33	0.03	0.34	0.04
Unstressed									
20/15 C	5	0.62	0.04	0.58	0.15	0.69	0.06	0.69	0.11
	12	0.74	0.02	0.64	0.07	0.77	0.01	0.73	0.05
	19	0.70	0.02	0.67	0.02	0.71	0.06	0.77	0.08
	26	0.66	0.00	0.58	0.02	0.63	0.02	0.59	0.03
	33	0.52	0.01	0.56	0.03	0.48	0.01	0.31	0.08
	40	0.28	0.03	0.49	0.06	0.21	0.02	0.31	0.07

¹ stressed pots cycled to ψ s of -2.0 MPa
unstressed pots maintained near ψ s of 0 MPa

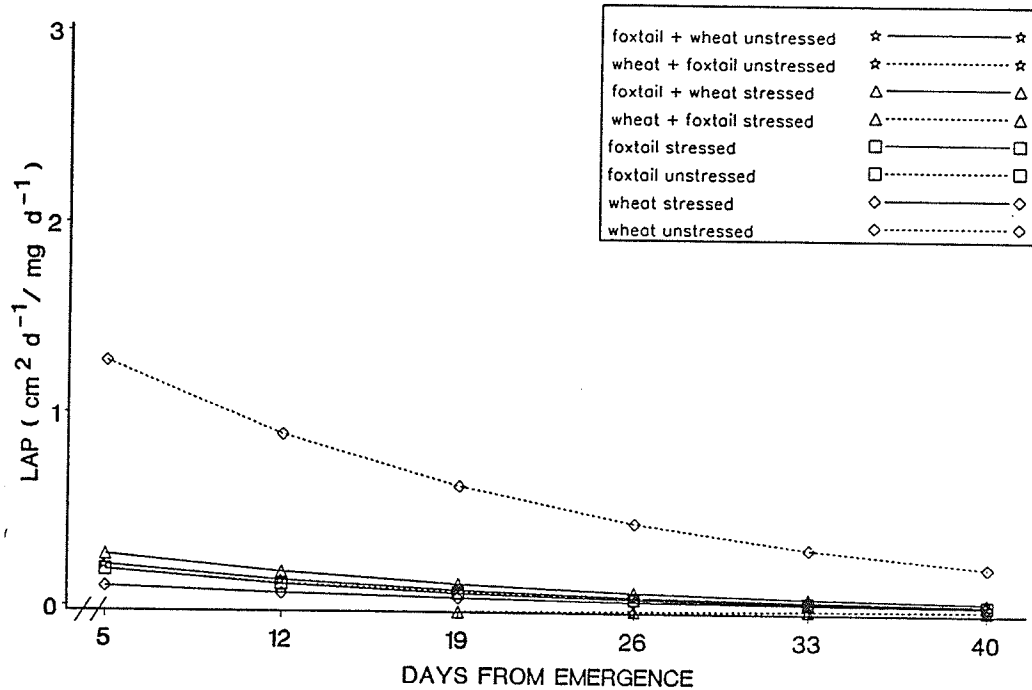
TABLE 18

Significance (F-tests) of parameters used in linear models fitted to the logarithms of measured and derived quantities in the growth experiment.¹

	Leaf Area	Leaf Weight	Stem Weight	Total Weight	Height	LAR	LWR
Days from emergence	**	**	**	**	**	**	**
Temperature regime	**	**	**	**	**	**	**
Watering regime	NS	NS	NS	NS	NS	NS	*
Species	NS	NS	NS	**	**	**	NS
Temp x Water	NS	NS	NS	NS	NS	NS	NS
Temp X Species	**	**	**	**	**	NS	NS
Water x Species	NS	NS	NS	NS	NS	NS	NS

¹ **, *, and NS refer to probability levels of 0.01, 0.05 and non-significant, respectively.

LEAF AREA PARTITION COEFFICIENT
30/25 C



LEAF AREA PARTITION COEFFICIENT
20/15 C

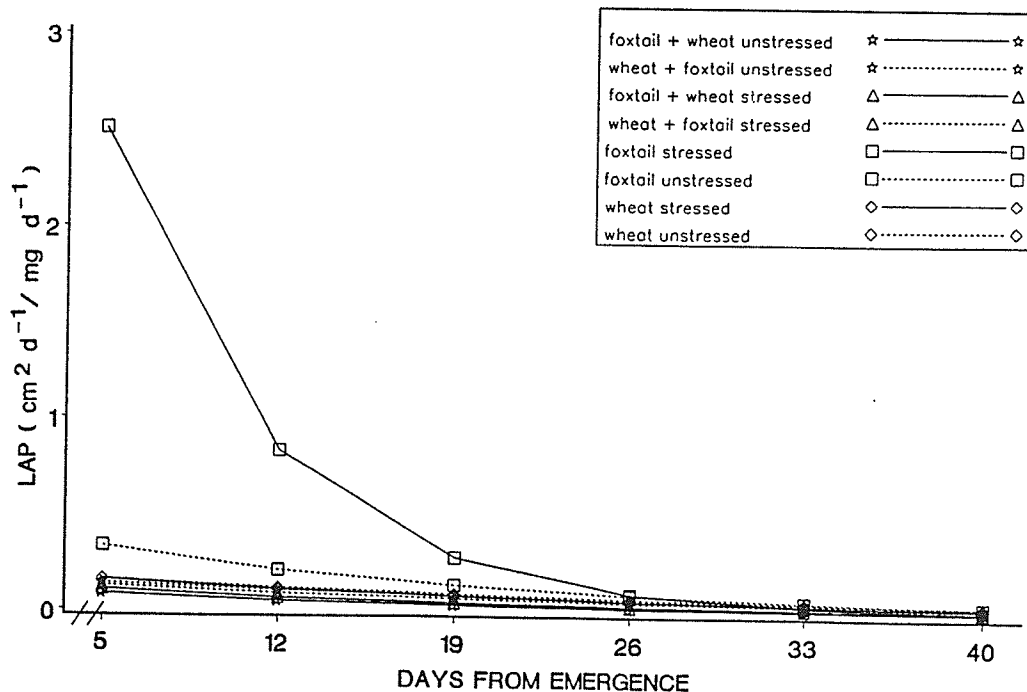


Figure 21: Leaf area partition coefficients (LAP) for green foxtail and wheat in a controlled environment under stressed and unstressed conditions.

wheat, on a relative basis, had a greater rate of leaf area and leaf weight increase than total biomass increase. LAP was greater in the stressed wheat + foxtail treatment, while LWP was greater in the unstressed treatment at 30/25 C. Thus wheat produced leaf area at a greater rate than leaf weight under stressed conditions but the opposite occurred under unstressed conditions. There was little difference in LWP values between species or treatments at 20/15 C, although foxtail had slightly higher values when grown alone. At 30/25 C the SWP coefficients for wheat increased, while those for foxtail declined (Figure 23). This was irrespective of whether the plants were grown in isolation or in combination, under stressed or unstressed conditions, although wheat in combination with foxtail had a greater rate and extent of increase in SWP. Foxtail generally had a decline in SWP at both temperature regimes.

The WUE for foxtail and wheat grown in isolation under both stressed and unstressed conditions at the two temperature regimes were variable (Table 19). The dry weight of the roots was included in the total dry weight of the plant for the calculation of WUE. Although the actual values for wheat and foxtail varied from harvest to harvest, in general foxtail had a greater WUE than wheat at 20/15 C, while the reverse was true at 30/25 C. This may be related to the actual amount of growth made and a greater transpirational water loss under the respective optimum conditions for each species. On a theoretical basis foxtail should have a greater WUE than wheat, at least at the single leaf level. However transpiration at the whole plant level is a function of stomatal conductance and leaf area, and as leaf area was greatest for foxtail at 30/25 C, and for wheat at 20/15 C, the water

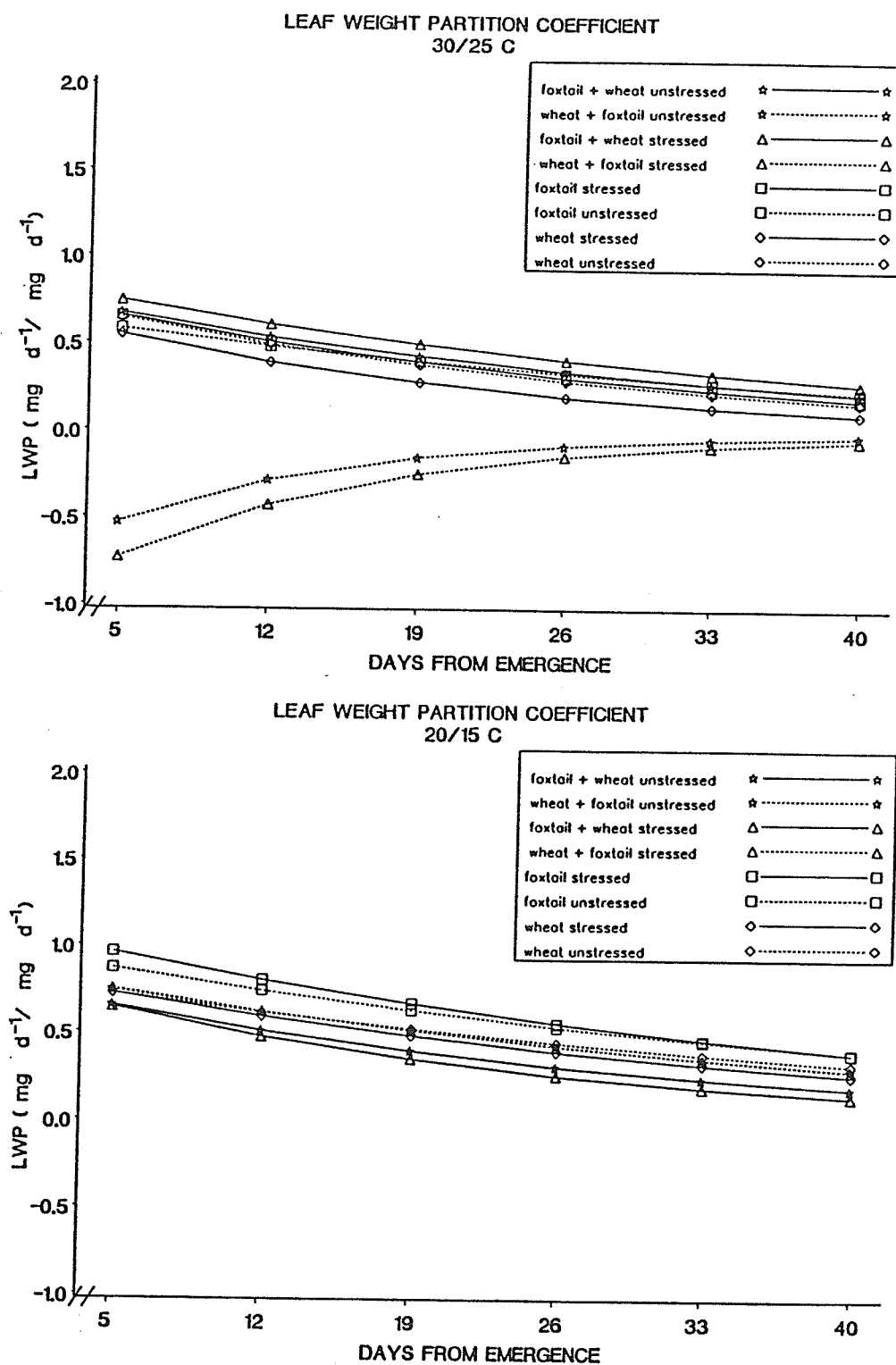


Figure 22: Leaf weight partition coefficients (LWP) for green foxtail and wheat in a controlled environment under stressed and unstressed conditions.

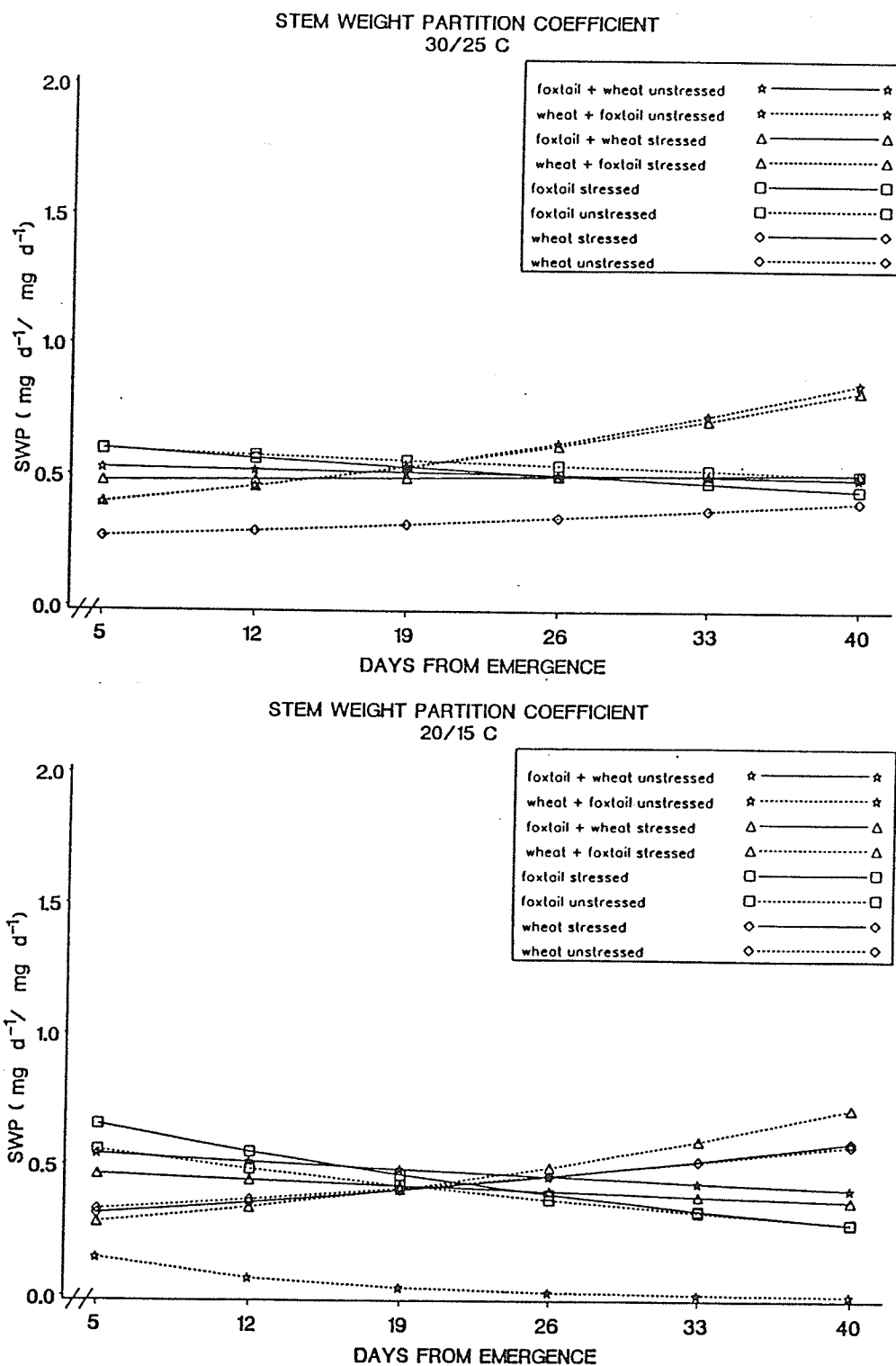


Figure 23: Stem weight partition coefficients (SWP) for green foxtail and wheat in a controlled environment under stressed and unstressed conditions.

TABLE 19

Mean (\bar{X}) and standard errors (S_x) of water use efficiency (WUE) (mg dry weight g^{-1} water used) of green foxtail and wheat grown in a controlled environment.

Temperature Regime	Days	Wheat		Foxtail	
		X	Sx	X	Sx
----- (mg g ⁻¹) -----					
Stressed					
30/25 C	5	0.34	0.03	4.17	0.98
	12	4.14	0.92	0.79	0.27
	19	0.82	0.12	0.17	0.03
	26	1.01	0.21	0.29	0.03
	33	5.05	2.77	0.26	0.01
	40	0.96	0.23	0.26	0.01
Unstressed					
30/25 C	5	0.43	0.08	5.26	1.39
	12	3.60	0.59	0.90	0.14
	19	1.43	0.29	0.23	0.04
	26	1.51	0.36	0.22	0.01
	33	1.69	0.50	0.22	0.01
	40	1.49	0.36	0.23	0.01
Stressed					
20/15 C	5	0.47	0.08	1.06	0.23
	12	0.73	0.12	4.31	1.12
	19	0.49	0.16	3.30	1.86
	26	0.23	0.04	1.10	0.36
	33	0.16	0.02	0.52	0.16
	40	0.10	0.01	1.03	0.63
Unstressed					
20/15 C	5	0.37	0.04	1.34	0.20
	12	1.02	0.22	10.89	4.72
	19	0.45	0.03	1.71	0.52
	26	0.19	0.03	1.72	0.60
	33	0.14	0.02	1.11	0.32
	40	0.10	0.01	1.09	0.29

¹ stressed pots cycled to ψ s of -2.0 MPa
unstressed pots maintained near ψ s of 0 MPa

loss for each species would be greater in the respective regimes. It should also be noted that the WVP of the two temperature regimes differed, so that instantaneous WUE would have differed in the two environments but the long term pattern of WUE over the entire life cycle of the plant is different from any instantaneous rate (Fischer and Kohn 1966a) . As has been emphasized, a high WUE in a seral competitive situation may not be an advantage. A less efficient species such as wheat will simply exploit the soil water to the detriment of the foxtail.

Patterson et al. (1978) proposed that the relative importance of ULR and LAP as determinants of plant growth depended on the type of experiment conducted. In the study by Potter and Jones (1977) the temperature of the growth environment was varied but the irradiance was held constant. They reported that temperature influenced LAP and LAR more than ULR, with the result that RGR was better correlated with LAP than with ULR. However Patterson et al. (1978) used a constant temperature regime (31/25 C) but three different PPFD levels: 90, 320, and 750 $\mu\text{moles m}^{-2} \text{s}^{-1}$. ULR varied more with PPFD than did LAR, LAP, or RGR. Within each species examined RGR was positively correlated with ULR, but negatively correlated with LAP and LAR when grown at different PPFD levels.

Thus the relative importance of LAP, LAR, and ULR in determining growth can be examined for two separate scenarios. During wheat-foxtail competition we can consider two different situations: 1) prior to canopy closure, and 2) following canopy closure. In the first case the RGR, RLGR and biomass allocation to the leaves (LAR , LAP) are the overriding factors in determining the extent of canopy development and the

potential for shading of one species by the other. Pearcy et al. (1981) and, Spitters and Aerts (1983) have emphasized the importance of seedling growth in C₃ and C₄ competitive relationships. This early season growth and competitive superiority is determined by environmental influences on RGR, RLGR, and LAP. Pearcy et al. (1981) reported that the competitive outcome between a C₃ and a C₄ species was determined primarily by temperature effects on growth prior to canopy closure. They also reported that, compared to the temperature effect, water stress had little effect on the outcome of competition.

Following canopy closure the ability to maintain ULR, by increasing LAR, would influence the competitive ability. The low Φ of C₄ species would be a detriment to foxtail under these conditions, particularly at low temperature (Ehleringer 1978). However any differences in Φ or ULR, or morphological adaptations to shade, such as increased LAR or SLA, are of less importance than the relative position in the canopy.

Tissue water relations in green foxtail and wheat.

The data on photosynthesis and transpiration determined with the portable photosynthetic system were inconsistent, with high variability over all experiments, so this data is not presented. The reasons for the variability are as follows: 1) the third leaf of wheat, and foxtail especially, are very small and even with the smallest chamber available for the instrument (0.25 liter) the photosynthetic rates were extremely low, 2) the humidity in the chambers decreased rapidly at the onset of measurement, resulting in stomatal closure and negative transpiration and photosynthesis rates, 3) the CO₂ levels in the growth room had large day to day variation, and 4) as the stress period increased the stomata

were closed and gas exchange was insignificant. A method is required to alleviate the direct effects of humidity on stomatal aperture (Bunce 1985).

The progression of decrease in ψ_s with time is presented in Figure 24. The ψ_s showed little change during the first four days of drying but thereafter rapidly declined. This is consistent with the general pattern of drying in sands (Kramer 1983a). In sands approximately 95% of the available water is at ψ_s greater than -0.01 MPa (Kramer 1983a) thus most of the available water had been extracted by four days of drying.

At any given ψ_s , foxtail had a higher ψ_l but a lower RWC than wheat (Figure 25). As the total water potential ψ is a function of the pressure potential (P) and the osmotic potential (π), the difference in ψ could be due to changes in either component. An attempt was made to assess the relative contributions of P and π to ψ using pressure-volume analysis (Tyree and Jarvis 1981) but the low volumetric water content of the leaves resulted in a poor relationship. Although wheat maintained a greater RWC than foxtail, this in no way relates to physiological functioning as the potential of the water was much lower than in foxtail. The water potential in wheat decreased and at the same time there was an increase in RWC. The following changes in P and π are proposed to explain this occurrence. The decrease in RWC, as a result of soil drying, resulted in a proportional decrease in P relative to π . Thus a passive and/or active accumulation of solutes occurred which lowered π and ψ_l . Then water uptake into the cell occurred and ψ inside was lower than ψ outside and the result was an increase in RWC (Molz and Ferrier 1982). The role of active solute accumulation and thus

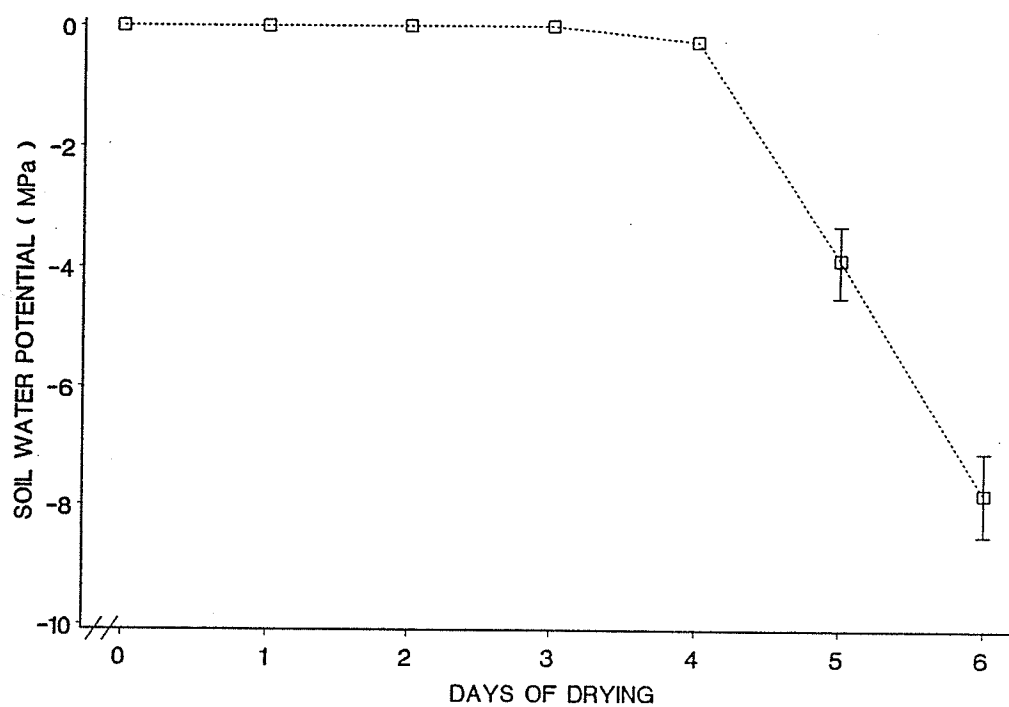


Figure 24: Soil water potential as a function of days of drying in a controlled environment (Almassipi sand).

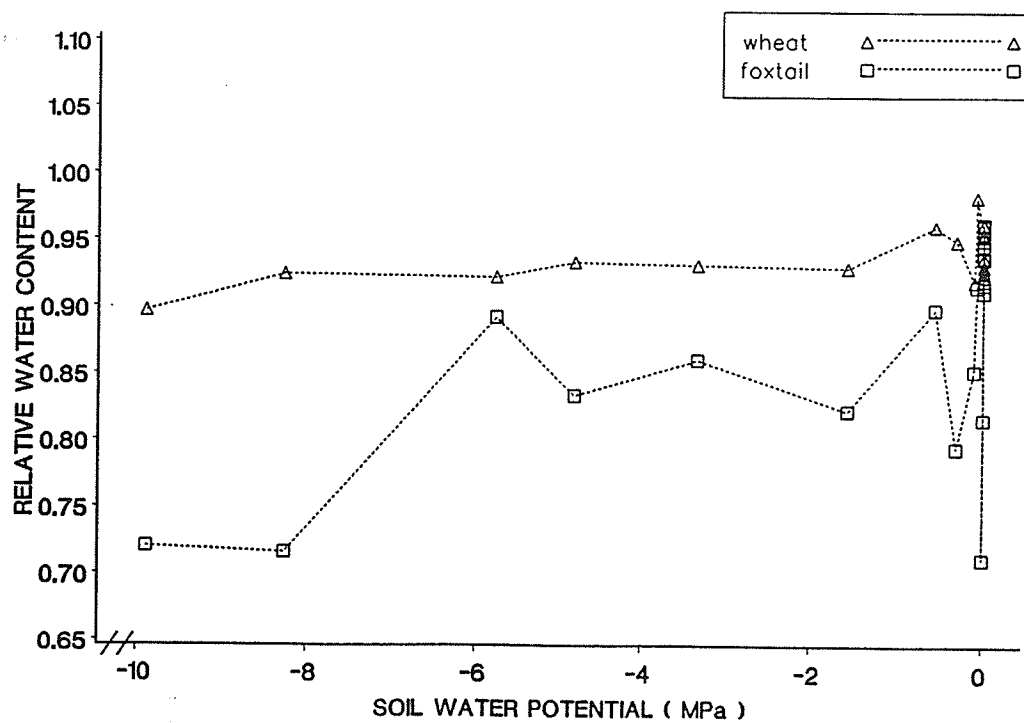
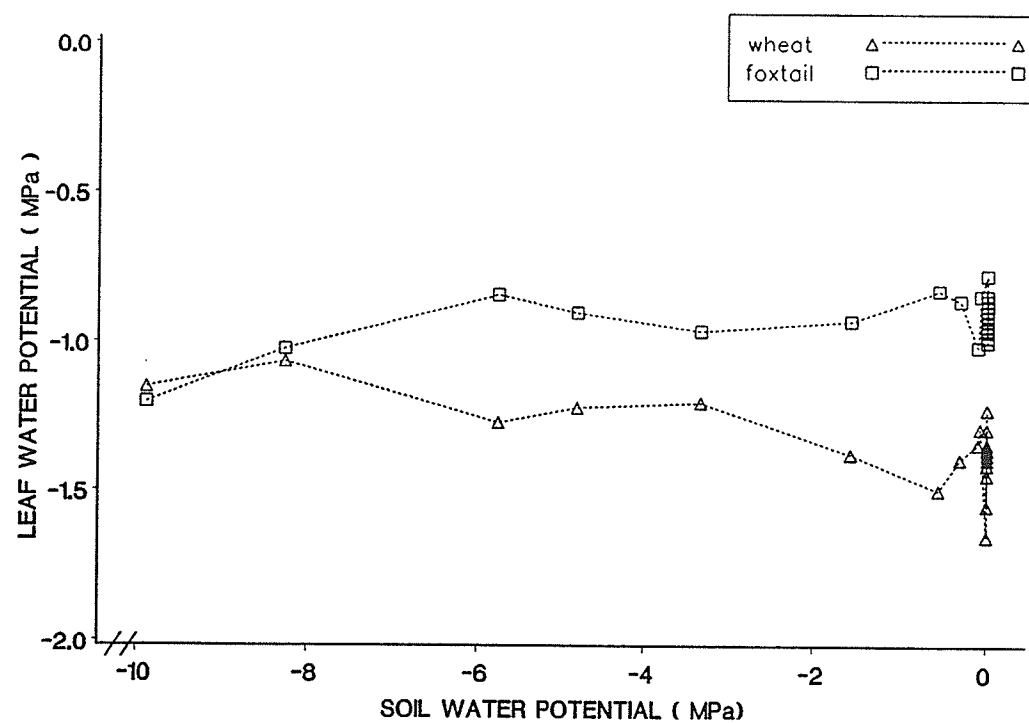


Figure 25: Water potential and RWC of green foxtail and wheat leaves over a six day drying period.

osmotic adjustment is merely speculation - some direct measurement of π and P would be required. The ψ_l in wheat subsequently increased as the RWC decreased. This could result from: 1) loss of solutes from the cell and thus a decrease in π , or 2) an increase in P due to cell shrinkage, i.e. a change in the elasticity of the cell wall. Morgan (1980) reported that the RWC of wheat plants was higher at low ψ_l in those genotypes which showed turgor maintenance through osmotic adjustment. There may also be substantial differences in wheat response of both π and RWC to ψ between different parts of the plant. Yang and deJong (1972) reported that the relationship between ψ_l and RWC depended mainly on the aerial environment of the plant and was independent of soil type. Under field conditions the RWC of wheat was reported to range from 0.65 to 1.03 at sunrise, and from 0.50 to 0.99 in the afternoon (Fischer and Kohn 1966b).

In foxtail ψ_l increased with RWC, as would be anticipated due to increased P, but thereafter ψ_l steadily declined with RWC (Figure 26). Although foxtail maintained a higher ψ_l than wheat the ability to compensate ψ_l for reduced RWC was greater for wheat than for foxtail. In general the leaves of most species are unaffected by RWC from 0.90 to 1.0, but cell expansion usually is reduced when RWC drops below 0.90 and ceases completely at 0.70 to 0.75 (Milthorpe and Moorby 1979).

There was no relationship between ψ_l and leaf temperature for either species (Figure 27). Under field conditions leaf and canopy temperature increase with increasing water deficit as latent heat exchange is reduced (Campbell 1977 ; Jackson 1983) but the radiation regimes and extent of water stress are different in controlled environment conditions (Macklon and Weatherley 1965 ; Gates 1968 ; Patterson 1983).

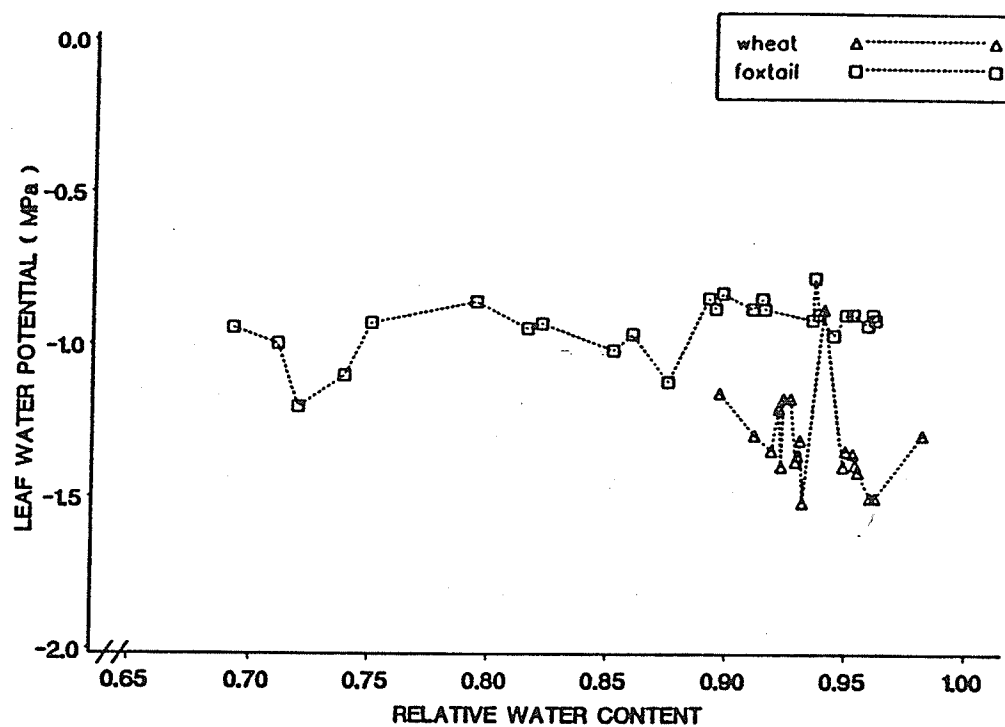


Figure 26: Leaf water potential versus RWC for green foxtail and wheat leaves over a six day drying period.

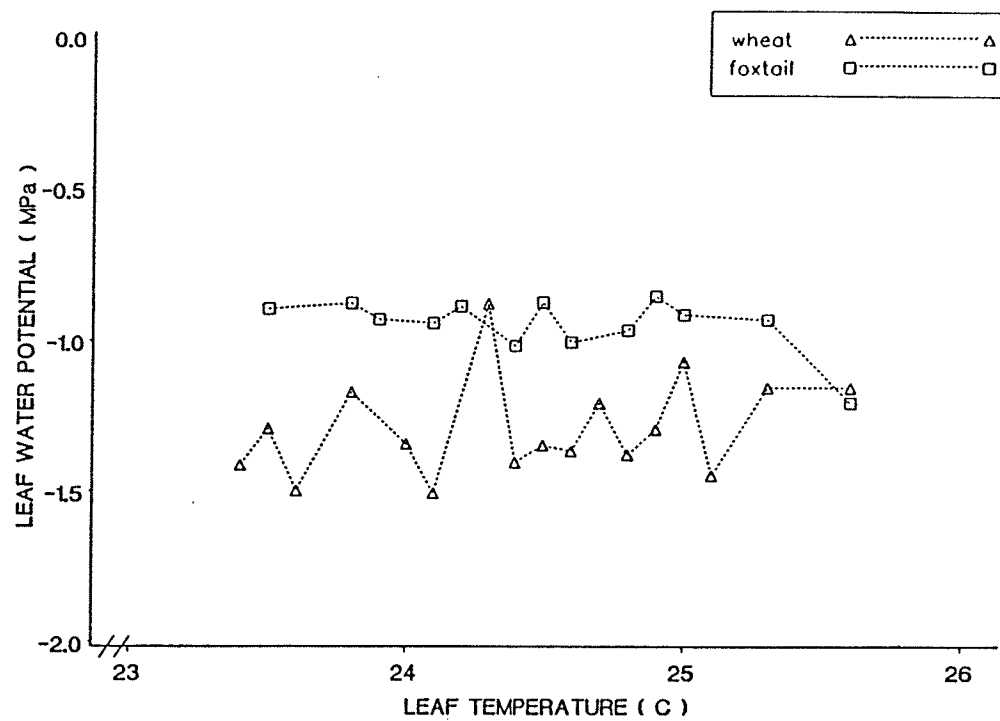


Figure 27: Leaf water potential versus leaf temperature for green foxtail and wheat over a six day drying period.

Additive experiments to examine wheat-foxtail competition.

In the additive experiment wheat had greater seed number per spike and greater total seed weight per spike at 20/15 C than at 30/25 C (Figure 28). There were significant temperature water stress, and interaction effects on seed number and seed weight. Water stress at 20/15 C severely reduced both parameters. Foxtail plants in this temperature regime became increasingly depauperate as the total density in the pots increased. No assessment of the vegetative characteristics of foxtail or wheat were determined as competitive and density effects are confounded (Harper 1977). The growth experiment has demonstrated the superior growth of foxtail at high temperature but the yield reductions at 30/25 C presented here are less evident than at 20/15 C. Although the yields were reduced significantly by both water stress and foxtail density, wheat yield was severely reduced by the high temperature regime. Thorne et al. (1968) reported that increased temperatures hastened the time to anthesis in wheat. This faster development resulted in smaller spikes and decreased spikelet numbers. Thus high temperature, density, and competitive effects on yield are confounded but the design more closely approximates the real situation than do substitution experiments.

The mean seed weight (Figure 29) was lower at 30/25 C than at 20/15 C. Although the differences in mean seed weight due to water deficit were significant, within a temperature regime, the differences were small compared to the effect on seed number and total seed weight. The potential for yield in wheat is influenced most by environmental conditions occurring from floral initiation to anthesis, while the actual yield is determined by conditions during grain filling (Thorne et

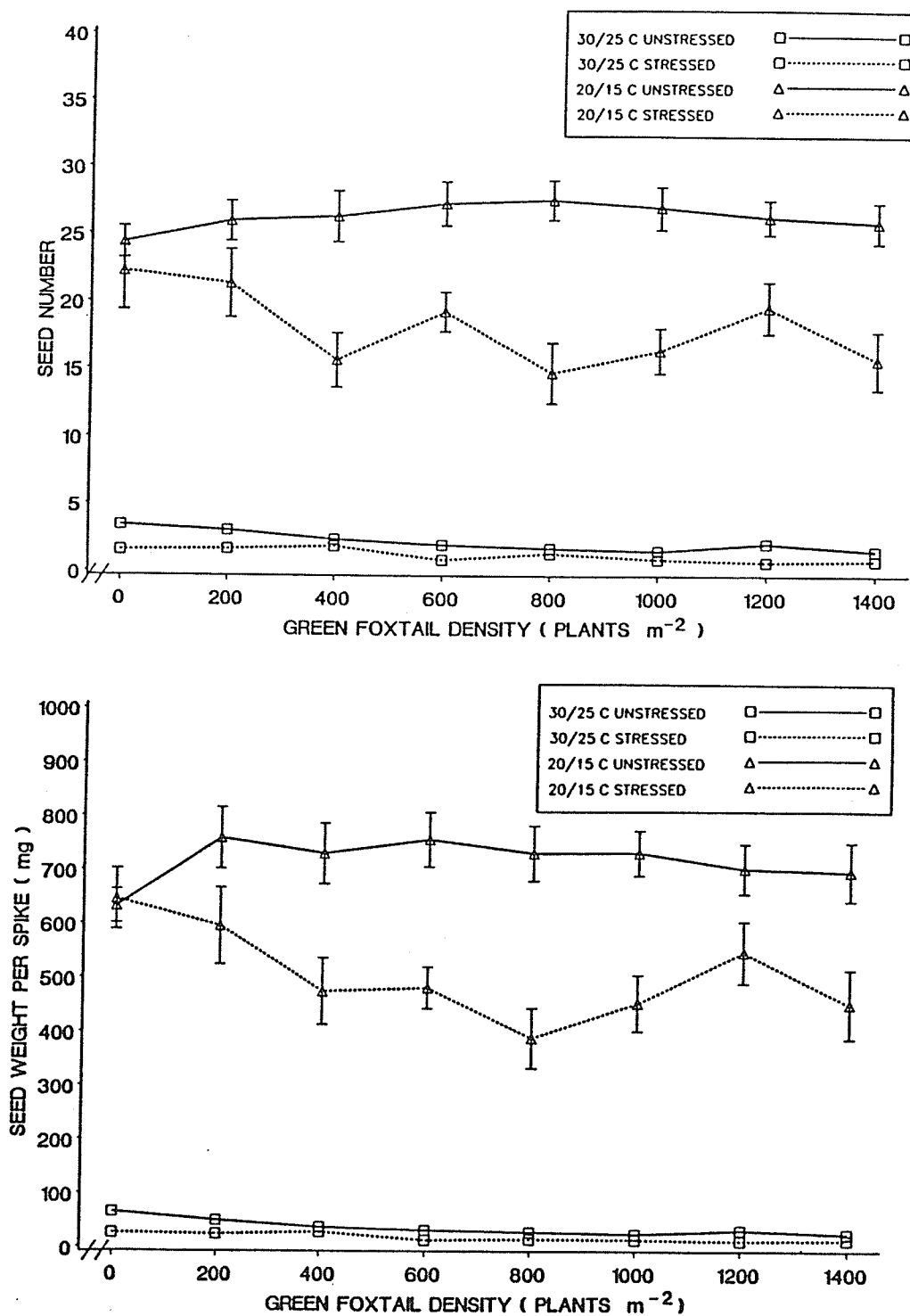


Figure 28: Seed number and total seed weight per spike of wheat plants in competition with green foxtail.

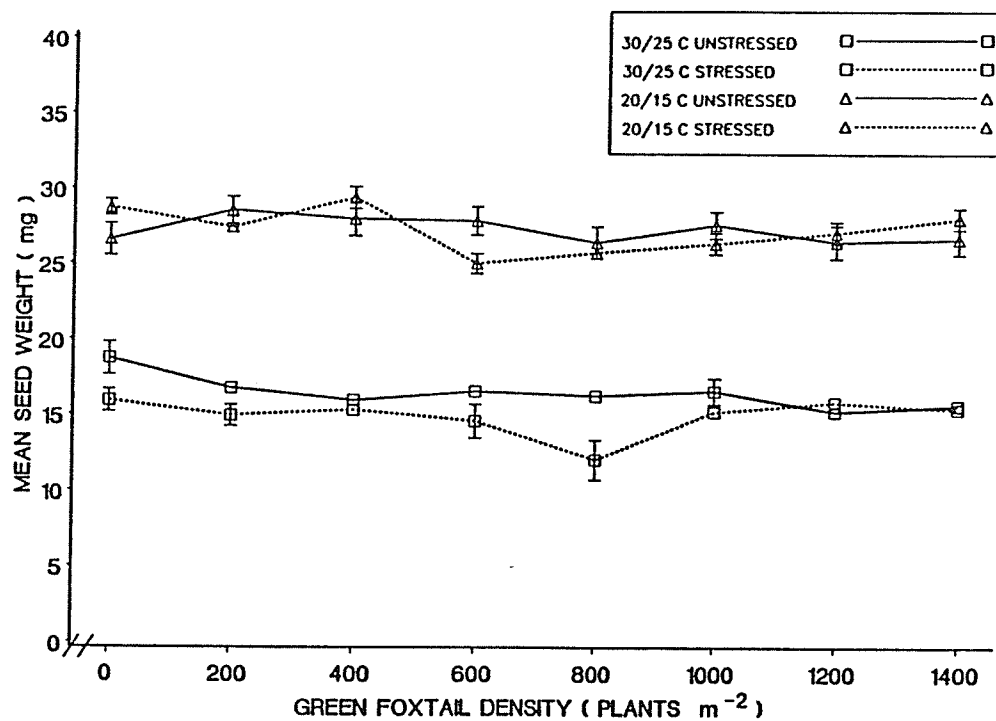


Figure 29: Mean weight of wheat seeds produced when grown in competition with green foxtail .

al. 1968). Thus the time of onset of water deficit during grain filling is crucial. Many experimenters have reported that individual seed weight is the least plastic of plant characters (Harper 1977).

GENERAL DISCUSSION

The competitive situation in an agronomic crop differs substantially from that of a climax plant community, and while a weed may be able to grow and reproduce, significant crop yield reductions may not occur (Baker 1974). This study has not examined the topic of reproductive plasticity and seedbank dynamics but they are certainly important in the overall competitive aspects of a weed (Harper 1977 ; Spitters in press). The competitive effects of weeds are dictated by early season environmental conditions, while the reproductive effort can increase following crop maturity. It is likely that green foxtail can produce and mature seed after crop maturation if environmental conditions are appropriate.

The degree and extent of competitive interaction between green foxtail and wheat is determined primarily by the relative times of emergence of the two species and subsequent environmental conditions. In temperate climates early growth of wheat would provide an advantage if foxtail emerged at a later date i.e. the temporal separation of the growth activities of the two species is very important (Doliner and Jolliffe 1979 ; Barnes et al. 1983). This was emphasized in the studies by Blackshaw et al. (1981a,b). In the field studies in 1984 and 1985 cool and/or rainy, cloudy conditions favored the growth of wheat over that of foxtail. As both species emerged simultaneously temporal separation was eliminated, but the growth of wheat was greater than foxtail during the period prior to canopy closure. Even though the

seedlings are of different sizes the comparative advantage of large and small plants depends on the growth rates following emergence (Newbery and Newman 1978). Hofstra and Steinstra (1977), Baskin and Baskin (1978), and Pearcy et al. (1981) have demonstrated that RGR, rather than unit leaf rates of photosynthesis determine success in a competitive relationship. The partitioning of biomass into leaf area (both rate and extent) was greater for wheat than for foxtail during seedling growth resulting in shading of foxtail by wheat. The relative positions in the canopy at the time of canopy closure dictated the results for the duration of the season. Thus under conditions of adequate soil water the competition is primarily for light (Donald 1961 ; Aldrich 1984). In the dry treatment the total LAI was lower than in the wet treatment, and consequently shading of the foxtail by wheat was reduced. However there was no evidence that foxtail was adapted to dry conditions, although both species were able to reproduce. Pickett and Bazzaz (1978) studied the growth and competitive ability of giant foxtail along a soil water gradient from saturation to less than 10%, in a silt loam soil. Giant foxtail produced the largest biomass at intermediate water contents both in isolation and in competition. Competition had no effect on the water content at which the maximum biomass was produced. In comparison Amaranthus retroflexus L. (also a C₄ species) produced the greatest biomass in the driest soil regime. Clearly these species differences occur irrespective of the mode of photosynthesis.

The RGR of wheat and foxtail are determined primarily by the temperature regime in which they are grown. Foxtail was superior at 30/25 C while wheat was superior at 20/15 C. The effect of soil water

deficit on growth was of minor importance compared to the temperature effect. Similar results were found by Pearcy et al. (1981) in their study of C_3 - C_4 competition. The overall adaptation of a species to dry environments is determined largely by phenological and morphological traits, rather than by a single metabolic response such as osmoregulation (Hanson and Hitz 1982). Nobel (1983) has emphasized that such metabolic adaptations to water deficit, and their physiological significance in terms of growth, are much easier to evaluate in ecologically similar species. This is clearly not the case for foxtail and wheat. Although we can speculate that the ability to maintain turgor, and thus leaf expansion, in the seedling stage, is a determining factor in canopy development in dry environments, an early, rapid utilization of soil water and the establishment of dominance in the canopy is more important.

Wheat cultivars differ substantially in height, leaf area, leaf orientation, the ability to osmoregulate, and drought tolerance (Evans et al. 1975), so the specific results are only applicable to this situation, but the general effect of temperature would be similar for other cultivars. Previous studies which have examined the physiology of green foxtail have failed to consider temperature as a significant environmental variable (Maurice 1985 ; Nadeau and Morrison 1986). In addition the response of foxtail to water deficit was studied in isolation, not in a crop.

SUMMARY AND CONCLUSIONS

The field and controlled environment studies have demonstrated the importance of environmental conditions in determining the competitive ability of green foxtail. At high temperatures the growth and competitive ability of foxtail was superior to wheat, while at low temperatures the reverse occurred. The effect of water deficit and any morphological or metabolic adaptation to low ψ s are of less importance than temperature in the wheat-foxtail complex. Clearly the initial early advantage for wheat of achieving a greater leaf area is reinforced throughout the growing season through the maintenance of a greater LAD and this determines the outcome of the competitive interaction.

Given "normal" spring weather conditions in western Canada, wheat development would be substantially advanced by the time soil temperatures increased to the point at which green foxtail would germinate, and even if the wheat and green foxtail emerged simultaneously, wheat would have the advantage of being a taller species with larger leaves. As the relative growth of the two species is ultimately determined by temperature, with water having a lesser effect, weather conditions following germination determine the relative superiority of one species over another.

Although foxtail competition would be reduced under cool conditions, in terms of managing weed populations a farmer would have to weigh the cost of herbicide treatment against the potential seed production by green foxtail and the threat of continuing infestations.

This study hopefully provides a stimulus for developing more comprehensive foxtail-wheat, or simply weed-crop models in general, based on weed densities and environmental factors. Further more detailed studies of this type utilizing a range of foxtail densities would add to the current data set and aid in the prediction process. Spitters (in press) has proposed that more accurate estimates of the competitive effects of weeds on crop yields can be obtained by basing yield loss models on an estimate of the initial ratio between the leaf area of weeds and the crop, rather than economic thresholds with fixed weed densities. As plant growth is a function of radiation interception, models of the relative radiation interception of the two species, based on their respective proportion in the total canopy area, are necessary (France and Thornley 1984 ; Spitters in press). It is important to realize that competitive ability is a relative attribute of a given species and that competition in a multi-weed environment may be different than in the single weed - crop interaction. A multivariate approach utilizing degree-days, weed density, and the extent and rate of development of green foxtail and wheat canopies would be the next logical step in assessing the potential detrimental effects of green foxtail. This type of approach based on the fundamental response of a weedy plant species to environmental conditions could be successfully utilized for other species and for more complex weed - crop associations and would better define the concept of an economic threshold for herbicide based weed control programs.

The salient features of this study with both theoretical and practical implications are:

- 1) that the extent of competition between green foxtail and wheat is determined by the degree of niche overlap between the two species, the temporal and spatial niche characteristics being particularly important.
- 2) the temperature regime following green foxtail and wheat emergence dictates the early season growth of each species and thus the relative height and leaf area of the two species. These early season environmental conditions determine the relative position of the leaf area of each species in the total (crop and weed) canopy and to a large extent the outcome of the competitive interaction.
- 3) at high temperatures foxtail is able to outcompete wheat, while at low temperatures the converse is true. This difference in competitive ability with temperature reflects the inherent differences in ecology of the two species, rather than any intrinsic differences in the type of photosynthetic system.
- 4) competition between wheat and green foxtail depends very strongly on whole-plant attributes, particularly plasticity in biomass partitioning
- 5) a high water use efficiency is a poor competitive "strategy" for green foxtail in competition with a less efficient species such as wheat.

- 6) the implications for herbicide based foxtail control recommendations should be examined with the aid of the information detailed in this study regarding the competitive ability of green foxtail and wheat as determined by the environment.

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APPENDIX

Appendix Table 1. List of symbols, abbreviations and appropriate dimensions.

Symbol	Parameter Represented	Dimensions
A	leaf area	area
BMD	biomass duration	weight time
ca	atmospheric CO ₂ concentration	ppm
ci	intercellular CO ₂ concentration	ppm
DD	degree-days	--
DFE	days from emergence	--
g	stomatal conductance	moles m ⁻² s ⁻¹
LA	leaf area	area
LAD	leaf area duration	area time
LAI	leaf area index	--
LAP	leaf area partition coefficient	(area time) ⁻¹ (weight time) ⁻¹
LAR	leaf area ratio	area weight ⁻¹
LW	leaf weight	weight
LWP	leaf weight partition coefficient	(weight time) ⁻¹ (weight time) ⁻¹
LWR	leaf weight ratio	weight weight ⁻¹
NUE	nitrogen use efficiency	weight weight ⁻¹
Pa	Pascal	pressure
PCOC	photosynthetic carbon oxidation cycle	
PCRC	photosynthetic carbon reduction cycle	
PEP	phosphoenolpyruvate	
PEG	polyethylene glycol	
PPFD	photosynthetic photon flux density	μmole m ⁻² s ⁻¹
RGR	relative growth rate	time
RLGR	relative leaf growth rate	time
RUBP-C:O	ribulose biphosphate carboxylase-oxygenase	
SLA	specific leaf area	area weight ⁻¹
SW	stem weight	weight
SWP	stem weight partition coefficient	(weight time) ⁻¹ (weight time) ⁻¹
SWR	stem weight ratio	weight weight ⁻¹
ULR	unit leaf rate	weight area ⁻¹ time ⁻¹
VPD	atmospheric water vapor pressure deficit	pressure
W	total biomass	weight
WUE	water use efficiency	weight weight ⁻¹
WVP	atmospheric water vapor pressure	pressure
ε	bulk elastic modulus	--
φ	quantum yield	moles CO ₂ fixed mole ⁻¹ absorbed quanta
π	osmotic potential	pressure
θ	volumetric water content	volume volume ⁻¹
P	pressure potential	pressure
τ	matric potential	pressure
ψ	water potential	pressure
subscripts	a - atmospheric	
	l - leaf	
	s - soil	

APPENDIX TABLE 2. Precipitation and temperature recorded at Winnipeg, 1984.

Date	May		June		July		August	
	Rain (mm)	Temperature (C) max min	Rain (mm)	Temperature (C) max min	Rain (mm)	Temperature (C) max min	Rain (mm)	Temperature (C) max min
1		13 1	21 14		9.6	28 13		34 20
2		11 0	26 12			32 13		31 16
3		15 2	27 12			28 11		31 12
4		15 2	21 3			27 10		32 16
5	T	17 3	18 16			28 10	2.8	32 17
6	T	13 0	20 17			26 5		32 18
7		7 0	27 16		17.4	29 8		30 17
8		13 1	20 14		0.9	28 13		28 15
9	1.8	17 2	13 10			28 13	7.4	26 14
10	0.6	20 6	19 7			29 13		30 14
11	0.8	11 7	23 9			23 13		30 12
12	6.0	15 1	17 13	18.7		34 14		30 16
13	0.6	18 7	21 11			31 11		37 19
14		21 4	22 9		2.8	28 14	4.4	30 22
15		26 7	28 14	49.7	T	29 15		30 15
16		32 16	30 12		1.4	27 13	1.3	30 14
17		26 19	28 11			31 11		33 12
18		20 14	27 13			33 15		29 9
19	T	14 10	26 18			30 9		32 11
20	12.4	17 9	27 11			30 11	9.4	28 15
21		23 12	28 17	45.1		27 10		26 11
22		17 9	32 17	6.3		28 11		23 9
23		19 8	25 11			31 10		27 7
24	3.4	14 6	28 9			30 11		30 14
25		14 5	32 14		1.3	34 13		34 19
26		19 4	26 15	22.6	0.5	35 11		39 16
27		19 7	31 12			34 14		38 16
28		22 4	30 14			33 15		35 16
29		26 7	28 12			30 18		28 10
30		32 14	29 11		4.0	28 21		22 14
31		36 17				30 18		19 9

APPENDIX TABLE 3. Precipitation and temperature recorded at Winnipeg, 1985.

Date	May			June			July			August		
	Rain (mm)	Temperature max min	(C)	Rain (mm)	Temperature max min	(C)	Rain (mm)	Temperature max min	(C)	Rain (mm)	Temperature max min	(C)
1		23	2	1.1	12	0		24	14		28	12
2		24	3		20	5		28	9		28	19
3		26	12	6.9	22	3	0.6	29	17	25.5	25	19
4	13.8	27	11	1.1	18	3		26	15	32.7	24	18
5		28	10		24	2		29	12	2.8	26	18
6		29	9	3.5	27	12		32	17		27	17
7		27	10		34	11	17.4	32	17		24	12
8		33	11	2.8	26	15	0.9	27	13	0.9	30	12
9		34	10		24	11		23	15	7.4	21	14
10	12.3	26	9		18	2	0.5	24	14		19	16
11	8.5	14	4		20	8		27	8		17	13
12		14	3		20	3	0.6	29	13	11.0	15	15
13	3.1	10	3		24	7	3.5	27	19	25.0	18	13
14		26	2	9.0	20	8	0.8	23	12	7.2	17	10
15		19	9		23	14		24	9	0.3	21	9
16		20	7	3.5	19	8	8.2	30	14		20	10
17		32	5	3.3	19	7		26	12	52.2	14	10
18		30	4	0.5	20	11	0.9	26	12	8.8	14	9
19	0.9	19	2		24	4	2.8	28	12		18	8
20		24	0		24	12		21	13		21	7
21		27	1	1.4	21	12		20	10	0.6	21	8
22		31	8	0.9	12	8	2.7	25	10		24	11
23	1.4	33	8	T	21	6		25	18	40.0	22	15
24	3.3	27	10		22	7		22	13	1.3	25	12
25		20	12	9.6	20	14		24	10		25	14
26		22	11	22.2	19	11	0.6	26	7		26	17
27		30	4		13	11		28	12		20	9
28		25	10		18	10		21	9		18	8
29	2.4	24	15		21	11		26	5		20	7
30		24	9		23	14		27	11		24	10
31	3.3	26	9					29	12		24	18

Summary of F-statistic from ANOVA 1984¹

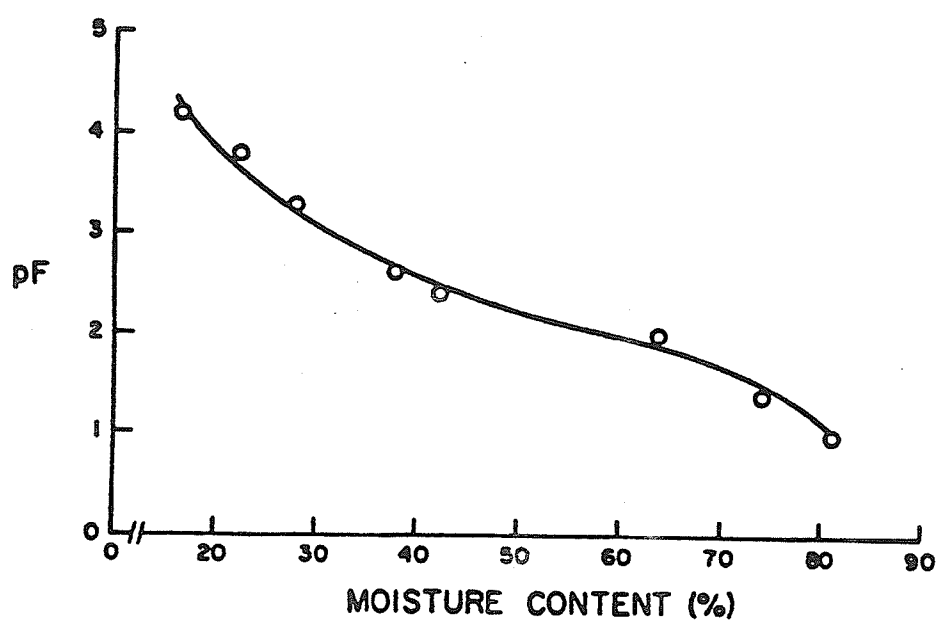
Source	Leaf No.	Leaf Area	Leaf Wt	Stem Wt.	Infl. Wt.	Total Wt.	LAR	LWR	SLA
PLOT			**						
TRT		**	*	*		*	**		*
PxTRT							*		
DATE	**	**	**	**	**	**	**	**	**
PxDATE									
TRTXDATE						**			
PxTxD			*	*		*			
SPECIES	**	**	**	**	**	**	**	**	**
PxSP	*	*	**	**		*			
TxSP			**	**		*	**		
DxSP	**	**	**	**	**	**	**	**	**
PxTxS			*	*		*			
PxDxS									
TxDxS								**	
PxTxDxS									

Summary of F-statistic from ANOVA 1985¹

Source	Leaf No.	Leaf Area	Leaf Wt	Stem Wt.	Infl. Wt.	Total Wt.	LAR	LWR	SLA	HT
PLOT										
TRT		**	**	**	*	*	**	*	*	*
PxTRT										
DATE	**	**	**	**	**	**	**	**	**	**
PxDATE										
TRTXDATE	**	**	**	**	*	**	**	**	**	*
PxTxD		**	*							
SPECIES	**	**	**	**	**	**	**	**	**	**
PxSP										
TxSP			**	**		**	**	**	**	*
DxSP	**	**	**	**	**	**	**	**	**	**
PxTxS										
PxDxS										
TxDxS				*			**	**	**	
PxTxDxS										

¹ Significance of the F test at p=0.05 * , p=0.01 ** .

Appendix Table 4. Summary of ANOVA from the outdoor experiment.

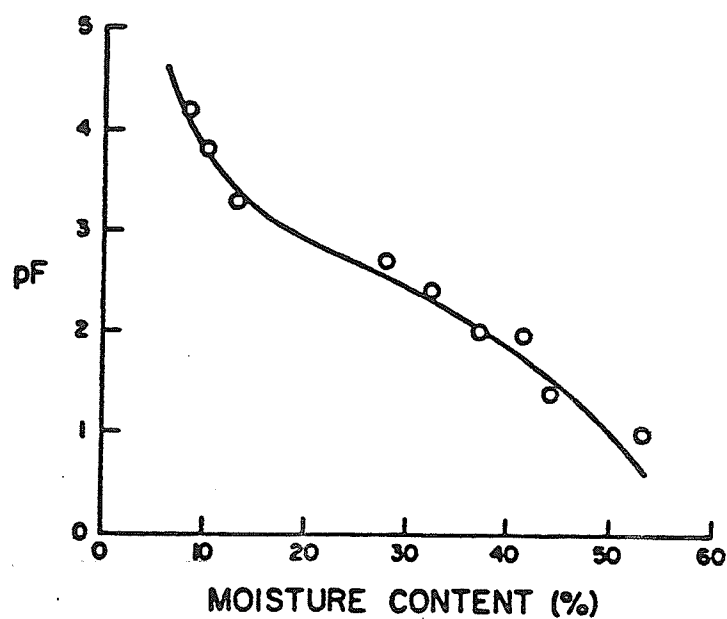


Appendix Figure 1. Moisture release curve for Altona clay loam.

$$y = 7.0583 - 0.2197x + 0.0036x^2 - (2.2335 \times 10^{-5})x^3$$

y = pF

x = soil water content (%)

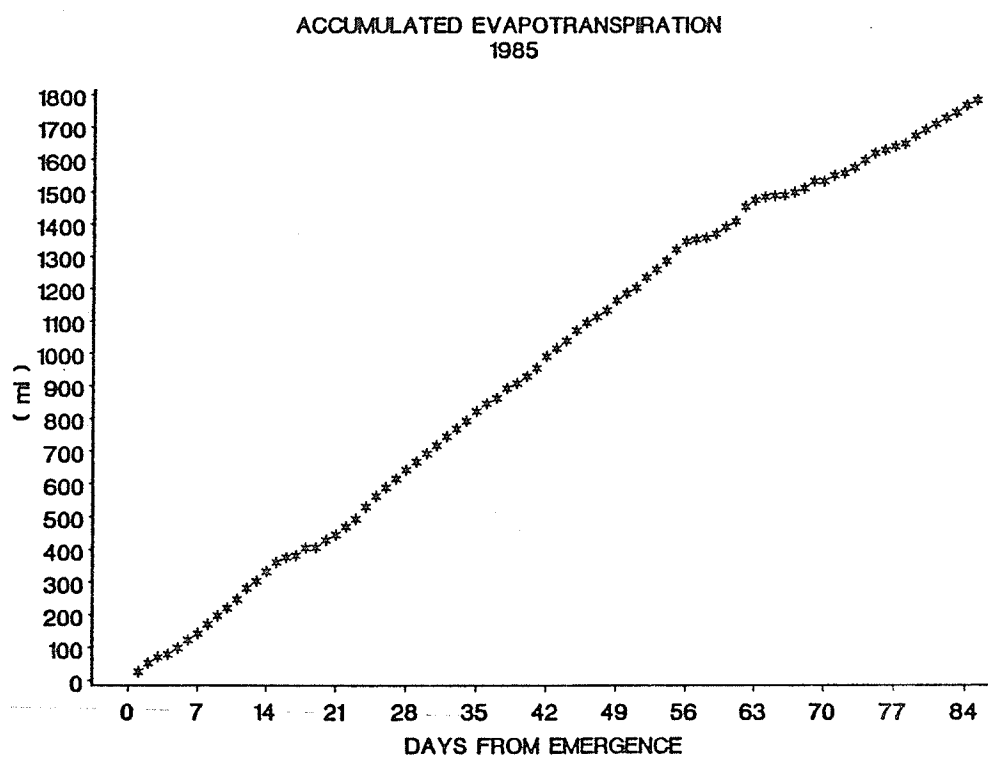


Appendix Figure 2. Moisture release curve for Almassipi very fine sandy loam.

$$y = 7.235 - 0.403x + 0.00085x^3 - (2.602 \times 10^{-5})x^5 + (2.238 \times 10^{-7})x^5$$

y = pF

x = soil water content (%)



Appendix Figure 3. Evapotranspiration from Bellani - plate atmometers in the outdoor experiment, 1985.