THE EFFECT OF SOIL MOISTURE ON THE GROWTH AND DEVELOPMENT OF GREEN FOXTAIL (*Setaria viridis* (L.) Beauv.) AND YELLOW FOXTAIL (*Setaria glauca* (L.) Beauv.)

A Thesis

Submitted to the Faculty

of

Graduate Studies

The University of Manitoba

by

Denise Cecile Maurice

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

Department of Plant Science

October 1985

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ACKNOWLEDGEMENTS

I wish to extend my sincere thanks to Dr. Ian N. Morrison for his helpful guidance and expertise which assisted during the course of research and preparation of this manuscript. I wish to express special thanks to Dr. B. Dronzek, whose encouragement and patience assisted in the completion of this project.

I would also like to thank the members of my advisory committee; Dr. G. Marshall, Dr. B. Woodbury and Dr. C. Shaykewich for their assistance and advice on the preparation of the manuscript. For financial assistance during this study, I express gratitude to the National Science and Engineering Council of Canada.

During my years of study at the University of Manitoba, I made many friends. Their understanding and constant encouragement, made the course of this project both enjoyable and memorable.

Above all, special thanks to my husband and family, for their loving support and encouragement.

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ABSTRACT

Maurice, Denise Cecile. M.Sc. The University of Manitoba, October, 1985. The Effect of Soil Moisture on the Growth and Development of Green Foxtail [Setaria viridis (L.) Beauv.] and Yellow Foxtail [Setaria glauca (L.) Beauv.]. Major Professor; I.N. Morrison.

The growth and development of green and yellow foxtail subjected to moisture stress was investigated both outdoors and in the growth room. In the outdoor study, plants were grown in a clay loam soil under four water regimes (0.3 cm water.week^{-1}; 0.6 cm water.week^{-1}; 1.2 cm water.week^{-1}; 2.5 cm water.week^{-1}) in 1980 and 1981. In the growth room plants were grown in a very fine sandy loam soil watered daily to soil moisture contents of 12%, 14% and 20% (representing soil water potentials of -2.4, -1.1, -0.3 bars, respectively). Significant reductions in growth occurred in both species subjected to moisture stress. Reductions were recorded in shoot height, leaf area, tiller number, inflorescence number and shoot dry weight. An increase in water stress resulted in a greater reduction in tiller number, leaf area and leaf number of green foxtail compared to yellow foxtail. As indicated by these growth parameters, green foxtail exhibited greater phenotypic plasticity than yellow foxtail. An increase in moisture stress resulted in reduced seed weights for yellow foxtail but no similar trends were observed for green foxtail under field conditions. The greater adaptability of green foxtail compared to yellow foxtail was further reflected in the minimal effect of water stress on leaf thickness and internal structure.

Optimum temperature for germination was 24°C for both green foxtail and yellow foxtail. Seeds collected from green and yellow foxtail plants subjected to various moisture regimes indicated the percent of germination of green foxtail seed was lower for seeds produced under the wettest moisture regime. No similar trend was observed for yellow foxtail.

INTRODUCTION

Weeds have been the subject of much research and because of their major economic impact on crop production throughout the world, weed research has been primarily directed towards discovering methods for their elimination. Weeds, however are excellent subjects for the study of adaptation (Baker, 1974). The ability of a weed to adapt to various habitats and to withstand adverse environmental conditions are major factors in determining the survival and competitiveness of a weed species (Nadeau, 1983). Hall (1981) hypothesized that characteristics which are adaptive will be present at intermediate levels, that environment and genetic background will determine the levels that are adaptive and the breadth of adaptation is dependent upon the plasticity of character response. It is for this reason that the biology and genetic makeup of green foxtail [Setaria viridis (L.) Beauv.] and yellow foxtail [Setaria glauca (L.) Beauv. Terrell, 1976] was closely examined and this followed by focusing on the effect of environmental factors on plant growth and development.

Reports by Alex and Switzer (1976) and Thomas (1981) indicate that green foxtail is more abundant and occupies a greater range of habitats than yellow foxtail. There is a need, therefore, to determine the possible mechanisms by which one species has become more abundant and widespread than the other. Moisture gradients could be a determinant factor influencing the present differences in distribution of green foxtail and yellow foxtail across the Prairie Provinces. Furthermore, plant competition among weeds and crops will differ under

various environmental conditions with water availability being one of the most important factors determining the ultimate competitive success of a species (Squire et al., 1981). Under dryland farming conditions of the Prairie Provinces, those plants that compete successfully for moisture will be the ones that will thrive.

The purpose of this study was to examine the effect of moisture deficit on the water status, growth and development of green foxtail and yellow foxtail both outdoors and under growth room conditions. Further this study was initiated to compare green foxtail and yellow foxtail in terms of their response to various moisture regimes and relate this to genetic background, and potential distribution and competitive ability.

LITERATURE REVIEW

General Ecology

Morphological Description

Green foxtail is an annual herb, culms erect to geniculate, branching at the base 10-100 cm tall. Leaf blades are 4-15 mm wide, 5-30 cm long, flat acumiate, light green nodding distinctly but finely veined with prominent midvein below, linear-lanceolate, scabrous on upper surface, scaberilous or glabrous on lower surface, margins overlapping, inner margin hyaline, outer margins ciliate; ligule a fringe of hairs 1.5-2.0 mm long fused at the base; auricles absent; inflorescence a narrow, terminal panicle, usually dense and spicate, erect or slightly nodding from the apex, 1-15 cm long, 4-14 mm in diameter, the rachis commonly pilose; spikelets borne on very short panicle branches, each spikelet subtended by 1-3 setae; the spikelet plus its associated setae known as a fascicle; the setae green or rarely purple, antrovsely scabrous, oval to ovate in outline, plano-convex, 1.8-2.7 mm long, 0.9-1.6 mm wide; each spikelet contains two florets, the lower floret sterile; the upper fertile; the rachilla is extremely reduced so that the glunes and lemmas are borne one immediately above the other; first glune one-third the length of the spikelet, triangular ovate, three nerved; second glume nearly equalling the fertile lemma elliptical, 5-6 nerved; sterile lemma slightly exceeding the fertile lemma, 5-nerved, enclosing a narrow, hyaline palea about 1/3 its own length; the fertile

lemma very pale green and very finely transversely rugose, indurate; fruit acaryopsis, 1.8-2.2 mm long, 1.0-1.3 mm wide enclosed by the lemma and palea; disarticulation below the glumes, the spikelets fall entire, the setae persistent (Douglas et al., 1985).

Yellow foxtail is an annual herb, roots fibrous, culms usually erect, mostly 20-130 cm tall, several tillers, branching at the base, sometimes geniculate below; leaf sheaths glabrous. On margins, keeled; ligule ciliate, up to 3 mm high with about 50 cilia per mm; leaf blades 4-10 mm wide, up to 30 cm long, loosely twisted, scabrous on upper surface about 80 (50 to 300) long hygoscopic hairs just above the ligule, panicles spike-like, usually 3-10 cm long; branches of the panicle less than 1 mm long, bearing one fertile spikelet with a cluster of bristles below it, bristles 3-10 mm long, yellow, orange or tawny at maturity, usually 4 to 12 below each spikelet; spikelets thick, awnless, plano convex, 3.0-3.5 mm long; glumes five-nerved, second glume covering about half the coarsely transverse - rugose fertile lemma. Seed elliptic in longitudinal section, depressed ovate in cross section, 2.5-3.3 mm long, 1.5-2.2 mm wide, 1.0-1.5 mm thick, articulating below the glumes (Steel et al., 1983).

Green foxtail is distinguished from yellow foxtail by its green or purple bristles, by the absence of long, white hairs on the upper surface of the leaf blade near the stem, and by its seed (Lee, 1979).

Geographic Distribution

The genus of Setaria comprises 125 species, many of which are of world-wide economic importance either as cultivated grains or as

noxious weeds. Records of fossilization dating back to the Oligocene epoch indicate the genus has been in existence since prehistoric times (Daubenmire, 1978).

Setaria species belong to the tribe Paniceae, which includes several species distributed throughout the temperate, subtropical and tropical regions of the world. In North America, the genus is represented by 25 native species, 10 introduced species from South America and 8 species that are adventives from the Old World.

Green foxtail and yellow foxtail were introduced to North America from Europe. Rominger (1962) reported that both foxtail species have similar distribution patterns in North America. Green foxtail is the most abundant of the two species; taking into account both frequency and density of infestation. By comparison, although yellow foxtail has the largest range of any Setaria species in the United States (Gregg, 1971), it is generally less abundant since it occurs at lower densities. Huemoeller (1967) stated that in 1965, surveyed wheat (Triticum aestivum L.) fields in the northeastern portion of South Dakota showed 78 % of the weeds present consisted of green foxtail and yellow foxtail. This estimate however, does not give any indication of the relative abundance of the two species. Later surveys in 1979 from North Dakota rank green foxtail as the most abundant weed and yellow foxtail as the fifth most prevalent weed in wheat fields (Dexter et al., 1981).

In Canada the distribution of green and yellow foxtail differs substantially. Early weed surveys indicated green foxtail was widely distributed across Canada (Groh and Frankton, 1948, 1949) but most

abundant in Western Canada (Frankton and Mulligan, 1970; Alex and Switzer, 1976) (Figure 1). Alex (1966) reported that green foxtail was present in nearly all municipal districts east and south of Edmonton, with the exception of an area in west-central Saskatchewan, north of the South Saskatchewan River. Survey results for Alberta, indicated green foxtail was rated tenth in terms of percent of fields infested (Dew, 1981). In Saskatchewan and Manitoba, green foxtail was the most abundant weed according to the latest weed survey results (Thomas and Wise, 1983; Thomas and Wise, 1984). In contrast, yellow foxtail is most widespread in coastal areas in British Columbia and east of the Great Lakes (Frankton and Mulligan, 1970) (Figure 2). However, it has been found in all provinces except Newfoundland (Scoggan, 1978). Interestingly, Manitoba is the only prairie province with known troublesome infestations of yellow foxtail (Morrison et al., 1981).

In the 1979 Manitoba weed survey, yellow foxtail was ranked fifty-second in terms of relative abundance (Thomas, 1979). Weed survey results for 1981 showed an increase in the yellow foxtail population, ranking it as the fortieth most abundant weed (Thomas and Wise, 1984). The 1981 seed drill survey further exemplified the increased incidence of yellow foxtail (Martin, 1981). Several areas in the southern portion of the province indicated detectable amounts of yellow foxtail seed present in the on-farm seed stock. Previous seed drill surveys did not list yellow foxtail as part of the weed seed component (Martin, 1965, 1976). Morrison et al. (1981) suggest that yellow foxtail's distribution is by no means static and is encroaching northward through Manitoba.

FIGURE 1. Distribution of green foxtail in Canada (Douglas et al., 1985).

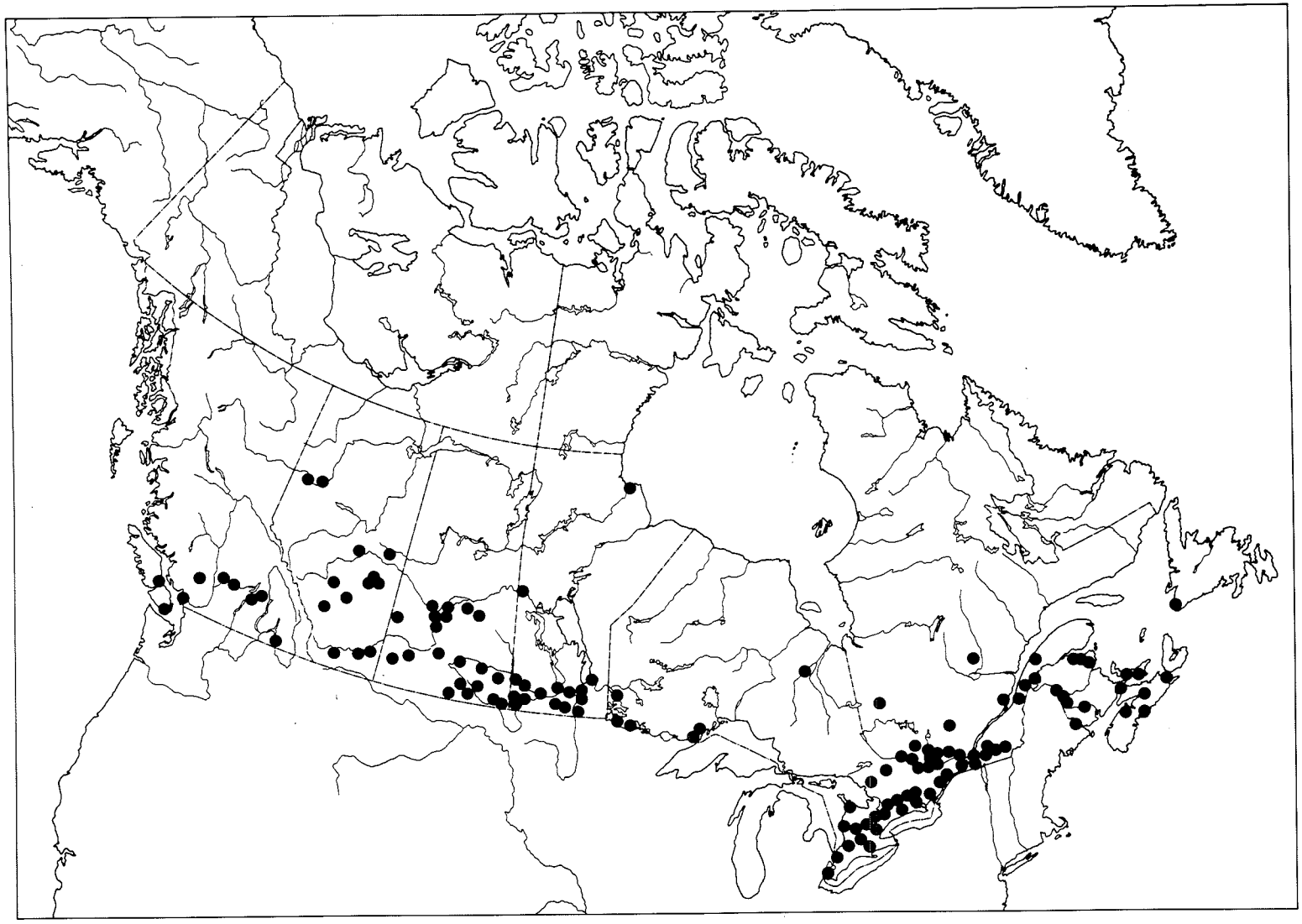
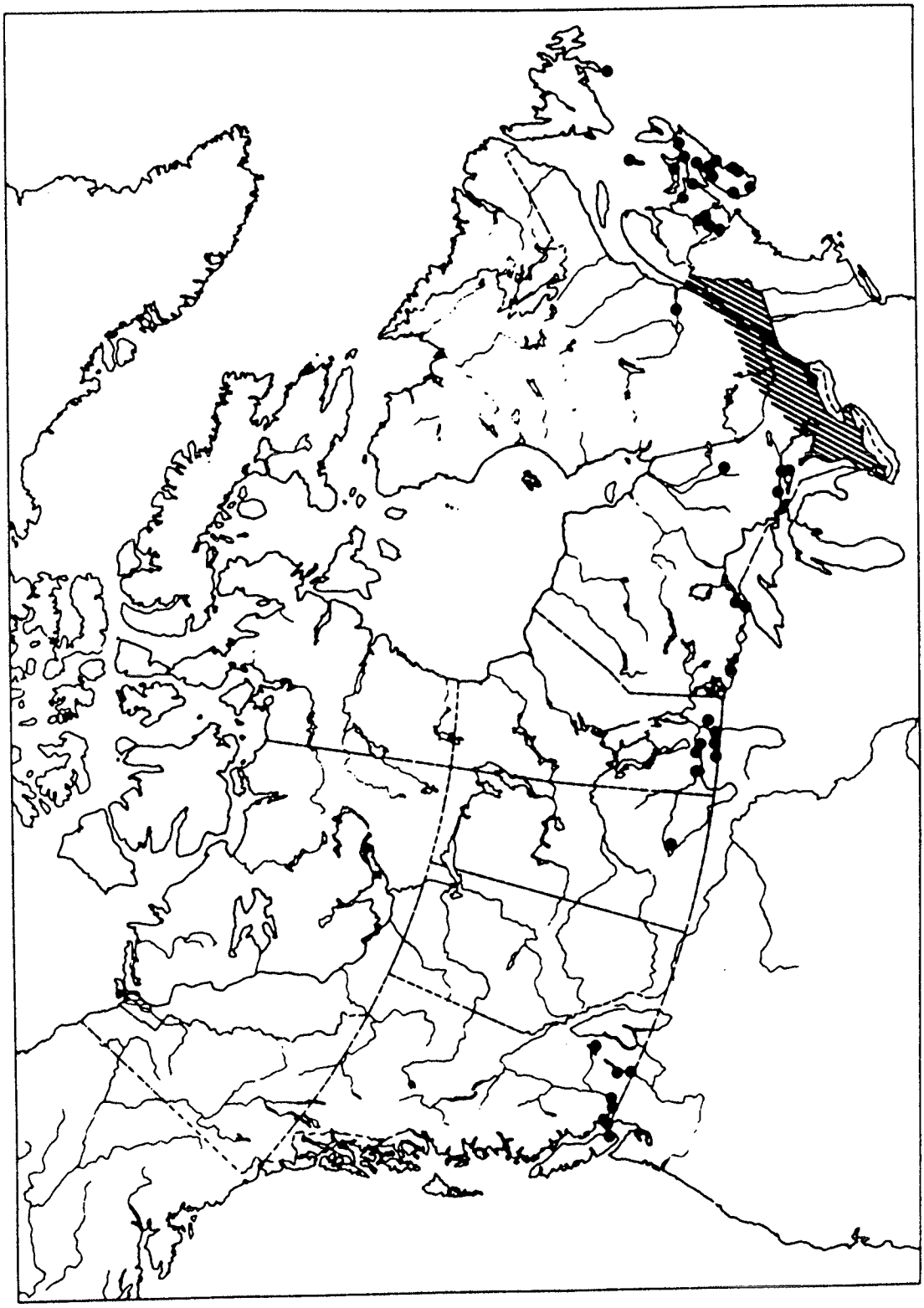


FIGURE 2. Distribution of yellow foxtail in Canada (Steel et al., 1983).



History

Green foxtail was first detected in Canada as early as 1821 and was reported to occur on the prairies in Southern Manitoba in 1883. Although these infestations were not considered to be of economic importance, it serves to illustrate the potential for green foxtail to spread rapidly (Alex et al., 1972). Dense infestations were becoming common in many of the rural areas on the Prairies by 1965. Green foxtail was found in 84% of the fields surveyed in Manitoba, compared to 32% and 28% in Saskatchewan and Alberta respectively (Alex et al., 1972). In 1972, green foxtail was recognized as a serious weed problem with nearly 28% of the total cultivated land across the Prairie Provinces being infested. More recently, estimates are that 50% to 60% of the cultivated acreage in western Canada is now infested (Morrison et al., 1981). In 1982, green foxtail was reported in the Peace River in northern Alberta. This constituted the first report of field infestations of green foxtail in these northern parts (K. Price, personal communication).

The first record of yellow foxtail in Canada was in 1821 in Quebec. This species was later detected in Eastern Ontario in 1882 and presently is the most widespread weed in oats (Avena sativa L.) and barley (Hordeum vulgaris L.) in Ontario (Steel et al., 1983).

Habitat

Green foxtail grows in a variety of locations including roadsides, waste places and cultivated fields (Frankton and Mulligan, 1970). Yellow foxtail exists in essentially the same locales but, as already stated, it is often less abundant (Lee, 1979). Yellow foxtail

attains maximal size on fertile, poorly colonized, exposed sites, where it may occur in pure patches or in mixed stands with other annual weeds (Gregg, 1971). On Oldfield Pennsylvania Piedmont, yellow foxtail was recorded as being a primary successional species possessing allelopathic characteristics (Gregg, 1971).

Schrieber (1977) investigated the competitiveness and survival of several foxtails including robust white foxtail, robust purple foxtail, giant green foxtail, giant foxtail and yellow foxtail, on undisturbed sites in Indiana to determine whether these foxtails posed a threat to cultivated land already infested with giant foxtail. Yellow foxtail was the only foxtail species that occurred in association with giant foxtail. Schrieber (1977) theorized that of the five species studied yellow foxtail was the only one to become a potential source of seed for further infestation from fence rows to cultivated fields.

To agriculturalists the occurrence of green foxtail and yellow foxtail in cultivated fields is of particular interest. Friesen and Shebeski (1960) recognized that green foxtail could significantly reduce yields of cereals. Many studies have shown conflicting results regarding the actual density of green foxtail required to cause significant wheat yield losses (Dryden and Whitehead, 1963; Alex, 1967; Rahman and Ashford, 1972; Sturko, 1978; Morrison et al., 1981; O'Sullivan et al., 1982).

For example, over a three year period Dryden and Whitehead (1963) observed that densities of green foxtail of 120-180 plants m^{-2} had little or no effect on the yield of barley or oats. Later studies

conducted in Saskatchewan also indicated that green foxtail did not affect the yield of barley (Rahman and Ashford, 1972b). By contrast, Alex (1967) examining green foxtail interference in wheat reported yield was reduced 20% by approximately 700 plants m^{-2} and 35% by 1575 plants m^{-2}. Morrison et al. (1981) also observed wheat yield reductions as a result of high green foxtail infestations. These researchers reported green foxtail populations over 500 plants/m^2 reduced wheat grain yield up to 25% compared to the weedfree plots.

Studies conducted in Manitoba indicated that the degree of competition between green foxtail and wheat varied with environmental conditions that prevailed at the time of seeding and seedling establishment (Sturko, 1978). Other researchers also contend it is the climatic conditions during germination and early plant growth that determines the competitiveness of green foxtail and not necessarily the direct effect of plant density (Rahman and Ashford, 1972; Blackshaw, 1979). The competitive ability of green foxtail when grown with corn (Zea mays L.) was reduced by high corn populations, good soil moisture conditions and an adequate supply of nitrogen (Moyer and Dryden, 1979).

These studies illustrate that the competitive effects of green foxtail is dependent upon the weed density, associated crop, the time of emergence of green foxtail relative to the crop and environmental conditions following emergence (Dryden and Whitehead, 1963; Blackshaw et al., 1981b). According to Douglas et al. (1985), the relative time of green foxtail and the crop is important but environmental conditions may override any effect due to temporal separation.

The competitive ability of yellow foxtail, by comparison, has been studied extensively in crops such as soybeans [Glycine max (L.)

Merr.], corn, sorghum [Sorghum bicolor (L.) Moench.], alfalfa (Medicago sativa L.) and wheat (Staniforth and Weber, 1956; Staniforth, 1958; Nieto and Staniforth, 1961; Staniforth, 1961; Staniforth, 1965; Huemoeller, 1967; Feltner et al., 1969; Morrison et al., 1981). Evidently, most of the research has been concentrated in the United States, where yellow foxtail has been a problem for several decades. Santelmann et al. (1963) reported that competition from yellow foxtail caused an estimated 16%, 11% and 15% yield reduction in wheat, oats and soybeans, respectively. Examining yellow foxtail's competitive ability in Chris wheat, Huemoeller (1971) observed that a foxtail density of approximately 200 plants m^{-2} reduced wheat yields by 12%. Further, Huemoeller (1971) determined that light and moisture dramatically affects the wheat-foxtail association. The author contends that under reduced moisture conditions wheat, because of its extensive root system, is a better competitor for soil moisture.

As with green foxtail, climatic conditions during the season are paramount in determining the extent of yield losses that result from various yellow foxtail population densities. Feltner et al. (1969) studied yellow foxtail competition in grain sorghum and observed that the competitive effects exerted by yellow foxtail were greatest during a year of above-average rainfall and when nitrogen fertility was high. Yellow foxtail's influence on soybean yields was also greater when above-average rainfall occurred (Staniforth and Weber, 1956; Staniforth, 1958; Weber and Staniforth, 1957; Feltner et al., 1969). In fact, the work done by Staniforth (1958) in soybeans indicates in seasons of limited moisture, yield reductions from moderate yellow

foxtail infestations were less than when moisture was normal or above (Weber and Staniforth, 1957; Staniforth, 1958).

Metabolism

Green foxtail and yellow foxtail are C_4 species (Downton, 1975). In the C_4 pathway, carbon dioxide is fixed by the enzyme PEP carboxylase to form four-carbon acids, malate or aspartate in the mesophyll cells, hence the name C_4 (Bjorkman, 1976). Aspartate and malate are then transported from the mesophyll cells into the bundle sheath cell where carbon dioxide is released to enter the Calvin cycle. The three-carbon carrier molecule returns to the mesophyll where it is converted to PEP to receive another carbon dioxide molecule. This mesophyll bundle sheath shuttle thus concentrates dioxide at the fixation site. Photosynthesis proceeds within the bundle sheath cells just as it does in the mesophyll cells of C_3 plants. It is important to note that the function of the C_4 pathway is to concentrate carbon dioxide in the bundle sheath cells thus permitting the Calvin cycle to operate at more favourable concentrations of this rate-limiting step, hence providing more efficient means of carbon dioxide fixation at low carbon dioxide levels in the intercellular spaces than does C_3 photosynthesis (Bjorkman, 1976). C_4 species are characterized by their ability to increase photosynthesis as light intensities increase, a requirement for high temperature for optimum photosynthesis and high water use efficiency. These properties led many researchers to postulate the C_4 pathway was more efficient than the Calvin cycle (Bjorkman, 1976). Black *et al.* (1969) theorized that plants with C_4

metabolism have a distinct advantage over species not possessing this pathway, further indicating it is a significant factor contributing to the competitiveness of certain weed species. Orwick and Schrieber (1975) concur that the mean extension rate of the seminal root system of the four Setaria species studied supported the hypothesis of Hackett (1973) that C_4 grasses have a mean root extension rate five to eight times higher than those of C_3 grasses. This factor may also be considered a distinct advantage when considering the competitiveness of a species.

The distributional patterns of certain plant species can also be influenced by the type of photosynthetic pathway the plant possesses. The distribution of C_4 species tends to be associated with conditions of relatively low moisture and relatively high temperature. Also C_4 species appear to be more restricted than C_3 species in the range of environments where they occur, suggesting an ecological specialized function (Doliner and Jolliffe, 1979).

Cytology and Morphological Variation

Interspecific Variation

Since growth is controlled by environmental factors interacting with genetically determined physiological and biochemical systems; species adaptability will depend upon its ability to respond to prevailing environmental conditions (Baker, 1974).

The genus Setaria exhibits extreme cytomorphological variations both at the inter and intra-specific levels (Khosla and Sharma, 1973). The basic chromosome number for the genus is n=9, or its multiples, the

ploidy level ranging from diploid to dodecaploid (Singh and Gupta, 1977). Khosla and Sharma (1973) suggest that polyploidy at various levels has played an active role in the speciation and separation into various taxa in the genus Setaria. Stebbins (1971) states trends from lower to higher level polyploid complexes are particularly useful for analyzing problems of plant geography.

Green foxtail exists at the diploid level, 2n=18. Yellow foxtail, by comparison, is known to exist at various ploidy levels, 2n=36, 2n=72 (Rominger, 1962). Later studies indicate another chromosomal race of yellow foxtail with n=44 (Khosla and Sharma, 1973; Singh and Gupta, 1977). Aneuploidy is also encountered in yellow foxtail, the only foxtail showing polymorphism in chromosome numbers (Khosla and Sharma, 1973). Mulligan (1960) investigated the frequency of polyploids in the weed population of Canada and reported that the chromosome number of green foxtail was 2n=18, as previously reported. Yellow foxtail was reported to have a chromosomal makeup of 2n=36, a tetraploid.

Li et al. (1945) suggested green foxtail was the ancestral stock of the genus Setaria from which several specific entities developed. Rominger (1962) also proposed green foxtail as the ancestral origin for the Old World Setaria. These researchers postulated that the tetraploid form of yellow foxtail originated from ancient crosses of green foxtail with an unknown diploid species.

Khosla and Sharma (1973) have confirmed that green foxtail is the ancestral stock from which present day members of the genus evolved. These researchers report that various processes like gene

mutation, repatterning of chromosomes, hybridization, and polyploidy played a major role in development of the genus as it exists today.

Williams and Schreiber (1976) compared the morphological characteristics, plant height, panicle length, first leaf width and first internode length of green foxtail, yellow foxtail, giant foxtail (Setaria faberi Herrm.) giant green foxtail [Setaria viridis var. major (Gaud.) Posp.], robust white foxtail (Setaria viridis var. robusta-alba Schreiber) robust purple foxtail (Setaria viridis var. robusta-purpurea Schreiber), bristly foxtail [Setaria verticillata (L.) Beauv.] and foxtail millet [Setaria italica (L.) Beauv.]. These researchers reported that yellow foxtail was the least similar of the seven species to green foxtail. These findings reinforce Rominger's view on the phylogeny of the Setaria viridis complex and it's allies, indicating the distal position of yellow foxtail from other members. These studies convincingly illustrate the basic genetic difference between these two Setaria species. This difference in ploidy level could influence the response of green foxtail and yellow foxtail to various environmental conditions (Williams and Schreiber, 1976).

Morphological and physiological effects of polyploidy have long been known (Stebbins, 1971). The most universal effect is an increase in cell size. This increase in cell size may be reflected in larger vacuoles; hence, a higher water content of the plant as a whole and a consequent reduction in its degree of resistance to drought and cold (Stebbins, 1971). Stebbins (1971) also states that as the ploidy level increases the leaves are generally thicker and the amount of branching is usually reduced particularly in tillering polyploidy grasses. In

addition, flowering and fruiting in polyploids is later compared to their diploid ancestors. These characteristics have been observed between green foxtail and yellow foxtail (Bubar, 1981; Nadeau, 1983). Green foxtail has been shown to have a greater number of tillers per plant than yellow foxtail (Bubar, 1981) and green foxtail was observed to start heading earlier than yellow foxtail (Nadeau, 1983). Field observations indicate the leaves of yellow foxtail are more succulent than green foxtail.

The influence that ploidy level has on plant distribution has also been explored. Stebbins (1971) proposed a general hypothesis, maintaining that polyploids in their initial stage depend upon especially favorable combination of circumstances for their survival and perpetuation. However, once established the polyploid species are more competitive and aggressive than related diploids. This may suggest that polyploids, like yellow foxtail, are able to adapt to very specific environmental conditions. In studies on the colonization of plants on disturbed sites in Canada, Mulligan (1960) found no evidence to suggest that polyploid weeds are particularly favored for the colonization of newly available sites. However there was evidence to indicate polyploid weeds, rather than diploid weeds, are better adapted to specialized habitats. In studying succession on old fields of Pennsylvania Piedmont, Gregg (1971) found yellow foxtail was one of the early establishing species, illustrating that this species has the ability to establish itself readily on disturbed sites.

Intraspecific Variation

Wide variation in morphology and development has also been recognized within species of Setaria (Schoner et al., 1978). Intraspecific variation in the morphology of green foxtail have been reported. Pohl (1951) observed that in stands of green foxtail there existed tall, vigorous, broadleaved forms with large panicles. Fairbrother (1959) also reported great variability in wild populations of green foxtail, with certain morphological characteristics such as width and length of blades, color of bristles on spikelets and leaf blades all showing high variability. Early studies by Hubbard (1915) suggested that many varieties of Setaria viridis exist. Two specimens of Setaria found in Indiana in 1961 did not fit any of the earlier taxa within the Setaria viridis complex (Schreiber and Oliver, 1971). After extensive study, these plants were given independent status as varieties of green foxtail. The two varieties of foxtail were robust white foxtail, and robust purple foxtail. They differ from one another in the color of their bristles and differ from green foxtail in their robust growth habit.

After examining green foxtail across the Prairie Provinces, Alex et al. (1972) postulated that green foxtail consisted of several ecotypes some of which were better adapted for growth on fine textured soils. The author suggested this could account for the different distributional patterns across Western Prairie Provinces. Chow (1972) also observed some differences in competitive ability as well as growth habits of green foxtail collected from different locations.

Santelmann and Meade (1961) demonstrated that morphological differences exist between yellow foxtail biotypes collected from different sites in Maryland. Schoner et al. (1978) examined yellow foxtail biotypes from several locations through eastern United States and California under uniform conditions in California. Significant variations in days from planting to heading, numbers of nodes per culm, leaf shape and size, and in final dry weight per plant were noted. Of particular interest were the distinct differences in growth habit; the California biotype exhibited a prostrate growth habit whereas the biotype from the eastern United States all had an upright habit. Schoner et al. (1978) states that a biotype adapted to California cultural conditions may have been selected over a period of several years.

Bubar (1981) compared two Manitoba yellow foxtail biotypes and an Ontario biotype and found no major differences in growth and development at the end of the season. Differences in growth early in the season were attributed to the later emergence and slower development of the Ontario biotype. The Ontario biotype was also slower in commencing heading and later to mature. Compared to the Manitoba biotypes, the Ontario biotype was somewhat more prostrate. Other studies show a wide variation in growth habit between selections of yellow foxtail collected from different sites in Maryland and Connecticut (Santelmann and Meade, 1961, Peters et al., 1963). Norris and Schoner (1980) also investigated yellow foxtail biotypes. A distinct difference in the time required for after-ripening of seed and stratification requirements between the biotypes was evident. Furthermore, these variations in germination requirements were considered to be genetically controlled physiological differences between geographically separate biotypes.

Both green foxtail and yellow foxtail display a considerable amount of variability. The dynamic nature of the variability of green foxtail and yellow foxtail shows the ability of both these species to adapt to varied environmental and cultural conditions. It may be this variability that enhances the species potential to invade new territories.

Not only does the variability of the species influence distribution, but the nature of the reproductive system may also have an impact. Several polyploid complexes are characterized by apomixis which is defined broadly as the replacement of sexual by asexual reproduction (Stebbins, 1971). The genus Setaria is characterized by this mode of reproduction (Singh and Gupta, 1977; Stebbins, 1971). This is a situation "par excellence" since populations tend to be genetically uniform (Harper, 1977) but leaves little opportunity for introduction of new genes. On a local scale, a single apomictic race might be expected to have shown its superiority over others races and the populations would be genetically monotonous. Natural populations that have been studied are found to contain an assortment of apomictic races, the mix varying from site to site (Harper, 1977). Plant populations characterized by apomoxis are found in temporary habitats and the plants tend to have efficient methods of seed dispersal. A single seed dispersed into a new locality may in one or two generations give rise to a large population (Stebbins, 1950). This constancy provided by apomixis may have a positive selective value in a rapidly expanding population.

Although the genus Setaria is characterized by this apomictic mode of reproduction little information is known about the extent of this type of reproduction and whether it varies from species to species. One species may be highly apomictic in nature while a closely related species may have little asexual reproduction (Solbrig and Simpson, 1974).

Response to Environmental Factors

The environment that surrounds a plant has a profound effect on its growth and development. A better understanding of the effects of various environmental conditions could assist in predicting whether a weed could prove to be a problem under specific climatic conditions.

Mukula et al. (1969) surveyed 2,710 fields in Finland and found soil type, temperature, water conditions and preceding crop were influencing factors on the distribution of several weed species in agricultural land. According to Blackman and Templeman (1938), cereals and annual weeds primarily compete for nitrogen and light. Therefore, environmental factors not only influence the distribution of various weed species but also the nature of the crop-weed balance.

Soil Fertility

Studies on the relationship between weed infestation, fertility and yield indicate weeds compete for essential nutrients and decrease crop yields even at high rates of fertilization (Zimdal, 1980). Nakoneshny and Friesen (1961) showed that increases in wheat yields resulted from fertilizer treatments, but these yield increases were approximately equal to the increases resulting from weed removal.

However, investigations by Blackman and Templeman (1938) led them to believe that high rates of nitrogen fertilizer was an economical means of suppressing moderate weed populations and the ability to compete for nutrients can account for an important part of a weed species success.

Hume (1982) investigated the effect of fertilizer applications and three crop rotations (continuous wheat, wheat-fallow, and wheat-wheat-fallow) on the weed species composition over a 22 year period. After spring seeding, green foxtail was the only species that had an increase in density in fertilized plots. Alex (1967) and later Moyer and Dryden (1976), reported that green foxtail competed well with wheat for soil nitrogen. Moyer and Dryden (1976) determined that green foxtail growing in the wheat crop lowered the nitrogen content of the grain. Sturko (1978) stated that high rates of nitrogen may enhance green foxtail's vegetative growth, causing the weed to be more competitive. By comparison, yellow foxtail was found to be competitive with wheat at low soil nitrogen levels (Huemoeller, 1967).

Bubar (1981) studied the response of green foxtail and yellow foxtail to applied nitrogen under growthroom conditions and reported that at low levels of nitrogen (50 and 100 ppm in 4000 gms of soil), yellow foxtail had a higher nitrogen use efficiency than green foxtail, in terms of shoot dry matter production per unit of applied nitrogen. Similarly, Schreiber and Orwick (1978) reported that yellow foxtail produced equal amounts of shoot dry matter at "normal" and "below normal" nitrogen fertility levels. These two studies substantiate yellow foxtail's efficiency under low nitrogen status. In addition, Bubar (1981) states that green foxtail is better able to utilize

additional increments of nitrogen at higher levels in the production of shoot dry matter. This may imply that these two foxtail species will not always occupy the same ecological niche. Yellow foxtail should be able to survive and reproduce efficiently when the available nutrients are low due to depletion by crop competition. Green foxtail conversely, requires higher levels of nitrogen to maximize it's growth potential (Bubar, 1981).

Light

Light constitutes a key external environmental variable of the photosynthetic process. Reduced light intensity during plant growth induces both morphological and physiological changes in plants. In general, plants respond to reduced light intensities by producing etiolated stems and leaves that are thinner with a less-developed internal structure and larger chloroplasts (Boardman, 1977).

The degree to which a plant species responds to the reduced light intensity is related to its metabolism. As previously mentioned both green foxtail and yellow foxtail are C_4 plants and well adapted for growth under conditions of high light intensity and high temperature. Lee (1979) surveyed the distribution of three Setaria species, bristly foxtail, green foxtail and yellow foxtail, in the vicinity of London, Ontario. Of the number of green foxtail infestations examined, 55% were growing in full sunlight. The corresponding figures for yellow foxtail and bristly foxtail were 50% and 85%, respectively. Lee (1979) concluded that all three species show a similar affinity for habitats with high light intensities. Interestingly, green foxtail and

yellow foxtail are primarily a problem in crop stands where light intensity may be reduced by as much as 88% by the end of the season (Bubar, 1981).

Some effects of reduced light intensity on foxtail development are known. In a greenhouse study utilizing parallel lathes to achieve 60 and 90% shade, Santelmann et al. (1963) reported that shading of yellow foxtail and giant foxtail plants decreased plant height, number of tillers and dry weight of both species. Knake (1972) investigated the effect of shade on giant foxtail under field conditions using shade intensities of 0, 30, 60, 70, 80 and 90%. Seed weight, total dry weight, number of stems and number of heads per plant decreased linearly with increasing shade. Height of the main culm was affected less than any other morphological characteristic. Unlike Santelmann et al. (1963), Knake (1972) reported that yellow foxtail plants under 30 and 60% shade were equal in height to those grown under zero shade. The length of the eighth and ninth internodes of the shaded plant were longer than those of unshaded plants.

Vanden Born (1971) studied the effects of light intensity on growth and development of green foxtail under growthroom conditions. Dry matter was directly proportional to light intensity, with both vegetative and reproductive development being substantially reduced. Reproductive growth was influenced more seriously by light intensity than was vegetative growth. The severely restricted growth of green foxtail under low light intensity was considered to partially account for the "weaker" competitive ability of green foxtail in field crops in Canada (Vanden Born, 1971).

Lee and Cavers (1981) reported that the green foxtail, yellow foxtail and bristly foxtail demonstrated morphological adaptations in response to shade. Yellow foxtail was the only species to show a significant increase in stem elongation with increasing shade. Investigating green foxtail and yellow foxtail's response to shade in the field under 0, 55, 73% shade and in-crop, Bubar (1981) also found yellow foxtail showed a significant increase in height as a result of increased shade. Green foxtail exhibited a relative increase in resource allocation to leaves with reduced light intensity while yellow foxtail had a relative increase in stem material (Lee, 1979). Lee and Cavers (1981) suggest this indicates different strategies in response to shade. Generally, weeds which are taller and produce higher yields of foliage material tend to be better competitors (Vengris and Damon, 1976).

Plant/Water Relations

Studies directed towards characterizing the effects of water stress on weed competition are important to dryland farming areas, such as the Prairie Provinces, where water availability may limit crop productivity. Weed competition may affect the water relations of the crop, as weeds compete for available nutrients, light and soil moisture. Several studies indicate species and varieties develop different degrees of water stress under similar conditions of soil water and evaporative demand (Blum, 1974; Peake et al., 1975). For example, Sullivan and Easton (1974) and Singh et al. (1973b) have shown that varietal differences exist in the tolerance of sorghum and barley to

severe moisture deficits. According to Hsiao et al. (1974), plant response to water deficits is multifaceted and encompasses physiological, developmental and morphological parameters. The concerted effect of these diverse plant phenomena, enable a species to function under water-limiting environments.

In this section of the review, attention is directed to the effects of moisture stress on plant growth and development. Since very few studies have considered the effect of water stress on growth of green foxtail and yellow foxtail, this review will concentrate on water stress effects on grass species, particularly sorghum. Orwick et al. (1978) developed a Setaria Simulation Model and observed that leaf water potential responses of robust white foxtail and robust purple foxtail were closely related to the C_4 species, sorghum. Hence the authors contend that the response of sorghum and these foxtails species to soil water deficits would be very similar.

Morphological Effects. The development of water deficits in plants leads to a wide range of morphological responses. According to Passioura (1976) under field conditions the control of leaf area and morphology is the most effective means a mesophytic plant has for influencing its fate to long-term moisture stress. Hence, one of the most discernible effects of water deficit on plant growth and development is it's effect on leaf development. Both leaf expansion and senescence are known to be very sensitive to water deficits and is ultimately manifested in a marked reduction in leaf area (Turner and Begg, 1981). Hsiao (1973) stated that in many species cell expansion

is one of the plant processes most sensitive to water stress. Boyer's (1968, 1970) experiments with corn, soybean and sunflower (Helianthus annuus L.) illustrated that leaf enlargement was strongly inhibited when leaf water potentials dropped below -4 bars. Later studies by McCree and Davies (1974) drew attention to the sensitivity of cell division to water stress. McCree and Davies (1974) reported that the leaf area of sorghum was reduced by approximately 60% when the plants were grown under hot dry conditions with periodic soil moisture deficits compared to when they were grown under warm, humid conditions and soil moisture maintained at field capacity. This reduction in leaf area was attributed solely to the decrease in the number of epidermal cells per leaf. More recently, Prasad et al. (1982) investigated the effect of water stress on growth and metabolism of wheat and determined that both cell division and cell elongation were decreased with the induction of water stress. Regardless of whether cell expansion or cell division is the more sensitive to water stress, these studies strongly indicate that leaf area is greatly affected by water availability.

Reduction of leaf expansion can provide an effective mechanism for reducing water loss. Similarly, leaf shedding or the accelerated senescence of the physiologically older leaves also provides a means for reducing water loss (Ludlow, 1975). For example, Fischer and Kohn (1966) observed that drought induced reductions in wheat grain yields were inversely related to the rate of leaf senescence after flowering. Stout and Simpson (1978) observed that leaf senescence of two cultivars of sorghum resulted in a large decrease in the leaf area of nonirrigated plants compared to irrigated plants. The two sorghum cultivars had an average of 65% loss in leaf material through senescence.

Water deficits have also been shown to reduce tillering in barley, sorghum, green foxtail and wild oats (Aspinall et al., 1964; Blum, 1973; Nadeau, 1983; Akey and Morrison, 1984). Generally, water deficits have been shown to reduce tillering or branching, the degree depends on the timing, duration and magnitude of the stress. As an adaptive strategy these reductions in tillering reduce the leaf area therefore effectively decreasing evapotranspiration by the plant (Turner and Begg, 1981).

Aspinall et al. (1964) reported that short periods of stress during which the soil water content was reduced from field capacity to the permanent wilting point, reduced barley tiller formation. The effect on tiller formation was independent of the time the stress was initiated i.e. during vegetative growth, at early flowering, at anthesis or during grain swelling. However, the most dramatic effects occurred at anthesis and during grain swelling. Other species show similar responses. Moderate and severe moisture stress at the tiller initiation stage significantly reduced the number of tillers produced in wheat and oats (Joffe and Small, 1964). Later studies by Connor (1975) on wheat indicated early stress tends to reduce tillering and spikelet numbers; while later stresses cause floret abortion and restricts the development of the grain. Akey and Morrison (1984) investigated the growth of wild oats (Avena fatua L.) under different moisture regimes in the field and in the growth chamber. For the most part, wild oat tiller formation responded similarly under both environmental conditions. For example, in the growth chamber, under the lowest moisture regime where the soil moisture content was held at

10% (-6.5 bars) for the duration of the experiment, the number of viable tillers per plant was reduced by as much as 38%.

Blum (1973) studied 21 agronomically adapted, high-performance sorghum hybrids under dryland and irrigated conditions in the field. Dryland plots represented the stored soil moisture from winter rainfall, while irrigated plots represented irrigation to maintain soil moisture above 50% of field capacity. Mild water stress experienced under dryland conditions significantly decreased tillering in all sorghum hybrids. In fact, those hybrids most susceptible to reduce moisture conditions performed better under irrigated conditions, and attained a yield advantage over the more tolerant hybrids, through increased tillering.

Studying green foxtail and yellow foxtail response to different soil moisture regimes under controlled conditions, Nadeau (1983) reported that of the two Setaria species, green foxtail had a greater reduction in tiller number. Water regimes, however, did not significantly affect the tiller formation until the fifth week after emergence. Rewatering to field capacity occurred after the various soil water contents reached the designated limit of -21.9 bars, -2.4 bars and -0.6 bars. This rewatering may have affected the tillering response. These results concur with Joffe and Small's (1964) studies with wheat and oats which illustrated an increase in tillering after rewatering. These researchers found that the final number of tillers were not significantly different between stress/rewatered plants and the well-watered control plants. Aspinall _et al._ (1964) findings with barley also drew attention to tiller formation of stressed plants which

were rewatered. Tillering, although suppressed during a drought cycle, was stimulated upon rewatering. Interestingly, the authors of both studies indicate that this enhanced tillering after rewatering may be related to mineral nutrition or the interaction of mineral nutrition and water stress.

Another strategy for reducing water loss by reducing evaporative surfaces, is to minimize the interception of solar radiation through changes in leaf angle. Leaves which are more parallel to the sun's rays are cooler since they intercept less solar radiation and have correspondingly lower rates of transpiration and photosynthesis (Hall et al., 1979). Rolling or folding of the leaf lamina greatly reduces the leaf area by creating a more vertical orientation (Turner and Begg, 1981). In grasses, leaf rolling is a common response to stress and may reduce transpiration by 50 to 70% (Oppenheimer, 1960 cited in Begg, 1980).

Merrill and Rawlins (1979) observed considerable leaf rolling and color change of sorghum leaves correlated with a significant decrease in leaf water potential. A study on the diurnal rolling of sorghum leaves revealed that this species is very sensitive to both onset and recovery from water stress (Begg, 1980). Thus, leaf rolling as an adaptive mechanism is unique in two ways. Firstly, it enables the plant to respond rapidly to periods of high evaporative demand, and secondly, unlike other morphological responses, it is reversible (Begg, 1980).

It is well established that the layer of epicuticular wax on the leaf surface of plants reduces cuticular permeability and assists

in protecting plants from excess water loss through transpiration (Chatterton et al., 1975; Ebercon et al., 1977; Turner and Begg, 1981). According to Ebercon et al. (1977), epicuticular wax formation is an effective component of drought resistance in sorghum. Similarly, Fischer and Wood (1979) concluded that the best morphophysological trait for predicting yields of spring wheat cultivars under drought conditions was given by a linear model containing total dry weight, kernel weight and leaf waxiness. Results from field experiments indicated that leaf waxiness readings taken 20 days after anthesis were a useful means of assessing drought tolerance of various wheat cultivars.

Svenningsson and Liljenberg (1982) did not find a significant difference in the amount of epicuticular wax formation between moisture stressed and non-stressed oat seedlings. In contrast, Akey (1982) reported that leaves of wild oats subjected to water stress under field conditions produced approximately 60% more epicuticular wax by heading than the leaves of wild oat plants grown under well-watered conditions.

Little is known about the effect of moisture stress on the chemical composition of epicuticular waxes. Tulloch (1980) studied 34 species of Gramineae, including green foxtail, and observed that only in one species did epicuticular wax composition changed with a change in growing conditions. A later study indicated that dryness of habitat was not necessarily associatd with greater wax content (Tulloch, 1981). Oat seedlings, subjected to short-term water stress under controlled environmental conditions, showed a shift in the components of epicuticular wax (Svenningsson and Liljenberg, 1982).

Numerous publications document total shoot growth reductions under water deficit conditions (Aspinall et al., 1964; Joffe and Small, 1964; Blum, 1973; Fischer and Wood, 1979). By comparison, there have been fewer studies in which the effect of reduced moisture on the development of root system has been studied, and even fewer that illustrated the effect of water supply on the integrated relationship of the shoot and root growth. The growth and distribution of the root system of a number of plant species, including wheat (Hurd, 1968; Connor, 1975), barley (Salim et al., 1965; Irvine et al., 1980), corn (Taylor and Klepper, 1973), and sorghum (Teare et al., 1973; Hsiao et al., 1976; Merrill and Rawlins, 1979) have been investigated under various moisture regimes. These studies concentrate on intraspecific and interspecific differences as they relate to rooting density, distribution and species performance under limited soil moisture.

Hsiao et al. (1976), compared the rooting system of both corn and sorghum to elucidate key features which could account for their differing drought tolerance. At the early seedling stage, root density was greater for sorghum, and the ratio of secondary to primary roots was twice as great for sorghum as compared to corn. Nevertheless these researchers stated that the differences were minor and insufficient to explain the differing yield behavior under limited water supply. Hurd (1968, 1974) compared various wheat varieties and observed an increase in root dry matter and deep soil penetration of the root system of the more drought tolerant varieties. Jordan and Miller (1980) determined that the sorghum varieties regarded as possessing the highest level of drought tolerance, had consistently higher root weights, greater root

volumes and lower shoot:root ratios under non-stressed conditions compared to other sorghum varieties. These parameters showed the same trends under moisture stress conditions. In addition, the roots of the tolerant strains penetrated an average of 15 cm deeper than the less-tolerant strains.

Nadeau and Morrison (1983) investigated the root development of green foxtail and yellow foxtail subjected to several soil moisture regimes under controlled environmental conditions. These researchers observed a significant increase in length of the seminal root of green foxtail under the driest moisture regime. Yellow foxtail showed a similar trend however, it was not as pronounced. The author concluded that the relatively greater increase in the seminal root length of green foxtail under the drier conditions compared to yellow foxtail was indicative of the higher degree of plasticity of green foxtail. Further Nadeau and Morrison (1983) examined the adventitious root development of these Setaria species and observed that the initiation of adventitious root was at first strongly affected by the water regimes. However, no significant differences in root numbers occurred between species or water regimes, 4 and 5 weeks after emergence. Water availability resulted in marked difference in the relative proportion of seminal and adventitious root oysters of green and yellow foxtail. Under the driest regime, 4 weeks after emergence, 55% and 68% of the total root length of green foxtail and yellow foxtail respectively were comprised of seminal roots. By comparison, only 5% of green foxtail and 14% of yellow foxtail total root length was comprised of seminal roots, under the wettest conditions.

The relative success of a species or biotype may be influenced by the allocation of fixed carbon to various portions of the plant (Stebbins, 1950). Abrahamson and Gadgil (1973) suggest the pattern of allocation, often referred to as resource allocation, will depend on the nature of the limiting factor. For example, if water is the limiting factor a larger fraction of the biomass could be in the form of roots. Increases in root:shoot ratio, sometimes coupled with enhancement of the absolute size of the root system, have been regarded as an adaptative response to drought (Passioura, 1981). Such increases have not always been observed and may depend on species, stage of growth, nutrient availability and soil physical structure. Gales (1979) reviewed several papers on the effect of drought stress on root:shoot ratios in different species. The general trend was toward an increase in the root:shoot ratio with increasing moisture stress. However, some studies showed lower or unchanged root:shoot ratios with induced drought. The author contends that the conflicting values for root:shoot ratios of a given species could be ascribed to differences in growth stage and nutrient availability. Further, it may simply reflect the variability between the methods of instilling moisture stress in each of the various studies. Merrill and Rawlins (1979) investigated the distribution and growth of sorghum roots in response to irrigation frequency, and observed that the root:shoot ratio tended to increase with less frequent irrigation.

Bubar (1981) reported that green foxtail had a greater shoot:root ratio than yellow foxtail at all sampling dates when grown in sand:soil:perlite mixture under greenhouse conditions. For example,

at the 4 to 5 leaf stage under adequate moisture conditions, green foxtail had an average ratio of 2.75, while yellow foxtail had an average ratio of 1.76. At heading the shoot:root ratios increased, green foxtail had an average ratio of 9.47; by comparison, yellow foxtail had an average ratio of 2.37 (Bubar, 1981). Huemoeller (1967) examined yellow foxtail grown under greenhouse conditions in clay soil and observed that 8 weeks after planting yellow foxtail had an average shoot:root ration of 3.75. In Huemoeller's (1967) experiments soil moisture was maintained at field capacity throughout the entire experimental period.

Examining the effect of different soil moisture regimes on the root system of green foxtail and yellow foxtail, Nadeau and Morrison (1983) observed a significant difference in the shoot:root ratios of the two Setaria species by the final sampling date. For example, 6 weeks after emergence, the shoot:root ratio ranged from 3.3 to 3.7 for green foxtail and 2.4 to 2.5 for yellow foxtail. When the shoot:root ratios of green and yellow foxtail were compared under the water regimes; namely reducing soil water potentials to -21.9 bars, -2.4 bars, and -0.6 bars then rewatering to field capacity once these water potentials were reached, no significant difference occurred in shoot:root ratios between the various moisture regimes for either species.

In a review of the growth and function of the root in relation to the shoot, Troughton (1974) clearly stated that shoot:root ratios may be misleading, particularly when comparing plants which differ in size. For example, a treatment which changes the rate of growth may

appear to change the ratio, compared to a control plant, however it may be the "normal" ratio for a plant of that particular size (Gales, 1979). Kummerov (1980) also concluded that no clue regarding the adaptation of plants to an arid environment can be obtained from observations of shoot:root or root:shoot ratios.

Reproductive Output. The long-term outcome of competition depends on the ultimate reproductive output of the competing species (Stebbins, 1950). The success of a species in a stressful habitat is determined by its reproduction and propagation. As Salibury (1942) clearly states the reproductive capacity and seed characteristics of a species are broadly correlated with its ecological status. An expression for reproductive allocation primarily used by plant breeders is harvest index (grain yield/total dry matter at maturity). Stress during seed filling will reduce the harvest index as a result of reduced assimilate production (Fischer, 1980). For example, the harvest index of semi-dwarf and normal-stature barley was decreased with increasing moisture stress maintained throughout the season (Irvine et al., 1980). Davidson and Campbell (1984) investigated the growth rate, harvest index and moisture use of Manitou spring wheat as influenced by nitrogen, temperature and moisture. These authors reported that moisture stress was the most important factor influencing the proportion of plant weight that was harvested as grain (harvest index).

It is evident that moisture stress can have an effect on yield. The specific nature of the yield response was investigated by several researchers (Aspinall et al. 1964; Blum, 1973; Connor, 1975; Irvine et

al., 1980; Davidson and Campbell, 1984). Drought stress reduces grain yield through its effect on individual components, with the different components being affected according to timing and magnitude of stress (Aspinall et al., 1964). Grain yield of grasses is a product of two components; the number of inflorescence per plant and the weight of the inflorescence. The inforescence weight can be broken down into its components, grain number and grain weight. The influence of the number of inflorescences per plant is directly related to the number of tillers produced. The effect of water stress on tillering has been discussed previously. Blum (1974) determined that water stress increased the number of sorghum grains per panicle and per branch; whereas, with barley, water stress reduced the number of grains per spike (Irvine et al., 1980). In field studies, Irvine et al. (1980) observed that 1,000-kernel weight was significantly different for semi-dwarf and normal-statured barley genotypes grown under differing levels of moisture stress. In Nadeau's (1983) studies with green foxtail and yellow foxtail, green foxtail seed production (as represented by seed number) was less affected by different water regimes than seed production of yellow foxtail. In his review of the influence of water stress on crop yield, Fischer (1980) stated that the greatest effects of water stress on grain yield are usually associated with reductions in seed number. Sensitivity of seed number to water stress tends to ensure consistency of seed size by restricting seed number (Stebbins, 1974). Harper (1977) contends evolution has favored homeostasis of seed size within most species due to the vital role the seed plays in maintaining continuity between generations.

Seed Dormancy. In spite of the extensive research on seed physiology, relatively few publication have dealt with the influence of water stress during seed maturation on seed dormancy. Seed dormancy can be innate, induced or enforced. Of these types, innate dormancy is most affected by growth conditions under which the seed matures on the parent plant, since it develops while the seed is still attached to the parent plant (Roberts and Smith, 1977).

Temperature and moisture conditions during seed development have been shown to affect the expression of dormancy. Early studies by Sexsmith (1969) details the effect of temperature and water deficits on seed dormancy of wild oats. Warm temperatures and water stress during wild oat seed development gave rise to less dormant seed. Sawhney and Naylor (1979, 1980) found that temperatures experienced by maternal plants of wild oats during seed development strongly influenced the expression of seed dormancy in dormant lines. Later studies by these investigators indicated that seeds produced by water stressed plants exhibited a shorter duration of primary dormancy. The magnitude of the effect varied among some of the dormant wild oat lines, but was consistently greater compared to the non-dormant lines. Sawhney and Naylor (1982) contended that expression of allelles conferring long-term dormancy depends on adequate soil moisture levels during seed maturation. Peters (1982) also studied the dormancy of wild oat seed from parent plants grown under various soil moisture conditions and similar results were found. He found hot dry conditions during seed maturation resulted in less-dormant seed than seed produced under cool moist conditions.

Several researchers have characterized some degree of dormancy in yellow foxtail (Peters and Yokum, 1961; Nieto-Hatem, 1963; Kollman, 1970; Rost, 1972, 1975). There is general agreement in the literature that freshly harvested seeds of yellow foxtail to germinate under optimal conditions of temperature and moisture. Innate dormancy present in the seed is disrupted by extended exposure to low soil temperatures during winter (Norris and Schoner, 1980) and most yellow foxtail seed dispersed in the fall, germinates the following spring (Stoller and Wax, 1974; Dawson and Bruns, 1975). Stratification experiments indicate that exposure of imbibed seed to temperatures of 5 to 10°C for 10 to 16 weeks is sufficient to overcome innate dormancy in 80 to 90% of the seed (Norris and Schoner, 1980). The expression of innate dormancy in the remaining 10 to 20% of the seed population after stratification is not well understood. Several studies attribute this persistent innate dormancy to the hulls of the yellow foxtail seed (Nieto- Hatem, 1963; Kollman, 1970; Rost, 1975). Schreiber (1977) found that of all the foxtail species he examined, only giant foxtail and yellow foxtail showed any seed dormancy. Studies of five yellow foxtail biotypes collected from Connecticut, Iowa, Massachusetts, Pennsylvania, and California and grown under California conditions, indicated substantial differences in seed dormany and germination requirements, leading the authors to speculate that the wide variation in seed dormancy may be due to genetically controlled variations between previously unrecognized biotypes.

Unlike yellow foxtail, green foxtail has not been known to show any innate dormancy once the seeds have been stratified. Primary

dormancy present in the seed at harvest time disappears rapidly (Banting et al. 1973). Vanden Born (1971) reported variations in dormancy of green foxtail seed at harvest and attributed the differences to variations in the conditions under which the parent plants were growing. The response of the second generation seed to cold treatment indicated that the degree of dormancy was not a fixed characteristic of each "ecological strain" (Vanden Born, 1971). Further investigations indicated that one strain sampled in mid-September was completely dormant, but the same strain sampled from the same location 31 days later showed 70% germination. This decrease in dormancy was a result of a cold treatment of seeds on the parent plant during the damp cool weather experienced between the first and second sampling dates (Vanden Born, 1971).

MATERIALS AND METHODS

Outdoor Study

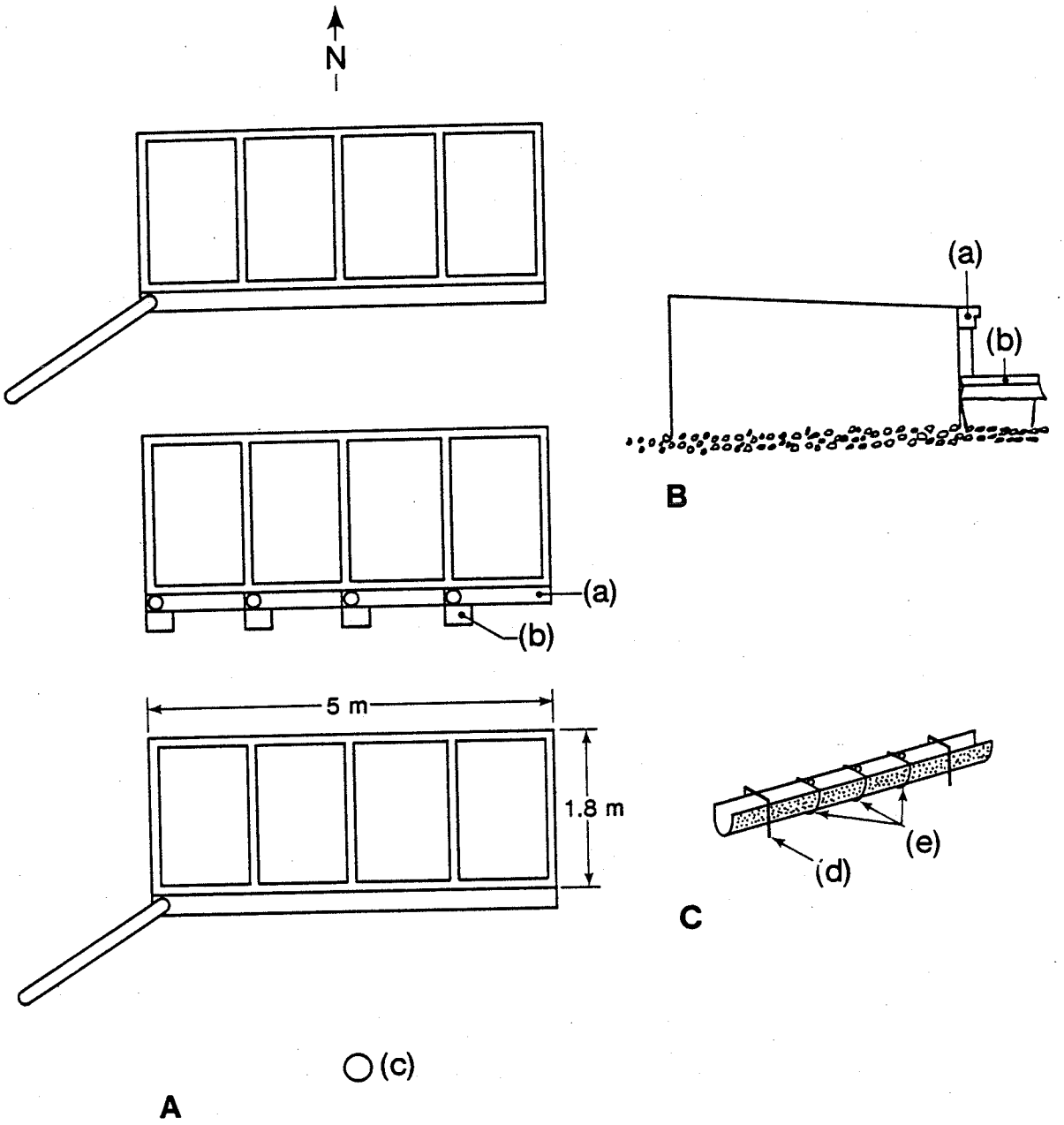
General Procedures

In the summers of 1980 and 1981, outdoor studies were conducted on a site at the University of Manitoba. Plants were grown in three specially designed wooden structures that allowed the manipulation of soil moisture while exposing the plants to prevailing environmental conditions (Figure 3A).

The structures were 5.5 m long by 1.8 m wide, 0.85 m deep at the rear and 0.75 m deep in the front. The differential in height represented a slope of approximately 5%, facilitating water removal by gutters placed in between the plant rows. Each structure was subdivided into four sections of equal size. Each subsection constituted an individual plot and each of the three wooden structures, a replicate. The interior walls of the structures were treated with wood preservative and the subsections were lined with 2 ply 6-mil clear polyethylene. The polyethylene was used to prevent water movement between plots. The wooden structures were placed on a solid gravel base and care was taken to ensure the structures were level. The exterior walls of the wooden structures were primed and painted with two coats of white exterior enamel, to reflect incident radiation.

In the spring of 1980, the structures were filled with Altona clay loam soil (39% sand, 32% silt, 29% clay; OM 4%, pH 7.8). A

FIGURE 3. Field layout used in outdoor study: A. overview of wooden structures used for growing green foxtail and yellow foxtail (a) eavestrough (b) wash tub (c) rain gauge; B. side view of wooden structure; C. gutter made of asphalt roofing paper placed between plant rows (d) copper wires (e) steel hoop.


N
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(b)
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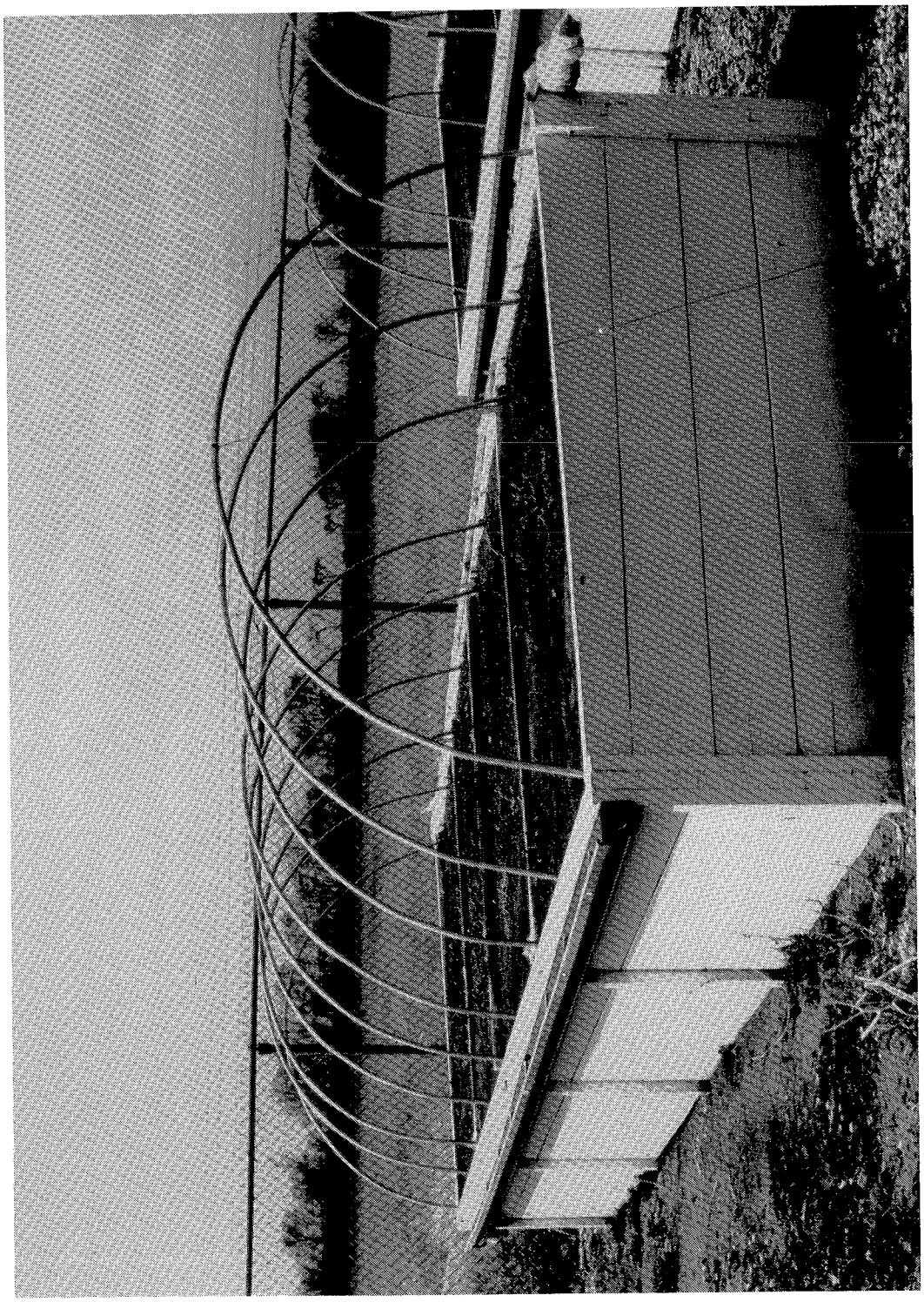
(e)
(d)
C
(c)
A

compacter was used to firm the soil to a bulk density of approximately 1.20 g. cm^3. The top 10 cm were raked to mellow the surface for seeding. All large soil aggregates were removed and the soil levelled flush with the top edges of the structure. After seedbed preparation, galvanized steel eavestroughing was secured to the exterior of the lower wall of all structures. The eavestroughing of the centre replicate was subdivided into four lengths corresponding to each of the four subsections or plots. Water could then be collected from each subsection via a guttering system described later. Water was funnelled into 56 l galvanized wash tubs covered with plastic. The plastic cover effectively minimized evaporation from the tubs and prevented the collection of incident rainfall (Figure 3B). For the remaining two replicates, the rainfall was drained off the plot area and not collected.

In 1980, an extended dry period occurred during the early part of the growing season and stress was easily instilled. In 1981, however, it was necessary to cover the structures with clear 6 mil polyethylene plastic tarps. These tarps were draped over the plot area during periods of rainfall that occurred between seedling establishment and the placement of the gutters. The tarps were supported by semi-circular hoops made from electrical conduit placed along the length of the structures. The hoops were secured with three lengths of steel wire strung along the top and sides (Figure 4). The tarps were removed as soon as possible after a rain.

FIGURE 4. Wooden structures used for growing green foxtail and yellow foxtail in the outdoor study in 1980 and 1981.



A soil fertility test[1] indicated the presence of 15.4 ppm nitrate-nitrogen (30 lb/ac), 55.6 ppm available phosphorous (100 lb/ac), 700 ppm available potassium (1400 lb/ac) and 20.0 ppm sulphate-sulphur (40 lb/ac) in 1980 and 22.0 ppm nitrate-nitrogen (44 lb/ac), 60.0 ppm available phosphorous (120 lb/ac), 700 ppm available potassium (1400 lb/ac) and 20.0 sulphate-sulfur (40 lb/ac) in 1981. No additional nutrients were added in either year.

Green foxtail and yellow foxtail seeds were planted by hand to a depth of 1 cm, in rows 15 cms apart and at a rate of 300 seeds per 1.8 m length of row. The foxtail seed used in this experiment was collected in 1978 from the University of Manitoba Graysville Research Substation and stored at room temperature until use. Initial seeding was done on June 18, 1980 and May 21, 1981. In 1981, a serious volunteer foxtail problem existed and, in order to maintain an even stand, it was necessary to reseed. This was done on June 15, 1981. In both years, 2.5 cm of water was applied immediately after seeding to establish the foxtail stand. Plants were thinned to 70 plants per row, at the four leaf stage, corresponding to a density of 222 plants m^{-2}. When the foxtail plants commenced tillering, three weeks after emergence in both 1980 and 1981, gutters were placed between the rows to channel off some of the incident rainfall. A second thinning was done at this time, establishing a stand of 55 plants per row (175 plants m^{-2}).

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[1] Analysis of soil fertility was performed by the Provincial Soil Testing Laboratory, Winnipeg, Manitoba.

The gutters were constructed of 2 m by 16 cm strips of asphalt roofing paper formed into channels with copper wire (Figure 3C). The width of each gutter was 10 cm. Steel hoops anchored in the ground secured the ends of each gutter. At the commencement of the experiment, the gutter system removed 50 to 70% of the rain falling on the plot area. This efficiency dropped to 30 to 50% by the end of the season. As a general observation, the gutters were more effective during short periods of heavy rainfall than during extended periods of light rainfall. In 1981, the tarps were used to overcome the need to rely solely on the gutters to intercept rain.

The experiment consisted of a split-plot design with three replications and four main treatments. The main treatments were 0.3, 0.6, 1.2 and 2.5 cm of water applied weekly, hereafter referred to as Treatments 1, 2, 3 and 4, respectively. Subplots consisted of four rows of each of the two foxtail species. The inner two rows were used for sampling. At each harvest date, 10 plants were selected randomly from these two sampling rows with the same number being removed from the guard rows. Thinning the guard rows ensured a uniform plant stand and eliminated any competitive effects due to differential plant number. In 1980, sampling occurred on six dates, while sampling was done on five dates in 1981. The experiment was terminated at an earlier date in 1981 since a severe hailstorm occurred before the sixth sample could be taken.

Total rainfall was monitored throughout each week and the percent efficiency of the gutters calculated. The following equation

was used to determine the amount of water necessary to bring each treatment to it's assigned water level:

$$x = a - [(b \times c) / 1000 \text{ ml } 1^{-1} - d]$$

where x = volume of water (l) to be added to the treatment each week; a = calculated volume of water (l) required weekly for each treatment; b = total weekly rainfall (cm) measured by a rain guage adjacent to the plot area; c = plot area (cm^2) and d = volume of water (l) collected per treatment weekly in each tub. Once the amount of water required was calculated, gutters were removed and water was applied by hand using a four litre watering can. Only eight litres were applied at a time since considerable puddling and run-off occurred if this amount was exceeded.

Soil Water Status. Soil water status was monitored throughout the experimental period. Soil water potential, soil temperature, and, in 1981, gravimetric soil moisture were recorded. A dew point microvoltmeter[2] and ceramic cup thermocouple psychrometer[3] were used to measure soil water potential and soil temperature. The thermocouple psychrometers were buried to a depth of 15 cm in the centre of each main plot in 1980, and in the centre of each subplot in 1981.

Gravimetric soil moisture was determined at 0-5, 5-10, 10-15 cm depths from two random samples per main plot. These values were

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[2] Model HR-33T, WESCOR, INC., Logan, Utah.

[3] Model PCT-55, WESCOR, INC., Logan, Utah.

subsequently converted to soil water potentials using a moisture release curve (Appendix 1). All readings on soil moisture status were determined on a weekly basis just prior to watering.

Plant Water Status. Leaf water potentials were taken in 1981, using sample chambers[4] and a dewpoint voltmeter. Sampling was done at 12:00 hr at the end of each week just prior to watering. The uppermost fully expanded leaf blade was selected randomly from a plant in Treatments 1 and 4 for both species. The restriction in the number of treatments sampled and the lack of replication was due to the limited number of sample chambers available. Two 25 mm^2 leaf sections, including the midrib, represented a single sample. Equilbration time was four hours.

Growth and Development. Once the plants commenced tillering, sampling was initiated and continued on a weekly basis just prior to watering. Sampling involved selecting ten representative plants from the centre two rows of each subplot. The following growth characteristics were measured: plant height (measured from ground level to the top of the extend leaf blades), tiller number, leaf and head number, leaf area, total fresh weight, total dry weight of the shoot and, later, the fresh weight and dry weight of the inflorescence. In 1980, plant height, tiller number, leaf and inflorescence number and leaf area were assessed on an individual plant basis. Leaf area was determined using

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[4] Model C-51, WESCOR, INC., Logan, Utah.

a leaf area meter.[5] Total fresh weight, fresh weight of the shoot and inflorescence and dry weight of the shoot and inflorescence were initially recorded on the bulk sample. However, on the final two sample dates, measurements were performed on the individual plants. In 1981, all measurements were taken on each of the ten plants. Upon termination, several heads were randomly selected from each treatment so that 1,000-kernel weights could be determined. All 1,000 kernel weights were counted by hand.

To further examine the effect of water stress on plant growth and development, additional observations were recorded in 1981. These included protein content of both the shoot and the inflorescence, epicuticular wax deposition and the anatomical differences in leaf structure.

Protein contents were determined by the Kjeldahl method[6] on a 1 g sample of tissue from each weekly harvest. The sample of tissue was obtained from the bulked ground dry matter sample of each treatment for each species. Three determinations were made on each tissue sample. Percent protein was calculated by multiplying the nitrogen content by a factor of 6.25.

Epicuticular wax determinations were recorded on two dates: August 1, 1981 and August 15, 1981. The colormetric method developed by Ebercon et al. (1977) was used to assess the effects of water stress

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[5] Model LI-3000, LI-COR Inc., Lincoln Nebraska.

[6] Protein content was determined by the Kjeldahl Laboratory, University of Manitoba, Winnipeg, Manitoba.

on wax formation for both green foxtail and yellow foxtail. Standard curves for green foxtail and yellow foxtail were determined by the following method: 50 to 70 leaves were immersed for 20 s in 200 ml of redistilled chloroform. This was repeated with several sets of 50 to 70 leaves. The extract was filtered and evaporated under vacuum at 25°C. The residue was weighed into four of each 1, 2, 3, 4 and 5 mg samples for both species and subjected to colorimetric analysis using $K_2Cr_2O_7$ as the reagent. Absorbance readings were taken at 590 nm using a spectrophotometer. From these values, standard curves were obtained and utilized to convert the absorbance values to the quantity of epicuticular wax present (Appendix 3). Five replicates of ten green foxtail leaves and five yellow foxtail leaves were used for each treatment. The leaves were placed through the leaf area meter to obtain the total leaf area of the sample and the leaf wax extracted. Extractions were then carried through the above analytical procedure.

For anatomical studies on leaf morphology, leaf blade samples were taken July 25, 1981 for each species in each treatment. Sampling consisted of selecting the last most-fully-expanded leaf of the main shoot. Several transverse sections 2 mm in length were cut from each leaf blade and placed in 5% phosphate buffered glutaraldehyde (pH 6.8). The specimens remained under vaccuum for 20 h, whereupon leaf sections were washed in four changes of 0.025 M phosphate buffer and post-fixed in phosphate-buffered 2% (w/v) osmium tetroxide for 1 h. Following two washes with the same buffer, the tissue was rinsed with three changes of distilled water and then gradually dehydrated with a graded ethanol series. The specimens were then infiltrated and embedded with epoxy

resin (Spurr, 1969). The tissue was subsequently infiltrated with three changes of the epoxy resin over 24 h and polymerized for 20 h at 70°C. Transverse sections, 2 μm in thickness, were cut with glass knives mounted on a microtome[7] and affixed to glass slides. These sections were stained with 0.1% toluidine blue O (TBO) in 1% (w/v) sodium bicarbonate (pH 9.0) for 2 minutes. Sections were viewed and photographed with a light microscope. Photomicrograph were printed from the negatives with a final magnification of 225x. The area occupied by various cellular components was determined by weighing the photographed image; from this the area of the mesophyll cells and intracellular space could be assessed. All photomicrographs represent the area between the midrib and the first major vein. Leaf thickness measurements were also taken from each photomicrograph, four measurements per print. In 1980, leaves were sampled on July 30, 1980 and subjected to the procedure mentioned above, with only leaf thickness measurements being taken.

Germination Study

In these experiments, seeds were considered matured when ready to drop from the panicle. Newly matured seeds were harvested from each species treatment combination from the outdoor study on August 27, 1980 and August 15, 1981. Seeds with intact hulls were dusted with the fungicide, Arasan[8] and stored at room temperature.

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[7] Porter-Blum JB-4, Dupont Co., Sorvall Operations, Newton, Conn., 06470.

[8] Arasan, active ingredient, 75% thiram (tetramethyl thiuramdisulphide) a product of Canadian Industries Limited.

The experimental unit consisted of 50 seeds placed evenly on Whatman No. 1 filters in standard 9 cm plastic petri dishes. A total of 3 ml of distilled water was added to each petri dish, an additional 1 ml was added on each sample date. Incubation occurred in the dark in germination cabinets regulated at 24°C. Replication consisted of four petri dishes randomly stacked in dark plastic containers spatially separated on germination cabinet shelves.

Germination tests for the 1980 seed collection commenced March 1981 and continued on a monthly basis until June, 1981. For seed collected from the 1981 outdoor study, testing was initiated in December, 1981 and continued monthly until March, 1982. To examine the influence of temperature on cumulative percent germination, two additional incubation temperatures were added, 16°C and 28°C, in 1981. Germination counts on all experimental units were made at regular two day intervals for the first four sampling dates. Counts, thereafter, were performed every four days for the remaining three sampling dates. Seeds were removed from the petri dishes following germination. Seeds were considered germinated when the length of the radicle was 2 mm or greater. Following the final sample date all ungerminated seeds were tested for "hardness". This involved gently pricking the seed with a probe; if the seed was hard, they were considered viable (Assoc. Off. Seed Anal., 1965). Generally, fungal contamination was light.

Growth Room Study

Four-litre plastic food containers were filled with 4 kg of air dried Almasippi very fine sandy loam soil (79% sand, 12% clay, 9% silt,

OM 4%, pH 7.7) to which 200 ppm N as NH_4NO_3; 50 ppm P as $Ca(H_2PO_4) \cdot 2H_2O$; and 160 ppm K and 65 ppm S as K_2SO_4 was added. The average soil moisture content was calculated for the air dried soil and determined to be approximately 2.0 to 2.5% (w/w). The 4 kg of air dried soil was watered to slightly above field capacity [20% (w/w)]. Fifteen seeds of either green foxtail or yellow foxtail were placed on the soil surface and 200 g of finely sieved Almasippi soil spread evenly on top. Water rose to the soil surface by capillary action, bringing the entire soil volume to field capacity.

The containers were placed in a growth room under day/night temperatures of 23/16°C, a relative humidity of 55 to 60% and illuminated with Gro-Lux WS Sylvania fluorescent lights yielding a photosynthetic photon flux density ranging from 170 to 220 $\mu Em^{-2}s^{-1}$. To offset the variation in light distribution, air movement and temperature, the containers were rotated systematically after watering. Containers were weighed and watered to field capacity daily.

Upon emergence, foxtail seedlings were thinned to four plants per container. Three soil moisture content (SMC) were used, 12, 14 and 20% (w/w) corresponding to soil water potentials of -2.4, -1.1 and -0.3 bars respectively. The soil water potentials were calculated using a regression equation derived from the soil moisture release curve developed from data obtained using a pressure plate apparatus (Appendix 2). By withholding water, the soil moisture content was allowed to decline to 14% SMC and 12% SMC: 14% SMC was reached two weeks after emergence and 12% SMC required an additional two weeks to attain. The plants were watered daily to maintain 12, 14 and 20% soil moisture content.

The experimental design was a split-split plot design with soil moisture content as the main plots, plant species and sampling date as the sub-plot and sub-sub-plot, respectively. The treatments were replicated once over three time periods, making a total of three replicates.

Once the 12% SMC was reached, sampling occurred 4, 5, 6, 7, 8 and 9 weeks after emergence. The foxtail plants from each container for all treatments were harvested and leaf area, height, tiller number, leaf number, inflorescence number, fresh weight of the shoot and root, dry weight of the shoot and root, were recorded. The shoot fresh weight and dry weight was further broken down into its component parts, leaves, stem and for later sampling dates, the inflorescence.

Statistical Analysis

Prior to analysis, means and variances for each parameter were examined for any departures from the assumptions for the statistical model. If no departures were detected, analysis of variance was performed on the raw data. However, if any departure occurred, a transformation was applied to ensure a normal distribution to conform to the assumptions underlying the analysis of variance. After transformation, if no differences in significance occurred between the raw data and the transformed data, the former was used. The multiple comparison procedure used to detect significant differences was the least significant differences test (LSD) at either the 1% or 5% level of significance.

RESULTS

Outdoor Study

Soil Water Status

The contribution of rainfall to the soil water status in the wooden structures is presented in Table 1. The average cumulative contribution of rainfall was 3.7 cm in 1980 and 3.1 cm in 1981 over the corresponding sample dates. Although the total amount of rainfall received on the plots did not vary greatly between the two years, the timing of the rainfall did differ. In 1981, the first rainfall occurred two weeks after gutter placement. This was one week earlier than the first significant rainfall in 1980. Rainfall patterns prior to seeding and gutter placement also varied greatly between the two years (Appendix 5). In 1981, the tarps were used to simulate the dry conditions experienced just prior to seeding in 1980. The tarps were effectively used to intercept all rainfall before seeding. Thereafter, the tarps were only used when extended periods of light rainfall were forecast.

On several occasions the amount of precipitation received on the plots exceeded the amount of water required to maintain the various treatments. This occurred on the 4th, 5th and 6th sample week in 1980 and the 3rd and 4th sample week in 1981.

The gutters removed 60 to 70% of the incident rainfall in the earier part of the season. However, in 1980 the efficiency of the gutters decreased to approximately 40%. The gutters by this time were shrouded by foxtail leaves.

TABLE 1. Weekly incident rainfall in the outdoor study in 1980 and 1981.

Week	Treatment Number	Treatment Level[a]	Rainfall 1980 Total[b]	1980 Received on plot[c]	1980 Excess of Treatment[d]	Rainfall 1981 Total[b]	1981 Received on plot[c]	1981 Excess of Treatment[d]
		(cm)						
1	1	0.3	0.0	0.0	-	0.5	0.0	-
	2	0.6	0.0	0.0	-	0.5	0.0	-
	3	1.2	0.0	0.0	-	0.5	0.0	-
	4	2.5	0.0	0.0	-	0.5	0.0	-
2	1	0.3	0.9	0.2	-	0.0	0.0	-
	2	0.6	0.9	0.2	-	0.0	0.0	-
	3	1.2	0.9	0.3	-	0.0	0.0	-
	4	2.5	0.9	0.3	-	0.0	0.0	-
3	1	0.3	0.4	0.2	-	2.1	1.4	+1.1
	2	0.6	0.4	0.2	-	2.1	1.3	+0.7
	3	1.2	0.4	0.2	-	2.1	1.5	+0.3
	4	2.5	0.4	0.2	-	2.1	1.7	-
4	1	0.3	3.0	1.4	+1.1	3.5	1.7	+1.7
	2	0.6	3.0	1.4	+0.8	3.5	1.8	+1.4
	3	1.2	3.0	1.7	+0.5	3.5	2.0	+0.7
	4	2.5	3.0	1.8	-	3.5	2.5	-
5	1	0.3	3.5	1.9	+1.6	0.0	0.0	-
	2	0.6	3.5	1.8	+1.2	0.0	0.0	-
	3	1.2	3.5	1.8	+0.6	0.0	0.0	-
	4	2.5	3.5	1.9	-	0.0	0.0	-
6	1	0.3	3.4	1.4	+1.1			
	2	0.6	3.4	1.4	+0.8			
	3	1.2	3.4	1.8	+0.6			
	4	2.5	3.4	1.7	-			
7	1	0.3	0.0	0.0	-			
	2	0.6	0.0	0.0	-			
	3	1.2	0.0	0.0	-			
	4	2.5	0.0	0.0	-			

[a] Amount of water applied weekly (cm).
[b] Measured by standard rain gauge.
[c] Total rainfall (cm) - amount intercepted by the gutter and tarp (cm).
[d] Amount received on plots (cm) - treatment level (cm).

Soil water potential, measured with psychrometers placed at a depth of 15 cm, decreased with time during the growing season (Table 2). In 1980, at the time of gutter placement (sample week 1), the soil water potentials were higher than the same period in 1981. Generally, the values were lower in 1981 than in 1980 with a greater distinction between the various water treatments.

In 1981, soil water potential readings were augmented with gravimetric soil moisture content readings determined at 0-5, 5-10, 10-15 cm depths (Appendix 6). Many of the soil water content values exceeded the limits of extrapolation from the moisture release curve determined for the Altona clay loam soil (Appendix 1). This was particularly evident for soil moisture contents taken at the 0-5 cm depth where values were below 10% soil moisture content.

Plant Water Status

In 1981, leaf water potential readings were measured at midday just prior to watering for Treatments 1 and 4 (Table 3). Under Treatments 1 and 4, the leaf water potential of yellow foxtail was higher than the leaf water potential of green foxtail. The only exception was at the initial sample date, where green foxtail and yellow foxtail had similar leaf water potentials under Treatment 1. With both species, the leaf water potential was lower under Treatment 1 than under Treatment 4. However, the leaf water potential for yellow foxtail was affected to a greater extent than was the leaf potential for green foxtail.

TABLE 2. Soil water potential in the outdoor study in 1980 and 1981.

Year	Sample Week	Soil water potential[b] Treatment 1	2	3	4
		(-bars)			
1980	1[a]	4.1	5.9	6.9	6.7
	2	16.5	17.2	3.9	0.3
	3	14.9	18.1	16.1	8.3
	4	17.4	14.4	9.3	1.3
	5	1.8	6.4	1.1	2.8
	7	7.4	10.5	10.4	0.3
1981	1[a]	32.3	18.6	15.3	15.1
	2	20.3	12.4	9.6	5.2
	3	23.5	9.6	7.2	2.3
	4	19.0	6.5	6.7	2.5
	5	13.9	7.0	8.5	4.2

[a] Gutter placement.
[b] An average of three measurements in 1980, an average of six measurements in 1981, taken with ceramic cup psychrometers buried at a depth of 15 cm.

TABLE 3. Effect of two water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on leaf water potential of green foxtail (GF) and yellow foxtail (YF) in the outdoor study in 1981.

Sample Week	Leaf water potential[a]			
	Treatment 1		Treatment 4	
	GF	YF	GF	YF
	(-bars)			
1	17.1	17.8	12.2	7.5
2	13.8	9.6	14.1	5.3
3	23.5	15.8	17.6	9.9
4	23.2	15.1	18.5	9.6
5	9.9	8.5	9.8	3.8

[a] Non-replicated sample of the last most fully expanded leaf.

Growth and Development

Sampling was initiated on the same date as gutter placement which corresponded to the first date of treatment. Calendar dates corresponding to sample dates in 1980 and 1981 are presented in Appendix 4. Hereafter the terms sample week, sample date and week will be used interchangeably.

In both years, green foxtail and yellow foxtail emerged five days after seeding, and were tillering approximately three weeks after emergence. At the first sample date, the two foxtail species were the same height regardless of water regime (Figure 5). Green foxtail was consistently taller than yellow foxtail in sample weeks 1 through 3 in all treatments and in both years. By the last sample date, yellow foxtail was taller than green foxtail regardless of treatment in both year. However, this difference was only significant under the wettest water treatment (Treatment 4). Under Treatment 4, yellow foxtail grew 17 cm and 15 cm taller than green foxtail in 1980 and 1981, respectively. Within species, at week 5 in 1980 and 1981, green foxtail was 40% shorter and yellow foxtail was 50% shorter under the lowest water regime (Treatment 1) than under the highest water regime (Treatment 4).

In 1980 and 1981, the number of tillers per plant increased gradually over all sample dates; with green foxtail consistently having a greater number of tillers (Figure 6). Green foxtail had an average of three more tillers more than yellow foxtail in 1980, whereas in 1981, the overall average was a difference of one. By sample date 5, in both years, the number of tillers per yellow foxtail plant plateaued

FIGURE 5. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on plant height of green foxtail (⊙—⊙) and yellow foxtail (△—△) in 1980 and 1981.

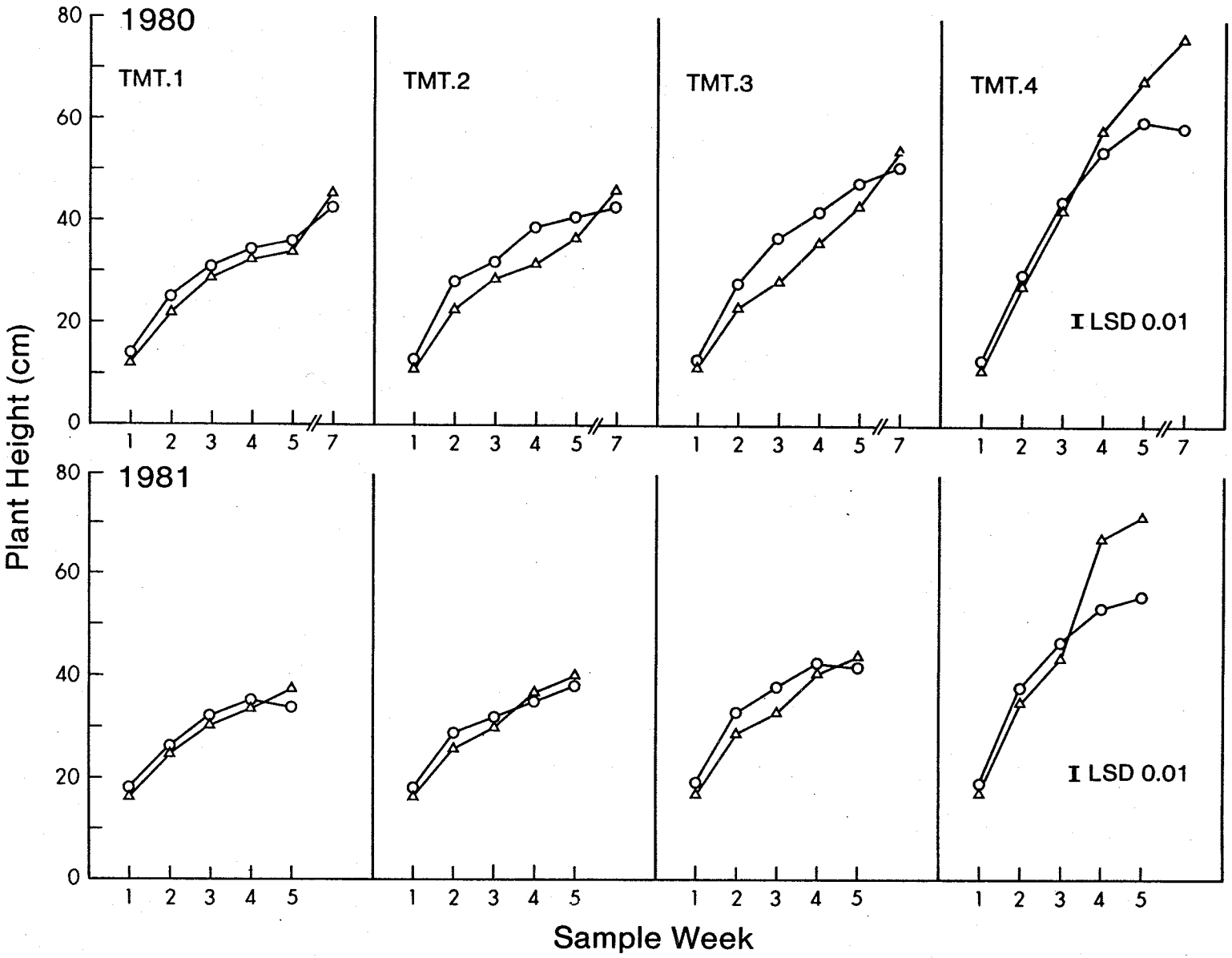
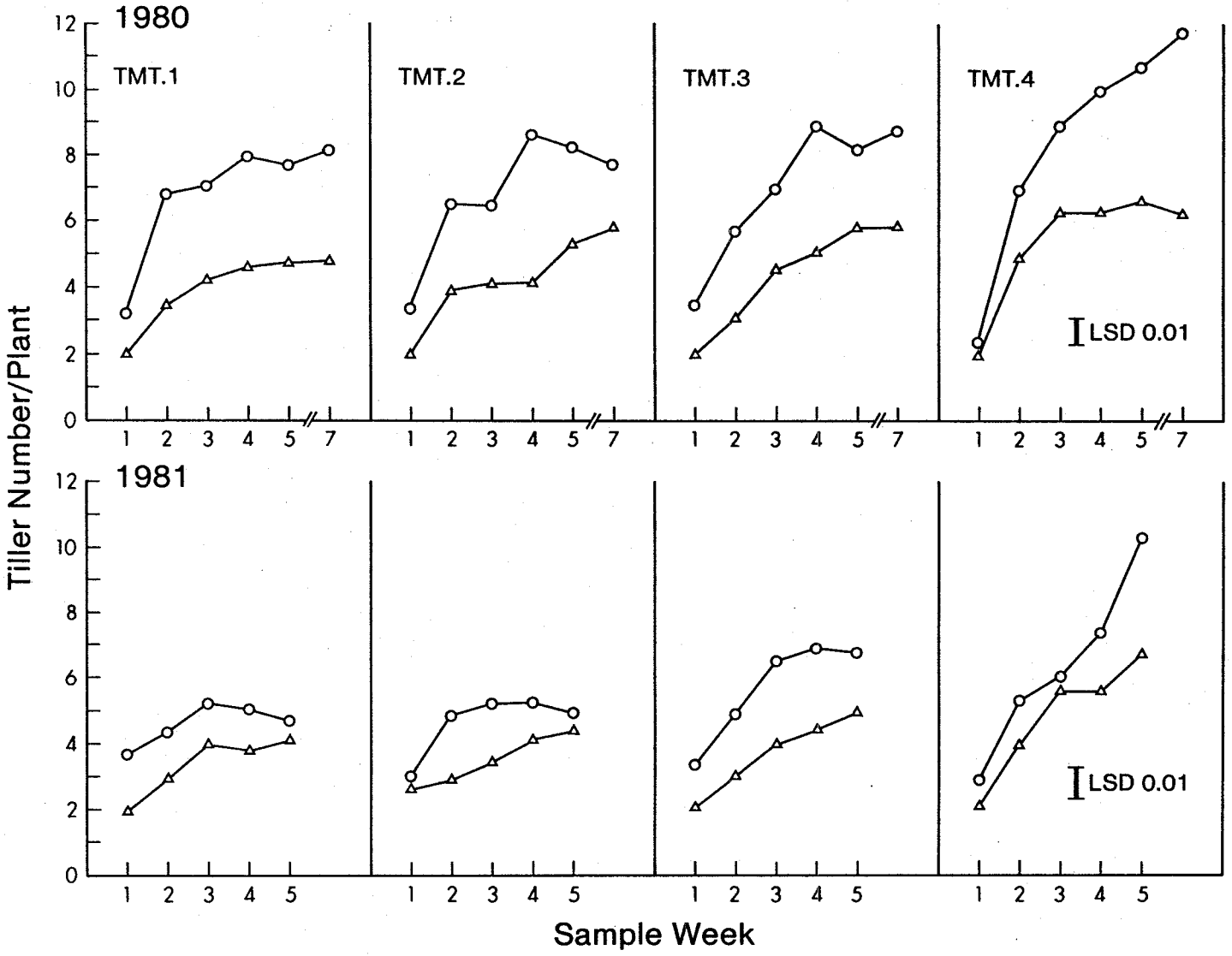

1980
TMT.1
TMT.2
TMT.3
TMT.4
I LSD 0.01
1981
I LSD 0.01
Plant Height (cm)
Sample Week
0
20
40
60
80
1 2 3 4 5 7
1 2 3 4 5

FIGURE 6. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the number of tillers per plant of green foxtail (⊙—⊙) and yellow foxtail (△—△) in 1980 and 1981.

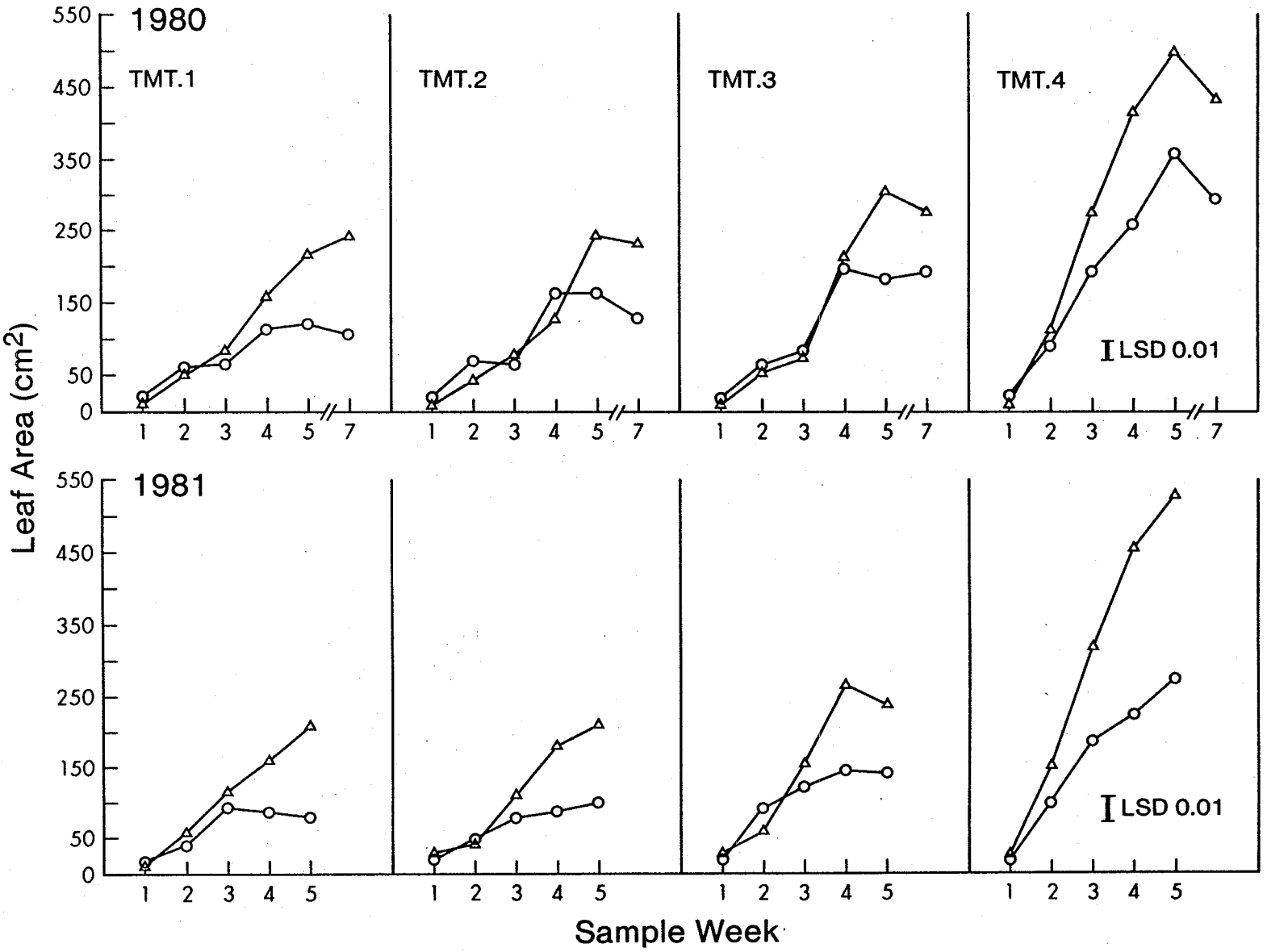

1980
TMT.1
TMT.2
TMT.3
TMT.4
LSD 0.01
1981
LSD 0.01
Tiller Number/Plant
Sample Week

under all water regimes. Green foxtail showed this same plateau under all treatments except under the highest water regime (Treatment 4) where tiller number continued to increase significantly over sample dates.

In 1981, green foxtail had fewer tillers per plant under Treatment 1, 2 and 3 than at the same sample dates in 1980. The number of yellow foxtail tillers per plant was the same in both years at the respective sample dates. At the fifth sample date in 1980, the number of tillers per green foxtail plant was increased by about 50% when comparing Treatment 1 and 4. By contrast, the number of tillers per yellow foxtail increased by 30%, when comparing the lowest and highest water regime (Treatment 1 and 4, respectively).

The leaf area of both species increased up to week 5 after which there was a tendency toward a decline in leaf area (Figure 7). At the first two sample dates, in 1980 and 1981, leaf area of green foxtail and yellow foxtail did not differ significantly. By week 3, the leaf area of yellow foxtail was comparable to that of green foxtail in 1980 and exceeded the leaf area of green foxtail in 1981. When comparing the highest and lowest water regimes (Treatment 4 and 1), it is evident that the leaf area of green foxtail was affected more by the lower moisture condition than the leaf area of yellow foxtail. The difference between the two foxtail species was greater under the highest water treatment (Treatment 4) where at week 5 the leaf area of yellow foxtail was 1.3 times and 2 times greater than green foxtail, in 1980 and 1981, respectively.

FIGURE 7. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the leaf area per plant of green foxtail (○—○) and yellow foxtail (△—△) in 1980 and 1981.


1980
TMT.1
TMT.2
TMT.3
TMT.4
LSD 0.01
1981
LSD 0.01
Leaf Area (cm2)
Sample Week
550
450
350
250
150
50
0
1 2 3 4 5 7
1 2 3 4 5

At week 3, in 1980; and week 2, in 1981, leaf folding was observed in both foxtail species under all but the highest moisture condition (Treatment 4).

The number of leaves of green foxtail was greater than or equal to the number of leaves of yellow foxtail (Figure 8). During the 1981 growing season, the number of leaves of green foxtail was greater under Treatment 3 and 4, however at the final sample date under the lower water treatments (Treatment 1 and 2) the number of leaves of yellow foxtail exceeded the number of leaves recorded for green foxtail. In both years, under the highest water regime (Treatment 4), the number of leaves of green foxtail was significantly greater than the number of leaves of yellow foxtail. At sample week 5, in both years, green foxtail had between 24 and 43 fewer leaves and yellow foxtail had between 17 and 14 fewer leaves under Treatment 1 compared to Treatment 4.

The number of inflorescences per plant increased gradually over time, with green foxtail heading one and two weeks earlier than yellow foxtail in 1980 and 1981 respectively (Figure 8). In both seasons, the number of inflorescences of green foxtail was greater than the number of inflorescences of yellow foxtail. The difference in the number of inflorescences between the two species was greater in 1981 than in 1980 and greatest under the highest water regime (Treatment 4) than any of the lower water regimes (Treatment 1, 2 and 3). As observed for leaf number, the magnitudes of the differences in inflorescence number between the two years when comparing the lowest and highest water treatment (Treatment 1 and 4) was greater for green foxtail. For

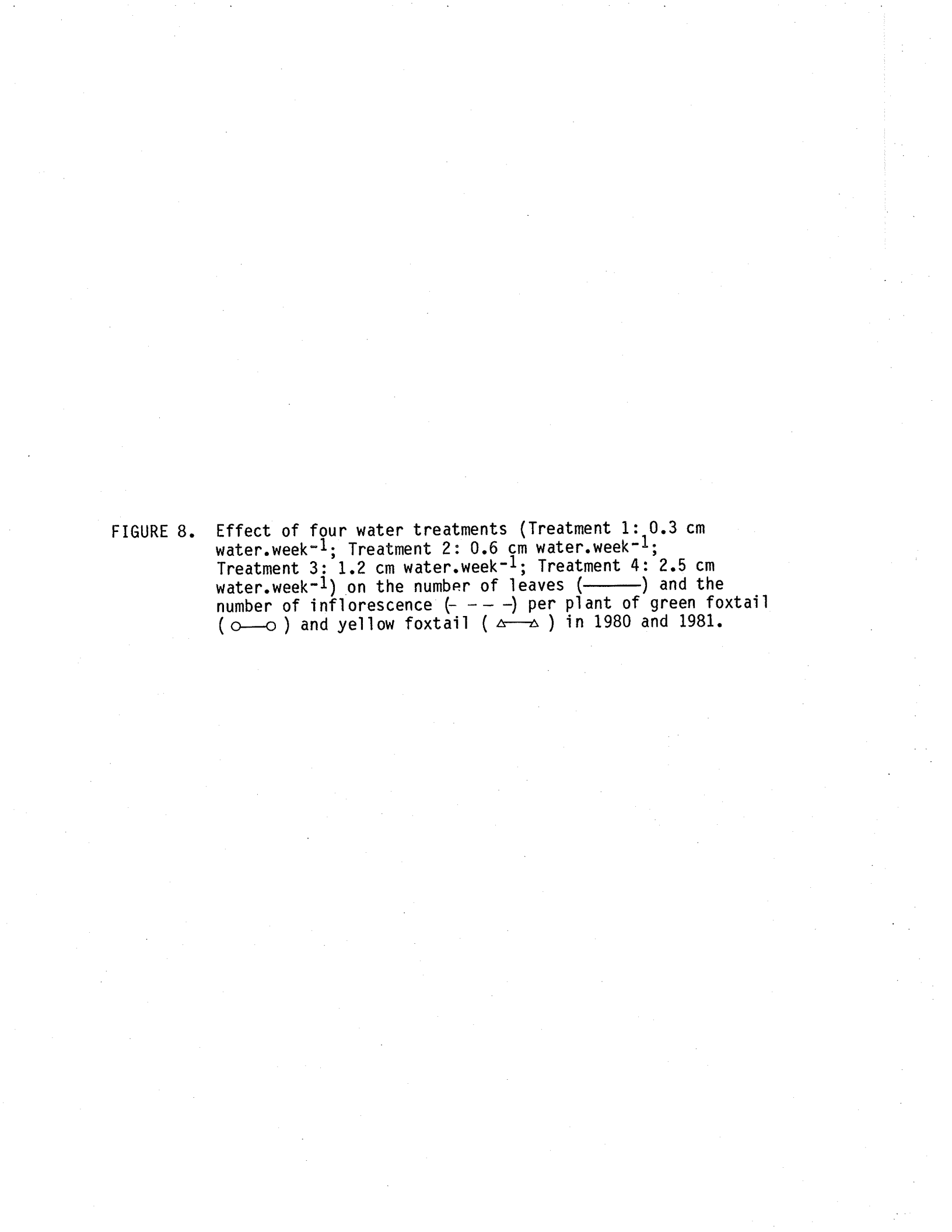
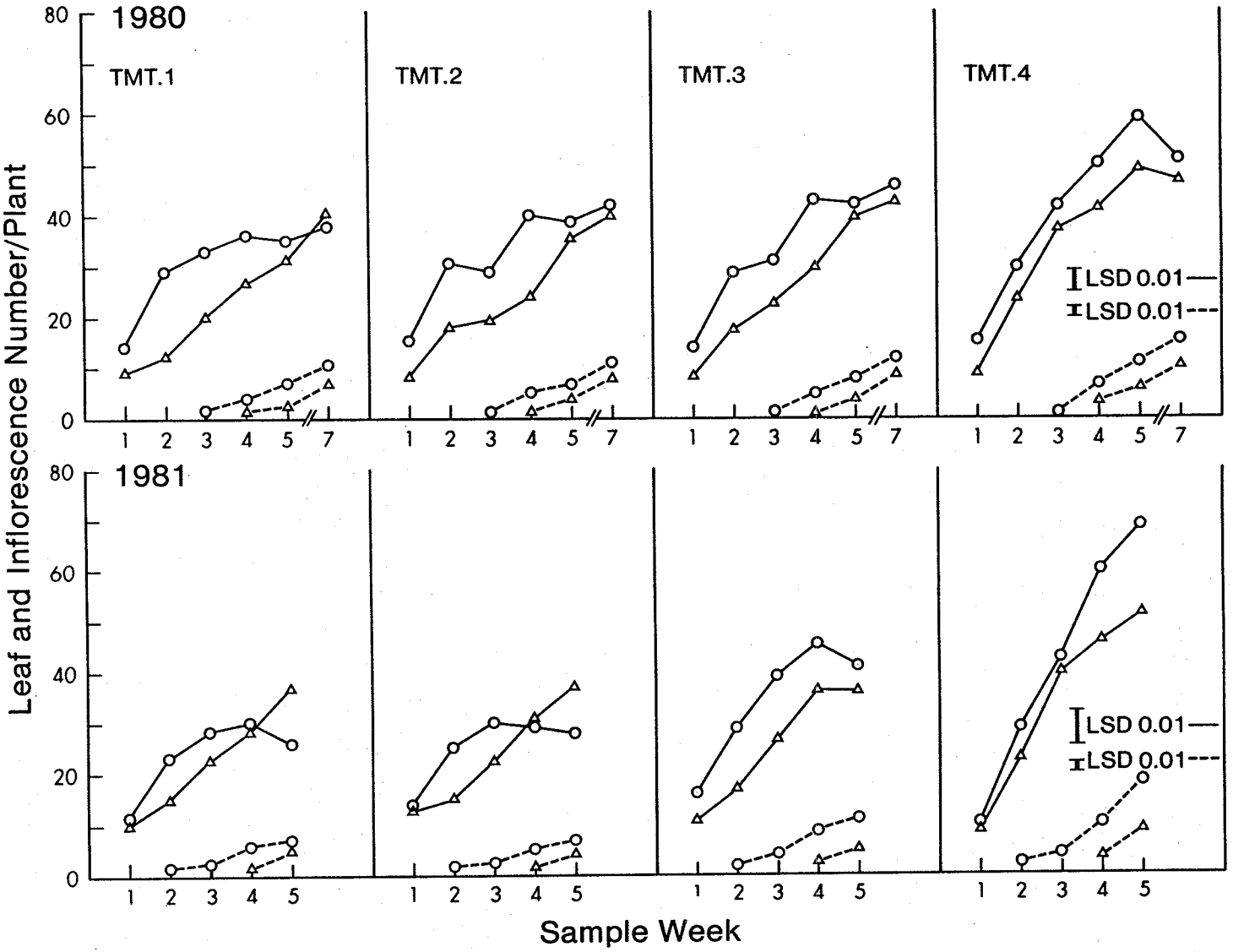


FIGURE 8. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the number of leaves (———) and the number of inflorescence (– – –) per plant of green foxtail (o—o) and yellow foxtail (△—△) in 1980 and 1981.


1980
TMT.1
TMT.2
TMT.3
TMT.4
1981
LSD 0.01
LSD 0.01
Leaf and Inflorescence Number/Plant
Sample Week
0
20
40
60
80
1 2 3 4 5 7

example, at sample week 5, green foxtail had between 10 and 4 fewer heads. By contrast, yellow foxtail had between 4 and 3 fewer heads under Treatment 1 compared to under Treatment 4 in 1980 and 1981, respectively.

The shoot dry weight of green and yellow foxtail increased over sample dates in both growing seasons (Table 4 and 5). Generally, green foxtail had a greater shoot dry weight than yellow foxtail. However, this difference was not significant. Significant dry weight differences within species were not evident until week 3 in 1980 and week 2 in 1981. For both species, a significant reduction in shoot dry weight occurred under Treatment 1 as compared to Treatment 4. At the last sample date in 1980, the shoot dry weight of both Setaria species was reduced by 50% when comparing the highest and lowest water regimes (Treatment 4 and 1, respectively). Whereas in 1981, the shoot dry weight of green and yellow foxtail was reduced by up to 70% when the water supply was reduced.

In 1980 and 1981, the ratio of shoot fresh weight to shoot dry weight of green foxtail was significantly less than for yellow foxtail (Table 4 and 5). These ratios were generally higher in 1980 than in 1981. Under the lowest water regime (Treatment 1), both green and yellow foxtail had lower ratios than under the highest water regime (Treatment 4). However these differences were not always significant. By week 5, the difference in the ratios within each species was not significant in either 1980 or 1981.

In both years, the dry weight of the inflorescence of green foxtail was greater than the dry weight of the inflorescence of yellow

TABLE 4. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the shoot dry weight and the ratio between the shoot fresh weight and the shoot dry weight of green foxtail (GF) and yellow foxtail (YF) in 1980.

Sample		Shoot Dry Weight		Shoot Fresh Weight / Shoot Dry Weight	
Week	Treatment	GF	YF	GF	YF
		--- (g/plant) ---			
1	1	0.09	0.08	7.74	8.28
	2	0.09	0.07	8.23	9.60
	3	0.09	0.07	7.73	9.55
	4	0.09	0.08	7.36	8.97
2	1	0.48	0.37	5.32	6.81
	2	0.55	0.33	5.72	7.49
	3	0.47	0.35	6.31	8.10
	4	0.45	0.52	7.43	9.21
3	1	1.17	0.79	3.76	5.61
	2	1.09	0.74	3.84	5.68
	3	1.48	1.11	3.69	5.09
	4	1.88	1.77	4.77	7.45
4	1	1.48	1.16	4.48	6.12
	2	1.98	0.84	4.58	7.63
	3	2.11	1.17	4.77	7.82
	4	3.04	2.66	4.56	8.17
5	1	1.95	1.65	4.06	6.25
	2	2.44	1.69	4.14	7.27
	3	2.87	2.19	4.90	7.39
	4	5.07	4.80	4.25	6.81
7	1	3.60	3.72	2.75	5.26
	2	4.05	3.82	3.14	5.04
	3	5.55	4.52	3.06	5.26
	4	7.71	7.50	2.90	5.19
LSD (0.05)[a]		1.03		1.19	

[a] LSD (0.05) for comparison within and between columns for all sampling dates.

TABLE 5. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the shoot dry weight and the ratio between the shoot fresh weight and the shoot dry weight of green foxtail (GF) and yellow foxtail (YF) in 1981.

Sample		Shoot Dry Weight		Shoot Fresh Weight / Shoot Dry Weight	
Week	Treatment	GF	YF	GF	YF
		--- (g/plant) ---			
1	1	0.18	0.14	5.04	6.75
	2	0.17	0.18	5.55	5.93
	3	0.19	0.15	5.04	6.09
	4	0.18	0.18	4.85	6.21
2	1	0.52	0.42	4.44	6.16
	2	0.74	0.44	4.55	5.99
	3	0.94	0.61	4.73	5.77
	4	1.08	1.03	4.84	6.83
3	1	1.18	0.85	4.13	6.07
	2	1.02	0.81	3.90	6.40
	3	1.47	0.92	4.87	6.92
	4	1.81	1.65	4.64	9.10
4	1	1.59	1.22	3.60	6.19
	2	1.43	1.37	4.77	6.53
	3	2.24	1.88	4.03	6.70
	4	3.62	3.25	4.04	8.83
5	1	1.84	2.21	3.54	6.39
	2	2.08	2.19	3.59	6.33
	3	3.40	2.43	3.53	6.38
	4	6.12	6.09	3.58	6.82
LSD (0.05)[a]		1.08		1.22	

[a] LSD (0.05) for comparison within and between columns for all sampling dates.

foxtail under all treatment (Table 6). At the final sample date, the dry weight of the inflorescence of green and yellow foxtail was reduced by approximately 50% in 1980 and 35% in 1981, as the water supply was restricted.

Generally, the ratio of inflorescence dry weight to shoot dry weight of green foxtail was approximately 1.6 times and 2.2 times greater than for yellow foxtail, in 1980 and 1981, respectively (Table 6). Treatment differences were not observed in either year for either species. Hence the only significant difference observed was the difference between the two Setaria species.

The percent protein of shoots dry weight of both green and yellow foxtail decreased over the course of the growing season (Figure 9). After the second sample date, the protein content of yellow foxtail was significantly greater than that of green foxtail. Differences within species among treatments were only evident at the final sample date. The protein content of green foxtail was significantly lower under Treatment 2 than under the other three treatments. By comparison, the protein content yellow foxtail was significantly lower under the highest moisture regime (Treatment 4) than under any other moisture regime.

Unlike the protein content of the shoot, the percent protein of the inflorescence did not show as substantial a decrease over sample dates (Table 7). At week 3, the protein content of green foxtail inflorescences was significantly higher under the highest water treatment (Treatment 4) compared to the lower water treatments (Treatment 1, 2 and 3). Yellow foxtail was not heading at this date. At sample week

TABLE 6. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the inflorescence dry weight and the ratio between the inflorescence dry weight and the shoot dry weight of green foxtail (GF) and yellow foxtail (YF) in 1980 and 1981.

Year	Treatment	Inflorescence Dry Weight[a]		Inflorescence Dry Weight / Shoot Dry Weight	
		GF	YF	GF	YF
		--- (g/plant) ---			
1980	1	1.61	1.04	0.45	0.26
	2	1.69	1.02	0.42	0.26
	3	2.51	1.34	0.46	0.29
	4	3.44	2.15	0.44	0.29
	LSD (0.05)[b]	0.43		0.05	
1981	1	0.78	0.42	0.42	0.19
	2	0.89	0.39	0.42	0.18
	3	1.36	0.43	0.39	0.18
	4	2.29	1.23	0.39	0.20
	LSD (0.05)[b]	0.26		0.04	

[a] Determined for plants sampled on the final sample date of each year.
[b] LSD (0.05) for comparison within and between columns for one year.

FIGURE 9. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the protein content of the leaf and stem material of green foxtail (o—o) and yellow foxtail (△—△) in 1981.

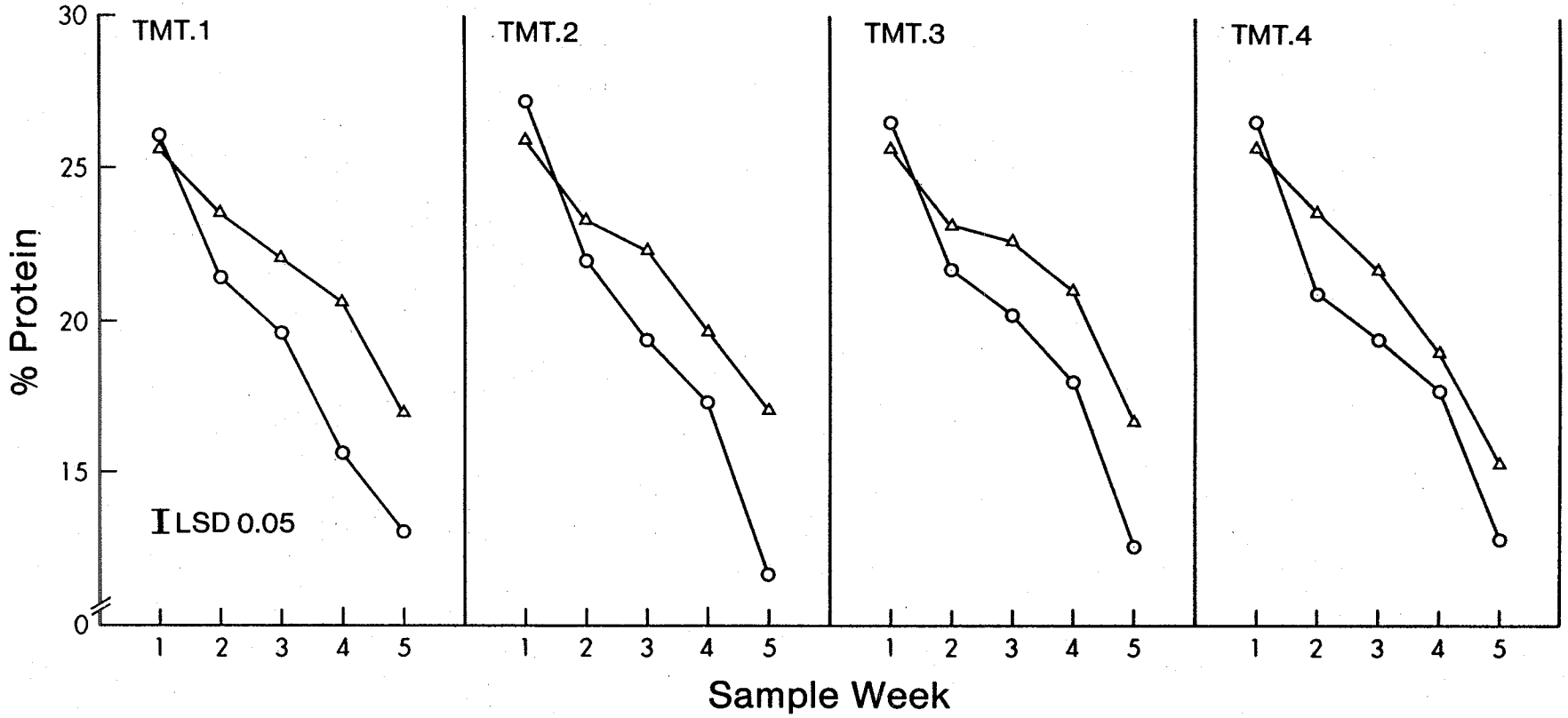

TMT.1
TMT.2
TMT.3
TMT.4
% Protein
30
25
20
15
0
LSD 0.05
1 2 3 4 5
Sample Week

TABLE 7. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on protein content (%) of the inflorescence of green foxtail (GF) and yellow foxtail (YF) in 1981.

	Protein Content					
	Week 3		Week 4		Week 5	
Treatment	GF	YF	GF	YF	GF	YF
	----------(%)----------					
1	18.8	-[a]	18.3	21.5	17.6	17.3
2	18.9	-	18.3	21.7	18.1	18.1
3	19.3	-	17.3	21.7	17.5	16.9
4	20.6	-	16.9	18.0	17.2	15.1
LSD (0.05)[b]	1.1		1.7		1.2	

[a] Yellow foxtail was not flowering at this date.
[b] LSD (0.05) for comparison within and between columns for one sampling date.

4, the inflorescence of yellow foxtail had a significantly lower protein content under the highest water regime (Treatment 4) compared to lower water regimes (Treatment 1, 2 and 3) at this date. Protein content of the inflorescence of green foxtail did not differ between treatments.

The effect of water stress on the production of epicuticular wax of green and yellow foxtail was measured in 1981, at two sampling dates (Table 8). The amount of epicuticular wax of green foxtail leaves was consistently greater than the amount of epicuticular wax of yellow foxtail leaves at both sample dates. For green foxtail, wax production did not differ significantly between treatments at both sample dates. Yellow foxtail, however, showed a significant increase in wax formation as the water supply was restricted.

In both seasons, leaf thickness values for yellow foxtail were greater than for green foxtail, irrespective of treatment (Figure 10). The only exception was Treatment 3 in 1981, where leaf thickness values for the two species were not significantly different. Under the wettest water treatment (Treatment 4), yellow foxtail leaves were up to 56 m thicker than green foxtail under the same conditions. Within species, the leaf thickness for green foxtail was less affected by the different water regimes than the leaf thickness for yellow foxtail.

The anatomy of leaves of green and yellow foxtail was also measured on samples collected on the third sample week in 1981 (Figure 11). Regardless of treatment, the leaves of yellow foxtail had a greater total area than the leaves of green foxtail (Table 9). The total area of the internal structure of yellow foxtail leaves increased by 30%, whereas the total area of the internal structure of green

TABLE 8. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on epicuticular wax formation of green foxtail (GF) and yellow foxtail (YF) in 1981.

	Wax Development			
	Week 3		Week 5	
Treatment	GF	YF	GF	YF
	----------($\mu g/cm^2$)----------			
1	15.77	12.17	19.27	11.98
2	15.72	12.48	18.29	12.37
3	15.38	11.96	18.77	12.92
4	14.72	9.89	19.30	11.06
LSD (0.05)[a]	1.12		1.03	

[a] LSD (0.05) for comparison within and between columns for one sampling date.

FIGURE 10. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on leaf thickness of green foxtail (GF) and yellow foxtail (YF) in 1980 and 1981.

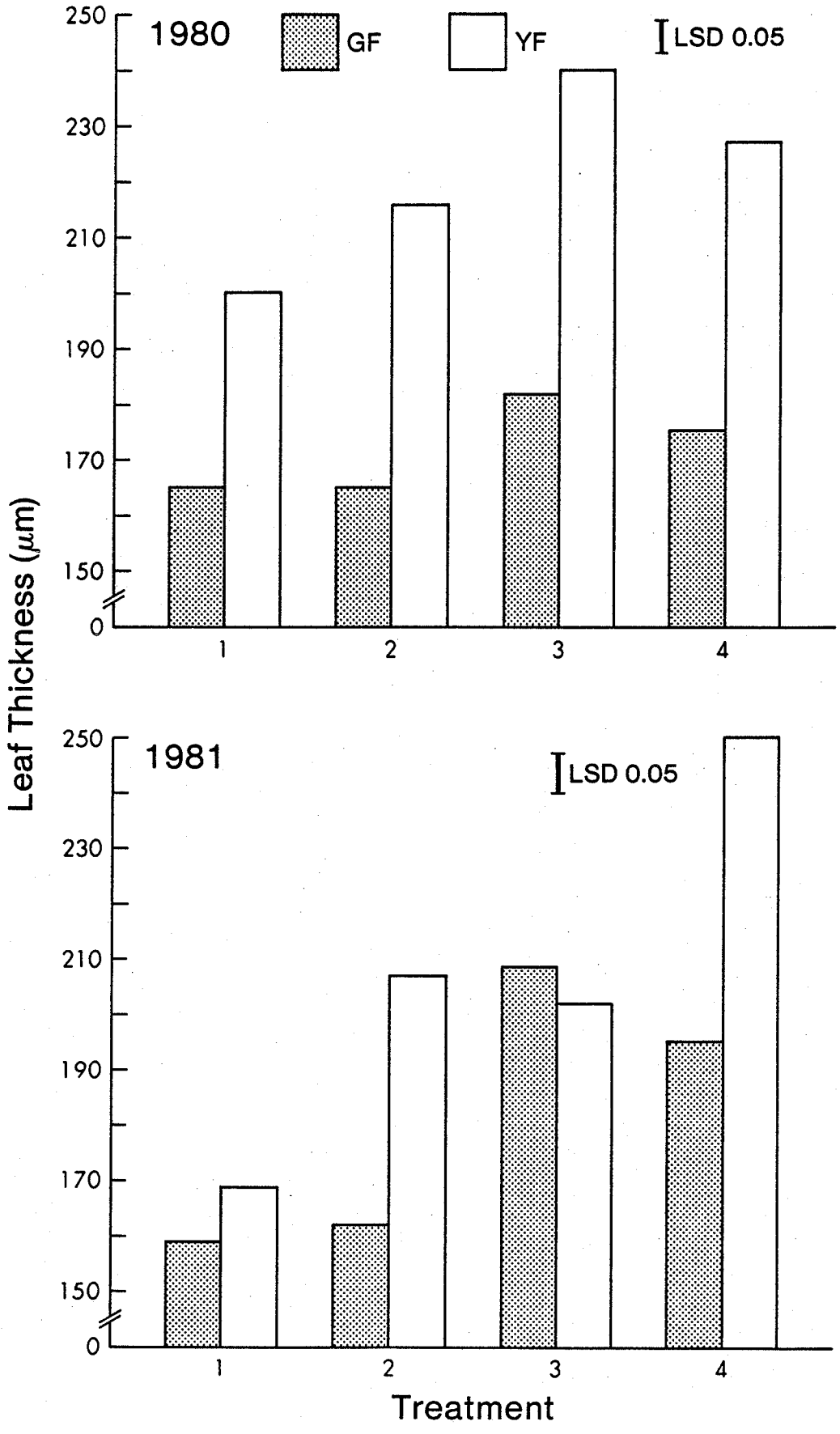
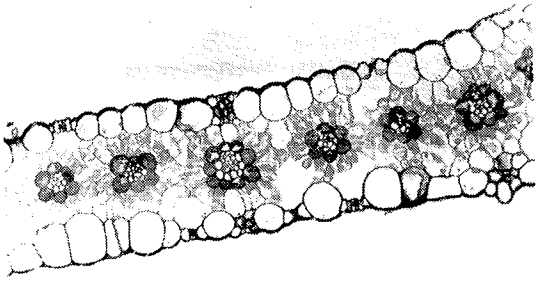
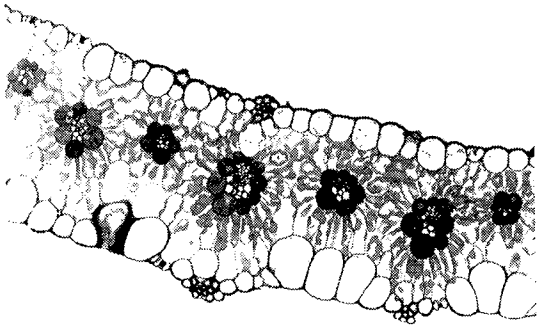

1980
GF
YF
LSD 0.05
1981
LSD 0.05
Leaf Thickness (μm)
250
230
210
190
170
150
0
1
2
3
4
Treatment

FIGURE 11. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the anatomy of green foxtail and yellow foxtail leaves in 1981. Photomicrographs represent the traverse section of the leaf of green foxtail and yellow foxtail magnified 225x.

Green Foxtail

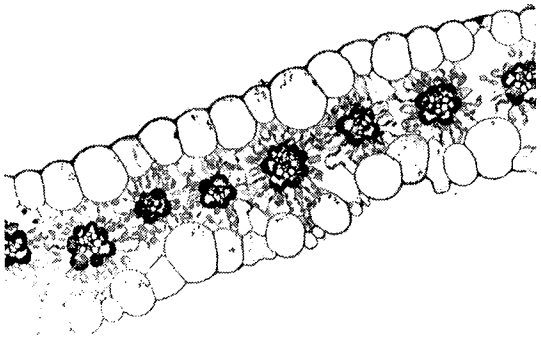


Treatment 1

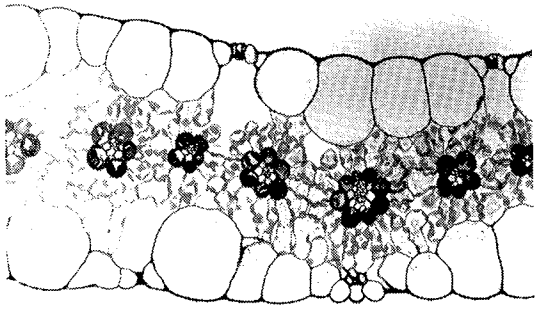


Treatment 4

Yellow Foxtail



Treatment 1



Treatment 4

TABLE 9. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the anatomy of green foxtail and yellow foxtail leaves in 1981.

Species	Treatment	Area[a]		
		Intercellular Spaces	Mesophyll	Total
		(μm^2)		
Green Foxtail	1	1.3	8.1	18.2
	2	2.1	8.1	18.3
	3	2.4	7.3	18.9
	4	2.6	9.8	21.5
Yellow Foxtail	1	2.3	4.9	18.8
	2	3.1	6.6	23.3
	3	2.8	10.8	27.3
	4	2.8	9.1	27.5

[a] Measured from photographs (225x) of transverse sections. Mean of two samples of the last most fully expanded leaf.

foxtail leaves increased by 15% under Treatment 4 as compared to Treatment 1. Within species, the general trend was one of reduced intercellular space, reduced mesophyll area and hence reduced total area as water supply was restricted.

In 1980, seed weights (g/1000 kernels) of yellow foxtail were approximately 3 times greater than the seed weights of green foxtail (Figure 12). In 1981, the difference in seed weights between the two Setaria species was not as great, with yellow foxtail seed ranging from 2 to 2.15 times the weight of green foxtail seeds. Yellow foxtail seed weights decreased 8% in 1980 and 21% in 1981, under Treatment 1 as compared to Treatment 4. By contrast, the weight of green foxtail seed did not differ under the various water regimes.

Germination Study

In 1980 and 1981, seed was collected on the final harvest date of each year to investigate the influence of water stress during seed development on the seed germination of green foxtail and yellow foxtail (Figure 13 and 14). For seed collected in the fall of 1980, germination trials were initiated in March 1981 and were conducted monthly until June 1981. For seed collected in the fall of 1981, germination trials were started in December 1981 and continued monthly until March 1982.

The results reveal a striking variability in response to water stress during seed development on subsequent germination (Figure 13 and 14). In March 1981, the percent germination of green foxtail seeds was generally greater than the percent germination of yellow foxtail seeds, irrespective of treatment (Figure 13). At this date, little difference

FIGURE 12. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) on the weight of green foxtail (GF) and yellow foxtail (YF) seeds in 1980 and 1981.

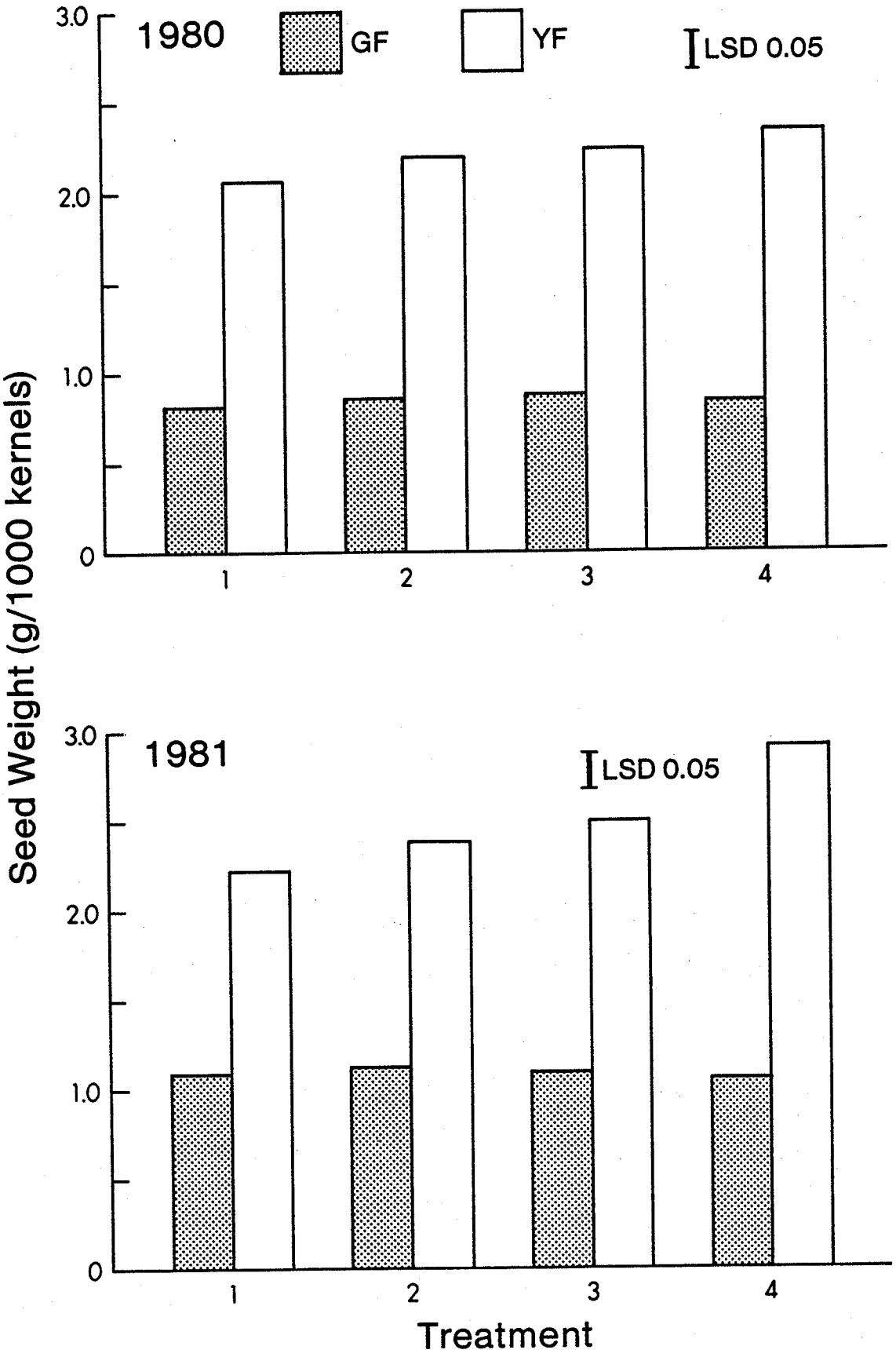
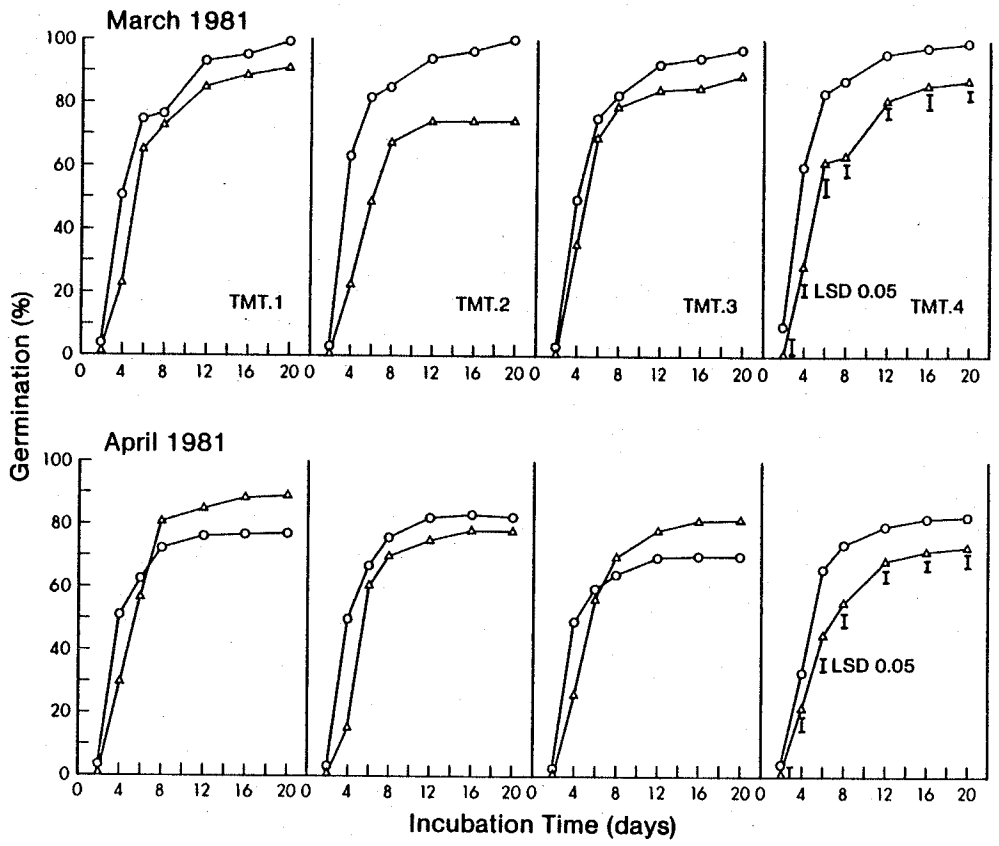
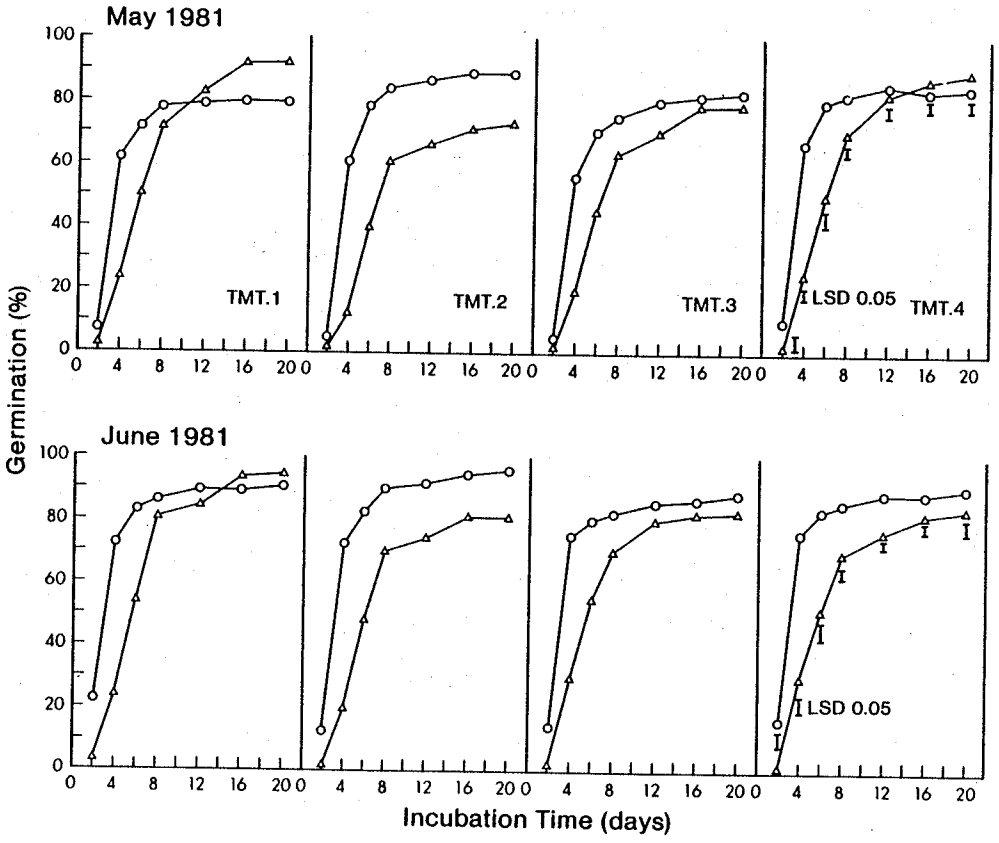
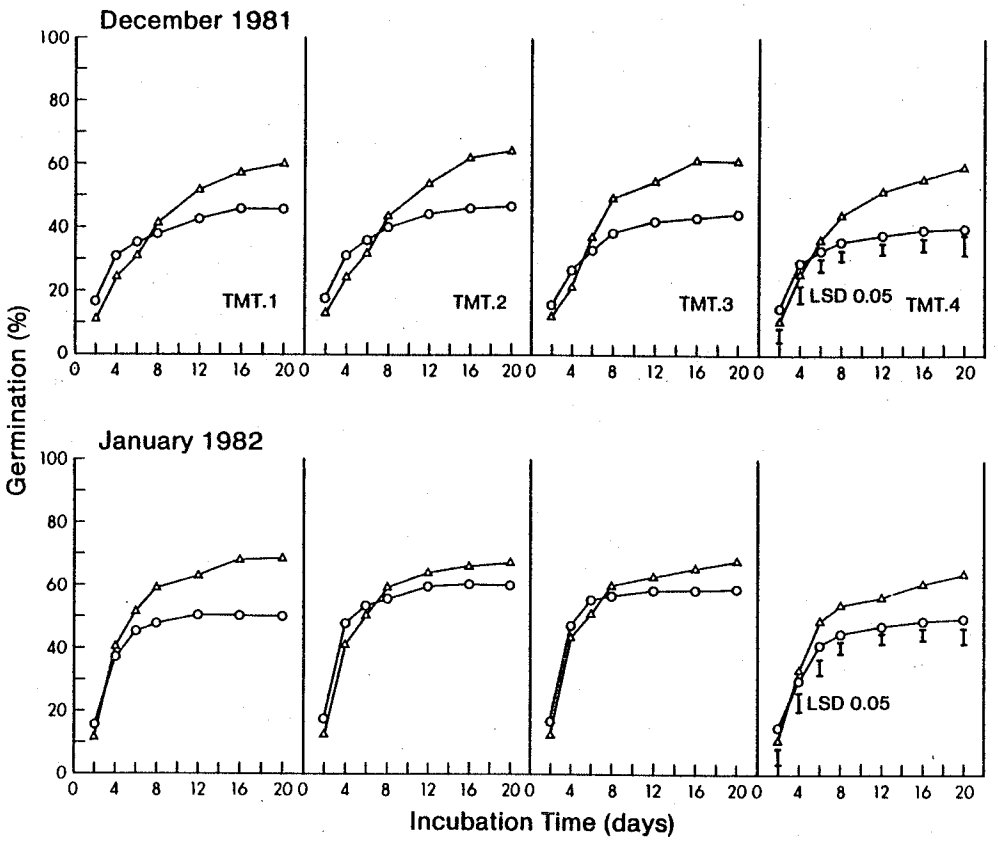
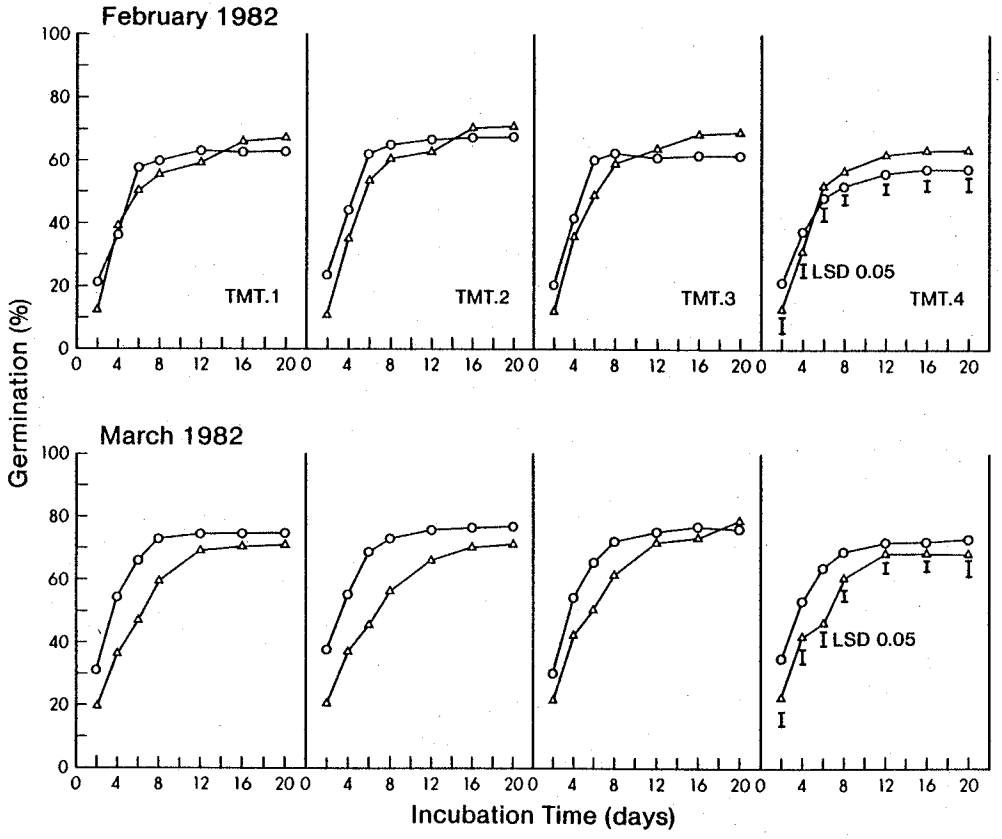

1980
GF
YF
LSD 0.05
3.0
2.0
1.0
0
1
2
3
4
1981
LSD 0.05
3.0
2.0
1.0
0
1
2
3
4
Seed Weight (g/1000 kernels)
Treatment

FIGURE 13 and 14 Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) during seed development on subsequent germination of green foxtail (⊙—⊙) and yellow foxtail (△—△) seeds. LSD (0.05) for comparison of each incubation time over all treatments and species for each month.


March 1981
April 1981
TMT.1
TMT.2
TMT.3
TMT.4
LSD 0.05
Germination (%)
Incubation Time (days)


May 1981
June 1981
TMT.1
TMT.2
TMT.3
TMT.4
LSD 0.05
Germination (%)
Incubation Time (days)


December 1981
January 1982
Germination (%)
TMT.1
TMT.2
TMT.3
TMT.4
LSD 0.05
Incubation Time (days)


February 1982
March 1982
Germination (%)
TMT.1
TMT.2
TMT.3
TMT.4
LSD 0.05
Incubation Time (days)

was observed in final germination of green foxtail seed between the various treatments. The final percent germination of yellow foxtail seed showed a significant decrease under Treatment 2 as compared to Treatment 1, 3 and 4. However, the final percent germination does not reflect the differences in percent germination at various incubation times. For example, in March 1981, four days after initiation of the experiment percent germination of green foxtail seed grown under the various water regimes showed a significant difference in response. However, beyond this date no consistent pattern was observed in either species. Comparing species, the percent germination of yellow foxtail seeds was always lower than the percent germination of green foxtail. This occurred two days after incubation during all the observed sample months.

In the second year of the study, germination experiments were conducted earlier after harvest in order to observe the influence of imposed water stress during seed development on the after-ripening of mature foxtail seeds (Figure 14). The change in percent final germination over sample months was more dramatic in the second season of the study. Green foxtail seed showed a 33% increase in the final percent germination over the course of the experiment. Yellow foxtail seed showed a 15% increase in final germination over the same period. The percent germination of seeds of yellow foxtail was unaffected by water stress imposed on the maternal plant since no significant differences were observed between treatments at any date. The percent germination of green foxtail seeds was generally lower for seeds produced under Treatment 4 than for seeds produced under Treatment 1, 2 and 3. By the

final sample month (March, 1982) this difference between treatments of green foxtail seed was no longer significant.

Two additional incubation temperatures, 16°C and 28°C were included in a second experiment to investigate the effect of temperature on the expression of dormancy (Table 10). Four and five months after harvest, seeds of green foxtail generally had a lower percent germination when compared to yellow foxtail seed produced under the same water regimes and germinated under the same incubation temperatures. Six and seven months after harvest these differences between the species were no longer apparent. The only exception was seed produced under Treatment 4, and incubated at 24°C and 28°C. Under these conditions, six months after harvest, green foxtail showed a significantly lower percent germination than yellow foxtail under the same condition.

Germination for both species increased over time, regardless of treatment or incubation temperature. When comparing Month 4 and Month 7, the largest increase in germination of green foxtail was evident under an incubation temperature of 28°C. Over the duration of the experiment, green foxtail seed showed the highest percent germination at 24°C or 28°C, while yellow foxtail consistently showed the highest germination at 24°C.

Within both species, seed developed under the highest water regime (Treatment 4), showed the lowest percent germination up to six months after harvest, regardless of temperature. By month 6, this trend was no longer evident for seeds of yellow foxtail. Green foxtail seeds developed under the highest moisture regime (Treatment 4) however continued to show a lower percent germination compared to the other moisture regimes through to the completion of the experiment.

TABLE 10. Effect of four water treatments (Treatment 1: 0.3 cm water.week^{-1}; Treatment 2: 0.6 cm water.week^{-1}; Treatment 3: 1.2 cm water.week^{-1}; Treatment 4: 2.5 cm water.week^{-1}) during seed development in 1981 on the final germination of green foxtail (GF) and yellow foxtail (YF) seed at three incubation temperatures.

Months[a] after Harvest	Germination Temperature	Final Germination[b]							
		Treatment 1		Treatment 2		Treatment 3		Treatment 4	
		GF	YF	GF	YF	GF	YF	GF	YF
	---(°C)---	----------(%)----------							
Month 4	16	3.6(26)	5.8(67)	3.9(30)	6.1(74)	3.7(27)	6.0(73)	3.1(19)	5.7(64)
	24	5.1(52)	6.1(74)	5.5(61)	6.2(76)	5.3(56)	6.3(79)	5.1(52)	6.1(75)
	28	5.2(54)	5.7(65)	5.3(57)	5.8(68)	5.2(55)	5.9(66)	5.2(53)	5.3(56)
	LSD (0.05)[c]				0.4				
Month 5	16	4.6(43)	6.4(83)	5.0(50)	6.4(82)	5.2(54)	6.4(81)	4.4(38)	6.0(72)
	24	5.3(57)	6.2(82)	5.5(61)	6.6(86)	5.9(70)	6.7(89)	5.2(55)	6.2(78)
	28	5.6(63)	6.0(72)	6.2(76)	5.8(68)	6.1(74)	5.7(65)	5.3(57)	5.7(64)
	LSD (0.05)[c]				0.5				
Month 6	16	6.2(77)	6.0(71)	5.9(70)	6.0(72)	5.7(66)	6.1(74)	5.3(56)	5.4(58)
	24	6.0(72)	6.4(81)	6.5(84)	6.3(80)	6.4(82)	6.6(86)	5.7(66)	6.4(82)
	28	6.0(73)	6.1(74)	6.1(75)	6.3(79)	5.9(69)	6.0(73)	5.2(55)	6.1(75)
	LSD (0.05)[c]				0.4				
Month 7	16	6.4(82)	6.2(78)	6.4(82)	6.2(77)	6.4(81)	6.4(81)	6.3(80)	6.0(72)
	24	6.7(90)	6.5(85)	6.7(89)	6.3(80)	6.6(87)	6.7(89)	6.4(83)	6.6(87)
	28	6.3(78)	6.4(82)	6.6(87)	6.2(77)	6.5(84)	6.6(87)	6.2(77)	6.3(79)
	LSD (0.05)[c]				0.4				
	LSD (0.05)[d]				0.5				

[a] Months after harvest; Month 4: December, 1981; Month 5: January 1982; Month 6: February, 1982; Month 7: March, 1982.

[b] For statistical analysis, the data was transformed to $(\sqrt{n \div 2})$ to conform to the assumptions underlying the analysis of variance. LSD values apply to the transformed data. Actual data is given in brackets.

[c] LSD (0.05) for comparison between and within columns for one sampling date.

[d] LSD (0.05) for comparison between and within columns for all sampling dates.

Growth Room Study

To augment and expand on the outdoor study, an experiment was conducted under growth room conditions. The first time this experiment was conducted 10%, 14% and 20% soil moisture contents (SMC) were used as the water regimes to be imposed. By the fifth week after emergence however, it was difficult to sustain foxtail growth under the 10% SMC regime. In order to maintain the various SMC, daily weighing and therefore movement of the pots was necessary. Since the foxtail plants under the 10% SMC at this stage did not develop a substantial adventitious root system, this mechanical agitation often resulted in the foxtail plants breaking off at the soil surface. In following experiments the soil moisture content was held at 12%, 14%, 20% SMC representing -2.4 bars, -1.1 bars, and -0.3 bars, respectively. It is important to note that daily waterings, even of the driest water regime, results in the soil reaching field capacity initially when wetted.

Plant Water Status

The weekly leaf water potentials of green foxtail and yellow foxtail grown under the 12% and 20% soil moisture content are presented in Table 11. Leaf water potentials were measured at 12:00 hr just prior to watering. Therefore these values likely represent the lowest water potentials reached by either species. Under 12% SMC, green foxtail consistently had a lower leaf water potential than yellow foxtail over all sampling dates. However, leaf water potentials were comparable for both species under the highest soil moisture content (20% SMC). Over the course of the experiment, leaf water potentials remained fairly constant within each treatment/species combination.

TABLE 11. Effect of two soil moisture contents (12% SMC: -2.4 bars; 20% SMC: -0.3 bars) on leaf water potential of green foxtail (GF) and yellow foxtail (YF).

Weeks after Emergence	Leaf Water Potential[a]			
	12% SMC		20% SMC	
	GF	YF	GF	YF
	----------(- bars)----------			
4	18.5	9.9	6.4	6.0
5	16.5	8.9	5.5	5.8
6	18.3	8.4	5.9	6.5
7	16.3	9.3	7.0	7.1
8	15.3	9.9	7.2	5.4

[a] Non-replicated sample of the last most fully expanded leaf.

Growth and Development

Yellow foxtail was taller than green foxtail over all sample dates, irrespective of soil moisture content (Table 12). There were however, several occasions where this difference in height was not significant. After week 6, significant differences in height between the two foxtail species were only observed under the highest soil moisture content (20% SMC). Under 20% SMC, yellow foxtail was up to 10 cm taller than green foxtail. Through the course of the experiment, this difference in height between green foxtail and yellow foxtail decreased and by week 8, yellow foxtail was only 12% taller than green foxtail under the highest soil moisture content (20% SMC). Within species, plants grown under the highest soil moisture content (20% SMC) were significantly taller than plants grown under the lower soil moisture contents (14% and 12% SMC). The only exception was yellow foxtail four week after emergence.

Similar to height, the number of tillers differed significantly between the two Setaria species. Green foxtail had up to 8 tillers more than yellow foxtail (Table 12). Generally the number of tillers for both species increased up to week 6, beyond which tiller number appeared to plateau.

The number of leaves differed significantly between species, under all water regimes at week 4, 5 and 6, with green foxtail having more leaves than yellow foxtail (Table 13). At week 7, leaf number differences between the species were significant under 12% SMC and 14% SMC but not under 20% SMC. At the following sample date, (week 8), the only difference between the species was under the lowest water regime

TABLE 12. Effect of three soil moisture contents (12% SMC: -2.4 bars; 14% SMC: -1.1 bars; 20% SMC: -0.3 bars) on the height and the number of tillers per plant of green foxtail (GF) and yellow foxtail (YF).

Weeks after Emergence	Soil moisture content	Height		Number of Tillers	
		GF	YF	GF	YF
		----(cm)----			
Week 4	12% SMC	19.7	31.6	10	6
	14% SMC	27.9	42.5	11	6
	20% SMC	38.2	47.3	9	6
Week 5	12% SMC	30.6	37.7	12	7
	14% SMC	38.5	48.4	16	9
	20% SMC	45.7	56.0	14	9
Week 6	12% SMC	38.0	40.8	16	8
	14% SMC	47.0	51.5	16	9
	20% SMC	53.2	62.6	16	11
Week 7	12% SMC	41.0	47.3	14	8
	14% SMC	48.4	55.3	17	9
	20% SMC	58.4	69.2	15	10
Week 8	12% SMC	43.0	51.4	15	9
	14% SMC	56.1	58.7	15	10
	20% SMC	62.0	70.6	16	13
LSD (0.05)[a]		5.5		3	

[a] LSD (0.05) for comparison within and between columns for all sampling dates.

TABLE 13. Effect of three soil moisture contents (12% SMC: -2.4 bars; 14% SMC: -1.1 bars; 20% SMC: -0.3 bars) on the number of leaves per plant and the leaf area per plant of green foxtail (GF) and yellow foxtail (YF).

Weeks after Emergence	Soil moisture content	Number of Leaves		Leaf Area	
		GF	YF	GF	YF
				-----(cm^2)----	
Week 4	12% SMC	39	21	81.97	101.74
	14% SMC	49	24	174.48	201.79
	20% SMC	40	27	199.26	281.78
Week 5	12% SMC	58	38	140.29	197.64
	14% SMC	66	40	233.13	312.81
	20% SMC	66	44	437.19	585.92
Week 6	12% SMC	73	41	253.64	256.48
	14% SMC	70	44	367.89	427.81
	20% SMC	71	57	581.73	726.79
Week 7	12% SMC	58	36	321.02	332.30
	14% SMC	66	42	492.95	459.77
	20% SMC	64	55	665.20	672.82
Week 8	12% SMC	62	45	342.15	411.87
	14% SMC	59	55	611.76	513.29
	20% SMC	75	68	851.41	778.83
LSD (0.05)[a]		10		38.29	

[a] LSD (0.05) for comparison within and between columns for all sampling dates.

(12% SMC). Maximum differences between the leaf number of the two foxtail species was under the lower moisture regimes (12% and 14% SMC), where green foxtail had up to 34 more leaves than yellow foxtail. Within species, no signficant differences were apparent for green foxtail, until the final sample date, where the number of leaves of green foxtail increase under the highest moisture regime (20% SMC). For yellow foxtail, no significant differences in leaf number occurred between the various soil water contents at week 4 and 5. However, leaf number was reduced by water stress at all the succeeding sample dates.

The leaf area of yellow foxtail was greater than the leaf area of green foxtail for all moisture regimes up to week 6 (Table 13). Within species, the leaf area of plants grown under all soil moisture contents were significantly different over all dates, except the first sample date.

Although the shoot dry weight of yellow foxtail was generally greater than the shoot dry weight of green foxtail, this difference was only significant for plants grown under 20% SMC, 6, 7, and 8 weeks after emergence (Table 14). Under the highest soil water content (20% SMC) at these sample dates, the shoot dry weight of green foxtail was on the average 28% less than the shoot dry weight of yellow foxtail. Significant differences in shoot dry weight between the various water regimes for green and yellow foxtail were observed after the initial sample date.

The effect of water deficit on the shoot:root ratios (S/R) of green foxtail and yellow foxtail are presented in Table 14. Both species, showed considerable variability in S/R ratios. A significant

TABLE 14. Effect of three soil moisture contents (12% SMC: -2.4 bars; 14% SMC: -1.1 bars; 20% SMC: -0.3 bars) on the shoot dry weight and the ratio between the shoot dry weight and the root dry weight of green foxtail (GF) and yellow foxtail (YF).

Weeks after Emergence	Soil moisture content	Shoot Dry Weight		Shoot Dry Weight / Root Dry Weight	
		GF	YF	GF	YF
		--(g/plant)--			
Week 4	12% SMC	0.39	0.68	3.01	3.46
	14% SMC	0.67	1.02	2.52	2.38
	20% SMC	0.89	1.27	2.39	2.70
Week 5	12% SMC	0.71	1.14	3.11	3.08
	14% SMC	1.31	1.83	3.21	2.40
	20% SMC	2.05	2.91	3.22	2.57
Week 6	12% SMC	1.53	1.61	2.65	2.40
	14% SMC	1.64	2.63	3.15	2.34
	20% SMC	3.25	4.67	3.09	3.03
Week 7	12% SMC	1.66	2.24	4.03	2.81
	14% SMC	2.59	3.60	3.68	2.54
	20% SMC	4.54	6.30	4.07	2.94
Week 8	12% SMC	2.63	3.28	4.03	2.84
	14% SMC	4.57	5.21	3.94	3.26
	20% SMC	7.00	9.29	4.12	3.39
LSD (0.05)[a]		1.05		0.64	

[a] LSD (0.05) for comparison within and between columns for all sampling dates.

difference was observed between the two species, 7 and 8 weeks after emergence. On the average, green foxtail had a S/R ratio of 3.34 and yellow foxtail had a S/R ratio of 2.82.

Green foxtail started heading five weeks after emergence under the lowest soil moisture content (12%) (data not shown). At week 6, green foxtail was heading regardless of water regime, whereas yellow foxtail was only heading under the 20% SMC (Table 15). The number of inflorescences per plant increased over the course of the experiment, with yellow foxtail having as many as 19 inflorescences per plant. By the final sampling date, yellow foxtail had about 1.6 times more inflorescences than green foxtail under the highest water regimes (14% and 20% SMC). Nine weeks after emergence, green foxtail, had a 25% reduction in the number of inflorescences per plant, while yellow foxtail had over twice the observed reduction for green foxtail under 12% SMC as compared to 20% SMC.

The effect of soil moisture content on the dry weight of the inflorescence of green and yellow foxtail is presented in Table 15. Yellow foxtail, under 20% SMC, consistently had a larger inflorescence dry weight per plant than green foxtail. By the final sampling date, the dry weight of the inflorescence was over 2.5 times greater for yellow foxtail than for green foxtail under the highest moisture regime (20% SMC). No significant differences in head dry weights between treatments was observed until eight weeks after emergence. At this date, yellow foxtail showed a significantly higher allocation in head dry matter under the highest moisture regime (20% SMC) than under the lower moisture regimes (12% and 14% SMC). By contrast, green foxtail

TABLE 15. Effect of three soil moisture contents (12% SMC: -2.4 bars; 14% SMC: -1.1 bars; 20% SMC: -0.3 bars) on the number of inflorescences per plant and the inflorescence dry weight of green foxtail (GF) and yellow foxtail (YF).

Weeks after Emergence	Soil moisture content	Number of Inflorescence		Inflorescence Dry Weight	
		GF	YF	GF	YF
				---(g/plant)--	
Week 6	12% SMC	2	0	0.03	0.00
	14% SMC	1	0	0.03	0.00
	20% SMC	1	3	0.04	0.17
Week 7	12% SMC	2	1	0.07	0.01
	14% SMC	1	2	0.08	0.15
	20% SMC	2	7	0.13	0.56
Week 8	12% SMC	8	3	0.49	0.16
	14% SMC	7	5	0.69	0.53
	20% SMC	5	15	0.65	1.81
Week 9	12% SMC	9	8	0.84	0.56
	14% SMC	7	11	0.86	1.08
	20% SMC	12	19	1.30	3.48
LSD (0.05)[a]		4		0.45	

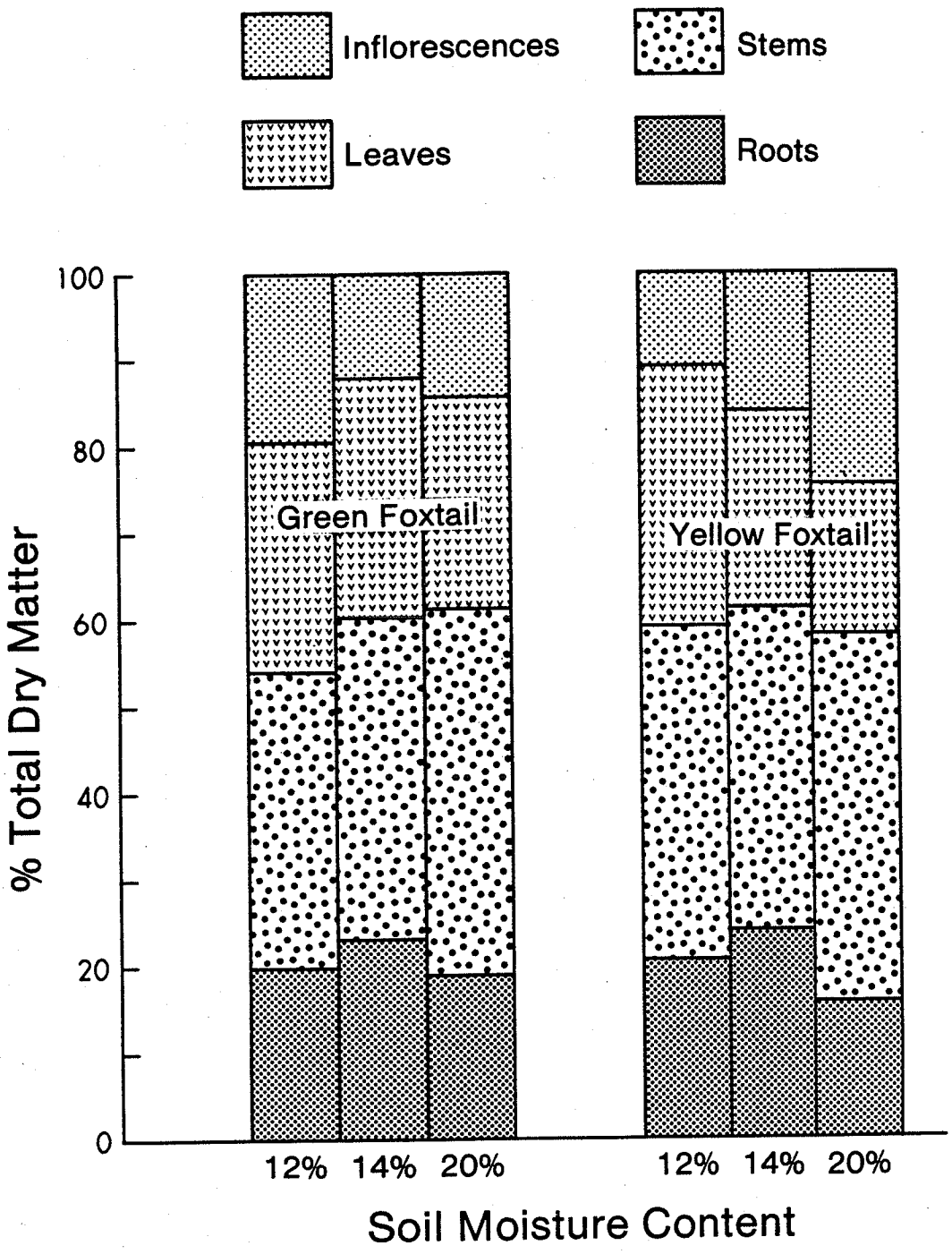
[a] LSD (0.05) for comparison within and between columns for all sampling dates.

did not show any significant shift in allocation to head dry weight under the various water regimes. At the final harvest date, the head dry weight of green foxtail was significantly greater under 20% SMC than under 14% and 12% SMC. Whereas the head dry weight of yellow under all three moisture regimes was significantly different.

Nine weeks after emergence, the pattern of dry matter distribution to the various plant parts was altered by the water regime imposed on both species (Figure 15). Within species, the general trend was; as water deficit increased, the amount of dry matter allocated to the stem decreased from 43% to 35% for green foxtail, and 42% to 38% for yellow foxtail. This occurred when comparing the 20% soil moisture content to the 12% soil moisture content. Both species showed a proportion increased biomass allocation to the leaves as water supply was restricted. This trend was more dramatic for yellow foxtail. The dry matter allocation to the leaves of yellow foxtail increased from 19% under the highest soil moisture regime (20% SMC) to 30% under the lowest soil moisture regime (12% SMC).

For green foxtail, as water deficit increased the dry matter allocation to the inflorescence increased. Yellow foxtail showed a reverse trend, as the moisture supply decreased the dry matter allocation to the inflorescence decreased.

FIGURE 15. Effect of three soil moisture contents (12% SMC: -2.4 bars; 14% SMC: -1.1 bars; 20% SMC: -0.3 bars) on the percent dry matter allocation to roots, stems, leaves and inflorescences of green foxtail and yellow foxtail, nine weeks after emergence.


Inflorescences
Stems
Leaves
Roots
100
80
60
40
20
0
% Total Dry Matter
Green Foxtail
Yellow Foxtail
12% 14% 20%
12% 14% 20%
Soil Moisture Content

DISCUSSION

Outdoor Study

Soil Water Status

In the Winnipeg area, the long term (40 year) average precipitation is 32.5 cm from May 1 to September 30 (Dunlop and Shaykewich, 1982). Assuming a uniform distribution over the growing season, this would be equivalent to 1.5 cm per week. The amount of water applied weekly in Treatment 1 and 2 (0.3 cm water.week^{-1} and 0.6 cm water.week^{-1}) corresponds to lower than average precipitation whereas Treatment 3 and 4 (1.2 cm water.week^{-1} and 2.5 cm water.week^{-1}) represents approximately average and above-average precipitation.

The different rainfall patterns and methods of intercepting this precipitation resulted in differences in initial soil water potentials between the two years (Table 2). In 1980, the first significant rainfall occurred on June 27 and 28 and was not prevented from reaching the plots. As a result, this rainfall contributed to the soil moisture content. However, in 1981 the tarps were used to prevent any precipitation from falling on the plot area prior to gutter placement (week 1) and hence, these two factors could account for the higher soil water potentials initially recorded in 1980 compared to 1981.

Soil water potential readings were taken at a 15 cm depth. The moisture status of the soil surface may have affected growth of foxtail in the early stages of growth but because the soil water potential readings were taken at a 15 cm depth, these possible soil moisture deficit would not be evident. To expand on information on soil water status, gravimetric soil moisture readings were taken in 1981 from 0-5, 5-10, 10-15 cm depths (Appendix 6). Soil moisture readings indicated that the upper 0-5 cm was the driest, these values were beyond the limits of extrapolation from the soil moisture curve determined for this soil (Appendix 1).

The wooden structures were effective in investigating the effects of moisture stress on the growth and development of green and yellow foxtail. In 1980, only the gutters were used to prevent rainfall from reaching the plots. However, over time the efficiency of the gutters to remove water from the plot area tended to vary between treatments (Table 1). Recognizing the shortcomings of the gutter system, a tarping structure was constructed in 1981. When rainfall was forecast, the plastic sheets were used to cover the plots. This greater ability to control incident rainfall may in part account for the greater difference in soil water potential between treatments in 1981 than in 1980.

The weather conditions experienced in 1980 and 1981 were similar (Appendix 8). In both years, the average maximum temperature through the duration was 25°C and the average maximum relative humidity was approximately 90%.

Plant Water Status

Leaf water potentials for both species varied over sample dates and showed a limited correlation with changes in soil water potentials (Table 2 and 3). The sample size used in determining leaf water potentials may have precluded the demonstration of a significant correlation between soil water potentials and leaf water potentials. Also, soil water potentials readings were taken prior to those on leaf water potential. This staggering of readings was necessary to facilitate the number of readings taken. Simultaneous readings of leaf and soil water potential could have enhanced the correlation between these two parameters. Shackel and Hall (1983) reported maximum differences in leaf water potential of stressed and unstressed sorghum which was observed at predawn rather than at midday. Readings were taken at midday.

In addition to restricted water supply, leaf water potential is dependent upon changes in radiation, relative humidity, temperature and leaf factors (Cowan and Milthorpe, 1968). Begg and Turner (1976) contend that the water potential of the leaf shows little dependence on soil water potential and that soil water potential merely sets the limit of recovery possible by the plant during the dark period.

It is clear from observations of Blum (1974) and Peake et al. (1975) that species and varieties develop different degrees of leaf water stress under similar conditions of soil water and evaporative demand. Leaf water potentials of green foxtail were generally lower than leaf water potentials of yellow foxtail. When comparing the highest (Treatment 4) and lowest (Treatment 1) water regimes, leaf water

potentials of yellow foxtail was affected to a greater extent than was the leaf water potential of green foxtail (Table 3). Blum (1974) evaluated the variability between sorghum cultivars with regard to drought response and identified key physiological response patterns in the drought resistant cultivars. Under increasing soil moisture stress, the most drought susceptible genotypes had reduced leaf water potentials, high diffusion resistance and the lowest total soil moisture extraction. More resistant cultivars had low leaf water potentials, which were associated with low diffusion resistance and greatest amount of soil moisture extraction.

Similar trends were observed in examining green foxtail and yellow foxtail. Leaf water potential of yellow foxtail was higher and reduced to a greater extent under water stress than the leaf water potential of green foxtail. Further, Nadeau (1983) observed that yellow foxtail generally had a higher stomatal resistance and a lower transpiration rate than green foxtail. According to Blum's theory, green foxtail would be considered better adapted to moisture stress conditions.

Under the lowest moisture regime (Treatment 1) leaf water potentials were detected as low as -23.5 bars and -17.8 bars for green foxtail and yellow foxtail, respectively (Table 3). In the closely related species, sorghum, Shearman et al. (1972) reported photosynthesis began to decline after the leaf water potential fell below -10 bars and declined rapidly as leaf water potentials approached -20 bars. However, Stout et al. (1978), also studying sorghum under moisture stress, observed that plant growth and yield were severely affected

before large detectable changes in plant water status could be detected. In field trials, Blum (1974) reported mean leaf water potential for all the sorghum cultivars studied, dropped to -15.3 bars and a minimum of -18.3 bars as the soil moisture was depleted. These leaf water potential readings are similar to those observed for green and yellow foxtail.

Growth and Development

Yellow foxtail and green foxtail showed morphological differences typical of differences observed for polyploid and diploid grass species (Stebbins, 1971). Green foxtail is the diploid ancestorial stock from which present day members of the genus evolved, including the tetraploid species, yellow foxtail (Khosla and Sharma, 1973). The enlarged effects of polyploidy was observed in yellow foxtail. These include thicker leaves, larger seeds, and a higher water content than that observed for green foxtail. Flowering and fruiting occurred later in yellow foxtail compared to green foxtail. This is also considered a universal effect of polyploidy (Stebbins, 1971). Further, an important distinction between polyploids and their diploid progenitors is the lowering of reproductive effort (Stebbins, 1971). This was an observed difference between green foxtail and yellow foxtail, as indicated by a reduced allocation of dry matter to inflorescence formation. Generally, the ratio of inflorescence dry weight to shoot dry weight of yellow foxtail under field conditions was one-half that observed for green foxtail. Nadeau (1983) reported that the average number of seeds produced by green foxtail was 3 and 6 times more than for yellow foxtail in the two years of the study.

The range of morphological variability encompassed by tetraploids is less than the total range of that found among diploids (Stebbins, 1971). Again, this feature of ploidy level was observed for green foxtail and yellow foxtail. In the discussion which will follow it will become apparent that green foxtail showed greater plasticity in its response to moisture stress than yellow foxtail. Rapid phenological development and developmental plasticity are considered key traits favoring the survival of plant species under water stress (Turner and Begg, 1981).

While differences in soil water status between treatments were small they were sufficient to cause significant differences in the growth and development of green and yellow foxtail. Both foxtail species showed a significant decrease in height as the amount of water was restricted (Figure 5). Under the highest water regime yellow foxtail was up to 17 cm taller than green foxtail. Akey and Morrison (1984) investigated the effects of moisture stress on the growth of wild oat plants and observed that stressed plants were as much as 23% shorter than unstressed plants. The final length of the main stem of sorghum was shorter for non-irrigated plants than for irrigated plants (Stout et al., 1978). Other evidence of this relationship between plant height and soil moisture status was observed for green foxtail and yellow foxtail exposed to similar moisture regimes imposed in this study. In field studies, Nadeau (1983) observed that yellow foxtail was shorter than green foxtail under the lowest moisture regimes (0.3 cm water.week^{-1} and 0.6 cm water.week^{-1}), but not under the

highest moisture regime (2.5 cm water.week^{-1}). Under the highest moisture condition, yellow foxtail was about 10 cm taller.

As observed with plant height, the number of tillers of green and yellow foxtail was significantly decreased under Treatment 1 compared to Treatment 4 (Figure 6). The number of tillers per green foxtail plant was affected to a greater degree than the number of tillers per yellow foxtail plant. This is similar to results observed for wheat and oats subjected to moderate or severe water stress, where tiller number was decreased in these species at the tiller initiation stage (Joffe and Small, 1964). Blum (1973) cited evidence of decreasing tillering in sorghum exposed to mild water stress. Reduced tillering due to water deficits has also been reported in the weed species, wild oats (Akey and Morrison, 1984).

Morphological responses such as leaf area development, duration and orientation of leaves are among the most effective means a mesophytic plant has for adapting to water stress in the field (Begg, 1980). A reduction in the leaf area in response to decreased soil moisture can be attributed to reduced leaf enlargement (Acevedo et al., 1971); to a decrease in the number of leaves formed due to inhibition of leaf primordia formation (Nicholls and May, 1963); to leaf rolling (Begg, 1980) or to a combination of these factors.

By sample week 5, leaf area and leaf number of both foxtail species decreased significantly when soil moisture was decreased (Figure 7 and 8). Although both species showed reduced leaf area and leaf number under water stress, it is evident that of the two species, green foxtail was more affected by reduced moisture. These data agree

with the results reported by Nadeau (1983) who observed that the leaf area of yellow foxtail was less affected by soil moisture deficits than the leaf area of green foxtail.

Positive leaf movement to orient the leaf parallel to the incident radiation and rolling of the leaves are additional adaptive mechanisms that reduce the effective leaf area and hence the energy load upon the plant (Begg and Turner, 1976). Considerable leaf rolling and color change accompanied the significant decrease of leaf water potentials of sorghum leaves subjected to water stress (Merrill and Rawlins, 1979). By sample week 3 in 1980 and sample week 2 in 1981, leaf rolling was observed in green and yellow foxtail under all moisture conditions except the highest water regime (Treatment 4). However, contrary to the observations of Merrill and Rawlins (1979) leaf water potential increased as a result of this leaf orientation.

For both species, the observed differences in dry weights between the moisture regimes further reflects the noted difference in leaf area, plant height and tiller number (Table 4 and 5). Unlike the other growth parameters, shoot dry weight did not differ between the species. Yellow foxtail generally had fewer tillers and fewer leaves than green foxtail, indicating a difference in allocation of dry matter between various plant parts.

A decrease in height, number of tillers, leaf area and dry weight of water stressed foxtail plants could alter their ability to compete with a crop species. A reduction in the number of tillers could result in a reduction in seed bearing culms and possibly the number of seeds produced, while, a reduction in leaf area would reduce

the photosynthetic tissue and its ability to compete for space. Vengris and Damon (1976) concur that weeds which are taller and produce higher yields of foliage are better competitors.

Although limited data is available on the effect of moisture on the competitive ability of green foxtail, some information is available for yellow foxtail. Research done by Staniforth (1958) with soybeans, indicated that in seasons of limited moisture, yield reductions from moderate yellow foxtail infestations were less than when moisture was normal or above-normal (Weber and Staniforth, 1957; Staniforth, 1958). Feltner et al. (1969) studied competition of yellow foxtail in grain sorghum and determined the ability of yellow foxtail to compete was greatest during a year of above-average rainfall. The competitive ability of green foxtail in corn by comparison, was reduced when soil moisture conditions were adequate (Moyer and Dryden, 1979).

The percent protein of green foxtail and yellow foxtail vegetative growth decreased linearly over the growing season (Figure 9). This decline can be attributed to the dilution effect from cellulose and other structural carbohydrates. Similar decreases in percent protein content with maturity have been reported in sorghum (Ajakaiye, 1984), barley (Singh et al., 1973) and wild oats (Akey, 1982). Hsiao (1973) reported that protein synthesis of most species was very sensitive to water stress. Other studies also indicate that moisture deficits inhibited protein synthesis (Singh et al., 1973; Dhindsa and Cleland, 1975). Green and yellow foxtail did not show a clear trend of a decline in percent protein with a corresponding decrease in soil moisture. This is similar to results reported by Akey (1983) for wild

oats. The protein content of wild oats was not significantly lower in stressed wild oats plants than in the unstressed wild oat plants.

Unlike protein content of the shoot, protein concentration of the grain when subjected to moisture deficits frequently increases (Barlow et al., 1983). This increased protein in the grain may be due to different patterns in starch and protein accumulation during grain filling or to different susceptibilities of protein and starch synthesis to water stress. Barlow et al. (1983) contend that the wheat grain is relatively protected from water deficits during drought. Any effect on protein synthesis would be manifested in the transport of nitrogen to the grain. The effect of water deficits on protein content of the inflorescence of green foxtail and yellow foxtail does concur with these earlier studies (Table 7). However, the trend of increased protein content with increased moisture stress was not observed until sample week 5 and was only significant for yellow foxtail.

There are several structural and anatomical characters that are considered to confer an adaptive advantage in plants subjected to water stress. The majority of these characteristics involve leaf structure and anatomy including cutinization of the epidermis, thickness of the leaves and the mesophyll surface area per unit leaf area (Begg, 1980; Nobel, 1980). The effect of water stress on the production of epicuticular wax differed between the Setaria species studied (Table 8). The leaves of yellow foxtail subjected to water stress produced more epicuticular wax than leaves grown under well-watered conditions. By comparison, wax development did not differ for green foxtail regardless of moisture status. Early studies indicated that water stress promoted

heavier cutinization of leaves (Skoss, 1955; Clark and Levitt, 1956). Baker and Procopiou (1980) also observed heavier deposits of wax on leaves of plants under arid conditions. Dryness of habitat was not necessarily associated with greater wax content (Weete et al., 1978). Further, Akey (1982) observed that the amount of surface wax present on leaves of wild oats subjected to moisture deficits did not differ significantly at jointing or the flagleaf stage. Not until heading that the leaves of wild oats subjected to water stress showed a 60% greater epicuticular wax production than leaves of wild oats grown under well-watered conditions. It is possible that if another sample was taken at heading, difference in epicuticular wax production between treatments may have been detected for green foxtail.

Water stress can affect leaf anatomy by causing changes in leaf thickness and the number and size of mesophyll cells (Nobel, 1980). Hsiao (1973) states that although indirect, leaf thickness is a good indicator of plant water status. Leaf thickness values were decreased with a decrease in water availability in both Setaria species (Figure 10 and 11). Leaf thickness of green foxtail was less affected than leaf thickness of yellow foxtail. Nobel (1980) reported a correlation between an increase in leaf thickness with an increase in maximum rates of photosynthesis.

Changes in the size of internal cellular components of leaves have been observed (Cutler et al., 1977). The general trend observed with increasing water stress for green and yellow foxtail was one of reduced intercellular space and reduced mesophyll. Although, the latter was not as pronounced in green foxtail (Table 9). The ratio of

mesophyll area to total area indicates that green foxtail on the average had a ratio 1.4 times greater than yellow foxtail. This ratio for leaves of yellow foxtail was affected by the imposed moisture stress. However, this same ratio for leaves of green foxtail remained unchanged. Nobel (1980) states that the greater the area occupied by the mesophyll cells compared to total area resulted in higher photosynthesis rates and higher water use. Cutler et al., (1977) concurred that cell size can affect the internal water relations and responses of plants to water deficits. These researchers concluded that cell size and an organism's ability to survive drought are inversely correlated. Although the mesophyll cells did not differ greatly, the area of the other components varied as water deficit increased. The results obtained on leaf parameters do not directly relate to those observed by Nobel (1980), since his data represented the total surface area of the various cell components. However, the result of this study may indirectly suggest that green foxtail would be considered to be better adapted to conditions of moisture stress.

The success of a species in a stressful habitat is determined by its reproduction and propagation, and the proportion of dry weight allocated to reproduction (Salibury, 1942; Stebbins, 1951). The number of heads per green foxtail and yellow foxtail plant was decreased under water stress conditions (Figure 8). The noted differences in inflorescence dry weight per plant further reflects the observed differences for inflorescence number between the moisture regimes (Table 6). The average ratio of inflorescence dry to shoot dry weight was .43 for green foxtail and .26 for yellow foxtail. However, the ratio of

inflorescence dry weight to shoot dry weight remained unchanged for both species regardless of treatment. This is contrary to results observed for wheat (Davidson and Campbell, 1984) and barley (Irvine et al., 1980) grown under conditions of restricted moisture. In both studies, harvest index was reduced as water availability was reduced.

By contrast, Hsiao et al. (1976) studying several sorghum varieties reported that the harvest index was increased under non-irrigated compared to irrigated conditions. A substantial difference in partitioning of assimilates did occur between the various sorghum cultivars examined and was reflected in the harvest index value. The timing, duration and severity of stress influences the affect water deficits on harvest index (Turner and Begg, 1981). Fischer (1980) contends that stress during seed filling will reduce the harvest index due to a corresponding reduction in assimilate production. Further, grain yield under water stress are highly correlated with size of the plant. The reproductive sink size is constantly adjusted during stress to result in a balance between vegetative size and grain yield (Fischer, 1980). Green foxtail and yellow foxtail when stressed over the growing season maintained this precise balance in allocation to the reproductive structures.

Under moisture stress, the inflorescence of both Setaria species emerged from the flag leaf normally, but part of the inflorescence had died. This "head blasting" has been observed in sorghum, when water stress was instilled at the beginning of head emergence (Hsiao et al., 1976).

As previously noted the various components of yield, number of inflorescence and inflorescence dry weight were affected by induced moisture stress in both foxtail species. Inflorescence dry weight, however, can be broken down into its components: the number of seeds per inflorescence and seed weight. Nadeau (1983) reported a substantial decrease in seed production in green and yellow foxtail under water stress. Seed production of green foxtail was less affected by the different water regimes imposed than the seed production of yellow foxtail. Similar to seed production, the weight of green foxtail seed was less affected by moisture stress than the weight of yellow foxtail seed (Figure 12). In fact, seed weights determined for green foxtail did not differ significantly under the various water regimes. In contrast, yellow foxtail seed weight decreased 8% and 21% in 1980 and 1981 respectively. This occurred under the lowest moisture regime (Treatment 1) compared to the highest moisture regime (Treatment 4).

Water stress decreased seed weights in sorghum (Stout et al., 1978) and wild oats (Sawhney and Naylor, 1982). Harper (1977) speculated that evolution has favored homeostasis of seed size within most species because of its vital role in maintaining continuity between generations. Although seed size was determined indirectly by 1,000 kernel weights, this adaptative strategy is congruent with that observed in green foxtail. However, homeostasis of seed size was not observed in yellow foxtail.

From these observations on the components of yield certain trends distinguish these two Setaria species. Green foxtail produces numerous small seeds, by contrast, yellow foxtail yields fewer larger

seeds. The interaction between seed size and seed number is of particular importance in determining adaptative strategies. Stebbins (1974) theorized that large seeds contain large embryos and/or large quantities of stored materials. As a result, these larger seeds produce more vigorous seedlings and enable a seedling to produce an extensive root system by relying on an abundance of stored food. The disadvantages of large seed is that it is at the cost of seeds number, larger seed take longer to develop and are less easily dispersed than smaller seed. By comparison, the great advantage of large seed number is the increased chance of random dispersal (Stebbins, 1971). Seeds of yellow foxtail decreased in weight under water stress may in turn have a detrimental effect on seedling vigor and the future establishment of this species.

Germination Study. "Effective" reproduction is not solely a matter of seed production. It involves germination and development to maturity of the next generation (Harper, 1977). Therefore dormancy and the physiological requirements for germination to a great extent control the potential weedy nature of a species (Norris and Schoner, 1980). Germination of foxtail seed subjected to various moisture conditions during development indicates the difficulty in conducting a study on climatic effects on seed dormancy. Although the results were variable, several trends were observed. Percent germination of green foxtail seed, 2 to 4 days after incubation was consistently higher than for yellow foxtail regardless of treatment (Figure 13 and 14). Following 8 months of dry storage in 1980, foxtail seeds had greater than 75% germinability, indicating that the necessary after-ripening had occurred

(Figure 13). In 1981, the storage period was decreased to 4 months. Over the course of the second year of study, germination of foxtail seed increased greatly with seeds of green foxtail showing the largest increase. The only treatment difference was observed for green foxtail seeds produced under the highest moisture regime (Treatment 4). The trend was one of reduced germination under high moisture conditions. This is in agreement with reports by Sexsmith (1969) that lower levels of moisture during seed formation decreased dormancy of wild oat seed. Vanden Born (1971) observed variations in dormancy of green foxtail seed at harvest, attributing the disparity to variations in the conditions under which the parent plants were grown. Contrary to the results presented herein, the author postulated that the decrease in dormancy was induced by the cool damp weather prior to sampling. Considerable variation in dormancy in various lots of green and yellow foxtail seed was also reported by Taylorson and Brown (1977). These researchers contend that differences in relative maturity could possibly account for some variability, as large collections of uniformly mature grass seeds are difficult to collect.

The variability in the germination results does not lend to clear interpretation of the data. Sexsmith (1969) stressed that if differences in seed dormancy are to be determined accurately, it is imperative that the germination test be conducted at the appropriate time or times. This researcher observed greater disparities in germination of wild oat seed 72 days after maturity than 28 days after maturity. In this study differences may not have been detected due to late initiation, ie. 4 and 8 months after harvest. The selection of

the optimum time is difficult and can only be overcome by initiating a large number of germination tests, at short intervals from the time of harvest until dormancy has completely disappeared (Sexsmith, 1969). More replication and earlier initiation of the germination study may have resulted in a greater separation in percent germination of green and yellow foxtail seed subjected to imposed water stress.

Best temperatures for germination of green foxtail seed was 24 to 28°C. By comparison, the optimum temperature for germination of yellow foxtail seed was 24°C (Table 10). These results correspond to those reported by Dawson and Bruns (1962). Under field conditions, yellow foxtail germinated at lower temperatures than green foxtail or barnyard grass (Echinochloa crus-galli (L.) Beauv.) leading the authors to speculate that yellow foxtail would likely germinate more readily during short periods of warm weather in the spring.

Growth Room Study

Plant Water Status

Similar to the results observed in the outdoor study, subjecting green and yellow foxtail to water stress reduced the leaf water potential of both species (Table 11). Unlike the field results, leaf water potentials did not fluctuate to any great degree. Under the highest moisture regime (Treatment 4), leaf water potentials of green foxtail and yellow foxtail were similar. In controlled environments such as growth rooms, radiation levels are usually low and constant, temperature and relative humidity are maintained about average. Thus leaf water potentials of plants grown under growth room conditions

would not be expected to fluctuate to the same degree as field grown plants. The only aspect of moisture stress generally under study in controlled environments is water deficit induced by restricted water supply (Begg and Turner, 1976).

Leaf water potentials did not decrease with time or age of the plant as reported by several researchers (Blum, 1974; Begg and Turner, 1976; Ritchie, 1981). Sampling of the last-most fully expanded leaf may have minimized the effect of leaf age on the leaf water potential readings.

Growth and Development

While the height, leaf area, shoot dry weight and inflorescence dry weight were reduced in stressed foxtail plants in both the outdoor and growth room study, observed reductions were not as great in the growth room.

This discrepancy in response to water deficits of plants grown in controlled environments compared to plants grown in the field has been reported by Begg and Turner (1976) and Akey (1982). These researchers reported a more pronounced effect of water stress on plants grown under growthroom conditions. Several factors contribute to a more pronounced effect of moisture stress in controlled environments. As was the case in this study, most indoor studies utilize small containers. Ritchie (1981) observed that the amount of water removed per unit volume of soil is usually much greater in container experiments than in the field. This tends to accelerate the rate of onset of stress when water is witheld. However, the fact that in growthrooms

radiation levels and wind velosities, are usually low and constant, temperature and relative humidity are above average, may have minimized the effect of small container size.

In addition, soil types differed between the two environments. In the outdoor study, Altona clay loam soil was used. For the growth room study, Almasippi very fine sandy loam was used. Examination of the soil moisture release curves of these soils indicates the Almasippi very fine sandy loam requires only a slight change in water content; below 10% to result in large decreases in soil water potential. As a result soil moisture contents were maintained above this level which resulted in maintaining a higher soil water potential than that experienced under field conditions.

Fertility has also been reported to affect water relations in plants. Increases in fertility would increase growth rates and water-use efficiency (Ritchie, 1974). Fischer and Kohn (1966) studied wheat under field conditions and reported that high fertilizer rates increased moisture stress as a result of increased crop growth. In the growth room study, a large amount of fertilizer was used, this may have influenced water use efficiency and alter the observed differences between the species. For example, under controlled environmental conditions, dry matter yield of yellow foxtail was greater than dry matter yield of green foxtail, regardless of water regime. In field experiments, where no fertilizer amendment were made, shoot dry weight did not differ significantly between the Setaria species. Bubar (1981) reported a distinct difference in the ability of these two species of foxtail in the uptake of nitrogen and in the utilization of nitrogen in

the production of top growth. More likely it is the combined effect of soil type, low irradiance, high fertility, and the method of instilling moisture stress which resulted in smaller reductions in the plant parameters observed under growth room conditions.

The primary purpose of the growth room study was to investigate the patterns of dry matter allocation in green and yellow foxtail. Of particular interest was the influence of soil moisture stress on shoot:root ratios (S/R) of these Setaria species. The S/R ratio of green foxtail was generally greater than the S/R ratio of yellow foxtail (Table 14). This is congruent with results reported by Nadeau (1983). This researcher observed that the smaller root mass of green foxtail compared to yellow foxtail was capable of supporting proportionately greater shoot growth. Troughton (1974) theorized that the size of the root system is the most influential morphological factor in determining the rate of water loss. A large root system relative to the shoot would be a disadvantage under water stress. Other researchers disagree with this theory Passioura (1980) states an increase in root to shoot ratio of a plant during drought has the advantage in assisting the plant to match it's water supply to evaporative demand. This researcher qualified this statement by emphasizing that such a response has a respiratory cost that may greatly reduce water use efficiency. Examining a range of drought tolerant sorghum cultivars, Begg (1980) reported the most tolerant genotypes possessed higher root weights, greater root volumes and lower S/R ratios.

Changes in S/R occurred over time (Table 14). No distinct trends however were observed for foxtail plants subjected to the

various moisture regimes by the final sample date. There exist several conflicting reports in the literature on the effect of moisture stress on the distribution of dry matter between roots and shoots (Gales, 1979). Kummerov (1980) concluded that no clue regarding adaptation of plants to arid environments could be obtained from the S/R ratio.

Water stress has been reported to enhance root growth not only relative to shoot growth but absolutely (Hsiao and Acevedo, 1974). A comparison of wheat varieties by Hurd (1974) indicated that plants with a more extensive root system could exploit a larger soil volume, thereby making more effective use of soil water. Rooting length, distribution and the ratio of secondary to primary roots also influence water uptake and these rooting characteristic may determine a species adaptability to water stress. Passioura (1981) postulated that under dry conditions where proportionately more seminal roots than adventitious roots are present, more water could be retained in the soil. This type of ratio between the two root systems ensures that soil water would be available for seed production and the survival of the species assured. A marked difference in the relative proportion of seminal and adventitious roots under moisture stress was observed for green foxtail and yellow foxtail (Nadeau and Morrison, 1983). Four weeks after emergence, 55% and 68% of the total root length of plants grown under the driest regime were comprised of seminal roots in green foxtail and yellow foxtail, respectively. Under the highest moisture regime, seminal roots comprised of only 5% and 14% of the total root length in green foxtail and yellow foxtail, respectively.

The relative success of a species or biotype may be influenced by the allocation of fixed carbon to various portions of the plant (Salibury, 1945). Assimilate translocation in plants is often reduced under moderate to severe water stress (Hsiao and Acevedo, 1974). Moisture stress reduces source strengths by decreasing photosynthesis and reducing sink strength by inhibiting growth, thus limiting translocation. Hsiao and Acevedo (1974) state that the altering of translocation may determine the partitioning of assimilates among different parts of the plant under stress. Biomass allocation to the leaves increased in a proportional manner due to increasing moisture stress in both foxtails (Figure 15). Contrary to results observed in the field, the percent dry matter allocated to the inflorescence was altered when plants were subjected to moisture stress. As water supply decreased the dry matter allocation to the inflorescence decreased in yellow foxtail but increased for green foxtail. This noted difference in allocation patterns under water stress between the outdoor study and the growth room study are likely due to the previously stated problems associated with controlled environment studies.

SUMMARY AND CONCLUSIONS

Morphological differences observed between green foxtail and yellow foxtail are typical of differences observed for diploid and polyploid grass species. The gigas effect of polyploidy was observed in yellow foxtail, including thicker leaves, higher water content, and larger seeds compared to green foxtail. Developmental differences between these foxtail species include later flowering and fruiting in addition to a reduction in allocation to the reproductive effort in yellow foxtail compared to green foxtail. Further, under water stress conditions, the range of morphological variability expressed by the tetraploid species, yellow foxtail was less than the range expressed by the diploid grass species, green foxtail. This phenomena is not unlike that observed for other polyploid and diploid species.

The shoot growth of green foxtail was reduced to a greater extent than yellow foxtail when comparing the lowest and highest moisture regime. This species difference was evident in both the outdoor and growth room study. However, it was less pronounced under controlled environmental conditions. Green foxtail was shorter, initiated fewer tillers, produced fewer leaves and less leaf area under the lowest water regime compared to the highest water regime. While yellow foxtail exhibited similar trends, the effects on these growth parameter was not as severe. By contrast the leaf water potential and fresh weight to dry weight ratio of yellow foxtail was lowered to a greater

extent than these same growth parameters for green foxtail under moisture stress.

Leaf characteristics were also altered under water stress. Leaf thickness was reduced in yellow foxtail when subjected to moisture stress. This trend was also observed for green foxtail. Epicuticular wax formation was increased under soil moisture deficits in both species. On the average, yellow foxtail had the greatest increase in epicuticular wax production as the amount of water supplied was restricted. This coupled with reductions in leaf area under water stress could severely hamper the herbicidal control of these Setaria species. Further experimentation in this area would be of benefit to farmers as well as weed biologists.

The reduction in number and dry weight of the inflorescence in green foxtail and yellow foxtail subjected to moisture stress was not correlated with a reduction in the ratio of inflorescence dry weight to shoot dry weight. In the outdoor study, this ratio was not significantly different under the various moisture regimes for either species. This same balance was observed for the S/R ratio of green and yellow foxtail. No distinct trends were observed as the amount of water was restricted. Seed weights of green foxtail also did not vary under the various water regimes imposed. However, seed weights of yellow foxtail decreased with decreasing water availability.

The greatest percent germination of yellow foxtail seed occurred at 24°C, whereas green foxtail had the greatest percent germination at slightly higher temperatures. The data also indicated that seed germination of green foxtail seed may be effected by the exposure of the parent plant to high moisture conditions.

From these results, green foxtail would likely be a stronger competitor than yellow foxtail under moisture stress conditions. However, yellow foxtail does appear to be able to utilize added moisture effectively, particularly in terms of increased height and leaf area. Although these foxtails are closely related and inhabit the same types of environments, their biological response to various environmental conditions could alter the extent to which the species becomes a problem in cultivated land. Further examination of the nature of the competitive ability of these Setaria species under varying moisture and fertility would be useful. It is likely that the interaction of fertility, moisture, light and temperature influence the extent to which each species would be competitive.

In addition there is some evidence indicating that moisture stress during development may influence subsequent germination. This could potentially effect the spread and estalbishment of these species in cultivated land.

In summary, further study is needed to understand the different biological strategies utilized by green and yellow foxtail, particularly when in competition with crop species. This research would enhance our understanding of crop losses due to these weeds, and prove helpful in defining cultural practice which could assist the produce in controlling these weeds.

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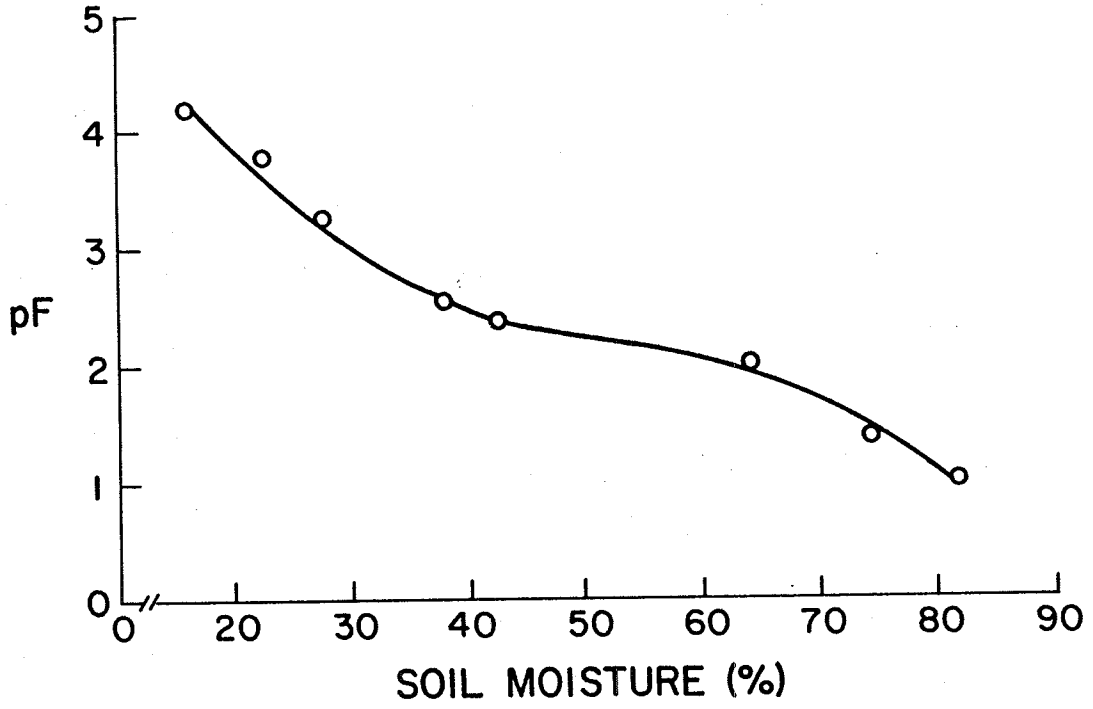
APPENDIX

APPENDIX 1. Moisture release curve for Altona clay loam soil determined from pressure plate apparatus data and gravimetric soil moisture content (%). The equation of the line is represented by the following polynominal regression equation (r = 0.99):

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

Y = pF

X = soil moisture content (%)

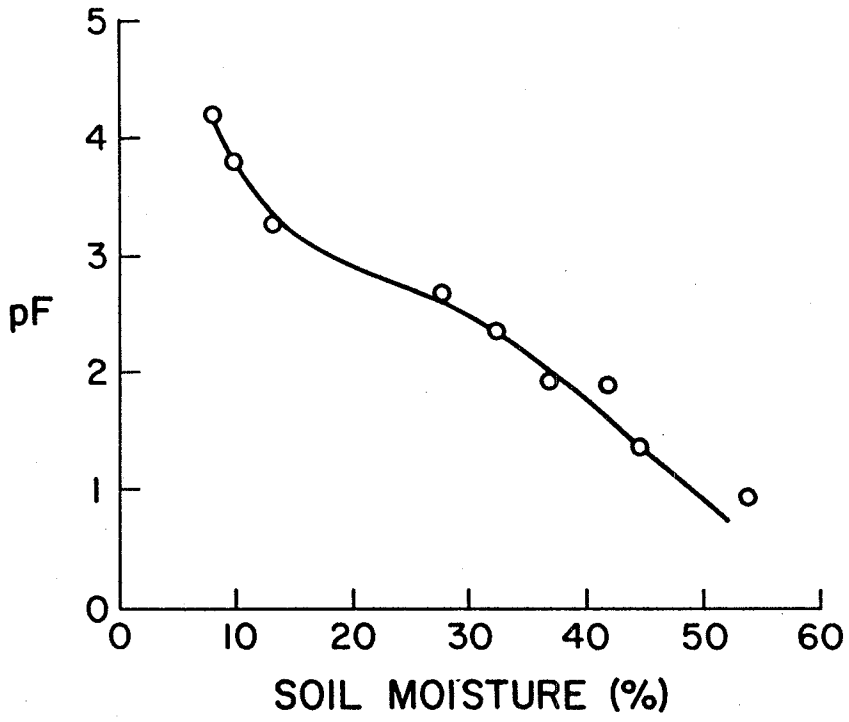

5
4
3
2
1
0
pF
0
20
30
40
50
60
70
80
90
SOIL MOISTURE (%)

APPENDIX 2. Moisture release curve for Almasippi very fine sandy loam soil determined from pressure plate apparatus data and gravimetric soil moisture content (%). The equation of the line is represented by the following polynominal regression equation ($r = 0.98$):

$$Y = 7.235 - (0.403)X + (0.00085)X^3 - (2.602 \times 10^{-5})X^4 + (2.238 \times 10^{-7})X^5$$

$Y = pF$

$X =$ soil moisture content (%)


5
4
3
2
1
0
pF
0
10
20
30
40
50
60
SOIL MOISTURE (%)

APPENDIX 3. Standard curve for epicuticular wax present on green foxtail (GF) and yellow foxtail (YF) leaves determined at an absorbance of 590 nm. The equation of the line for each species is as follows:

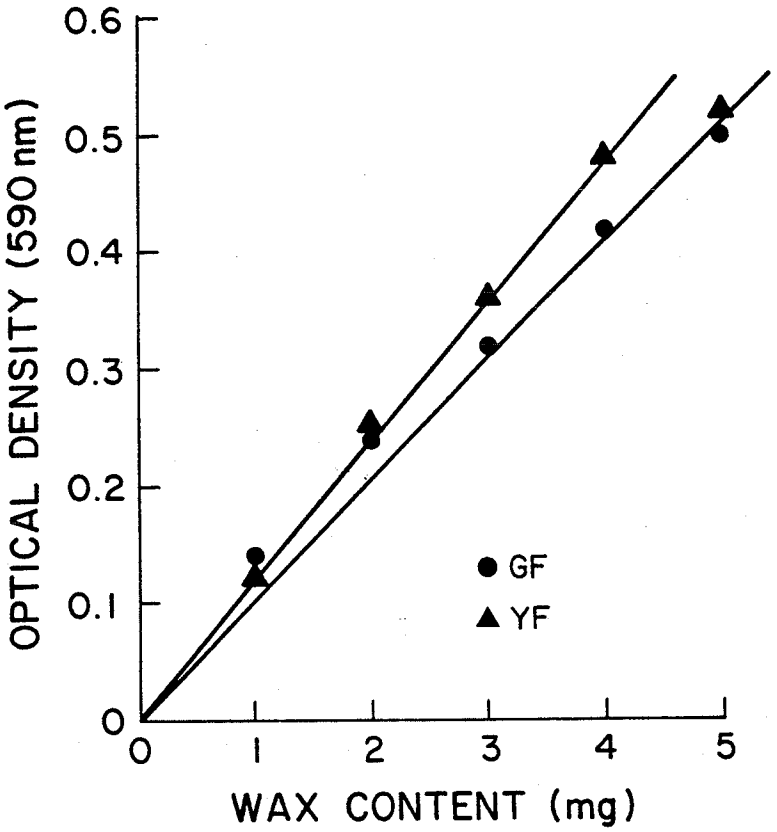
Green Foxtail

$$Y = .0258 + (.0972)X \qquad (r = 0.99)$$

Yellow Foxtail

$$Y = .0173 + (.1086)X \qquad (r = 0.99)$$

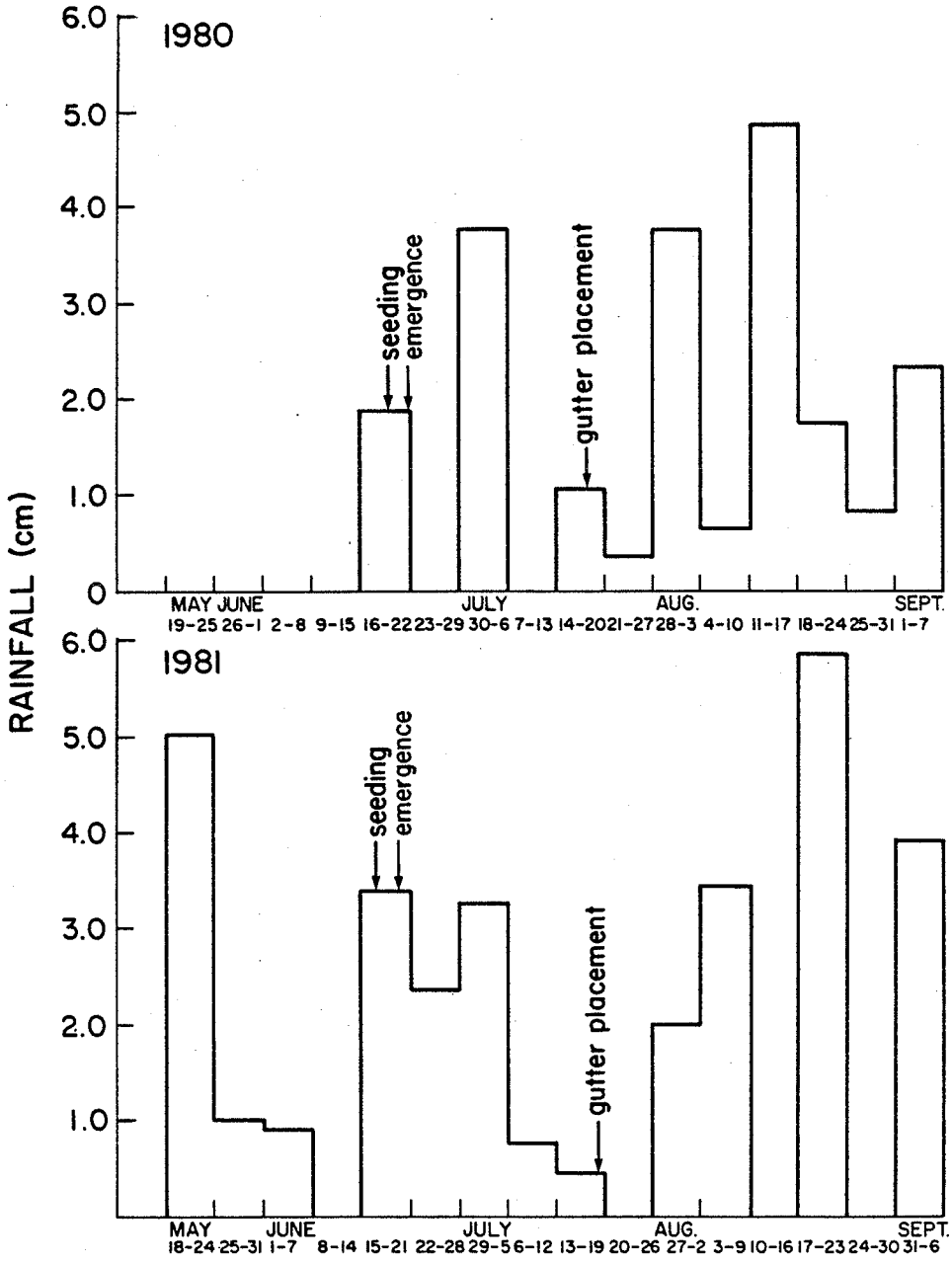
Y = absorbance at 590 nm
X = mg of wax


OPTICAL DENSITY (590 nm)
0.6
0.5
0.4
0.3
0.2
0.1
0
0
1
2
3
4
5
WAX CONTENT (mg)
GF
YF

APPENDIX 4. List of corresponding calendar dates for each sample week for 1980 and 1981 outdoor study.

Year	Sample Week	Calendar Date
1980	1	July, 16
	2	July, 23
	3	July, 30
	4	August, 6
	5	August, 13
	7	August, 27
1981	1	July, 18
	2	July, 25
	3	August, 1
	4	August, 8
	5	August, 15

APPENDIX 5. Rainfall Patterns in 1980 an 1981.


RAINFALL (cm)
1980
6.0
5.0
4.0
3.0
2.0
1.0
0
seeding
emergence
gutter placement
MAY JUNE JULY AUG. SEPT.
19-25 26-1 2-8 9-15 16-22 23-29 30-6 7-13 14-20 21-27 28-3 4-10 11-17 18-24 25-31 1-7
1981
6.0
5.0
4.0
3.0
2.0
1.0
seeding
emergence
gutter placement
MAY JUNE JULY AUG. SEPT.
18-24 25-31 1-7 8-14 15-21 22-28 29-5 6-12 13-19 20-26 27-2 3-9 10-16 17-23 24-30 31-6

APPENDIX 6. Gravimetric soil moisture content in the outdoor study in 1981.

Sample Week	Depth	Soil Moisture Content[a] Treatment 1	Treatment 2	Treatment 3	Treatment 4
	--(cm)--	----------(%)----------			
1	0-5	10.62	9.56	11.47	10.85
	5-10	16.46	14.88	16.20	16.09
	10-15	15.74	15.13	17.27	17.52
2	0-5	9.57	10.32	13.32	14.85
	5-10	13.32	14.52	16.42	17.33
	10-15	12.84	14.01	16.09	17.15
3	0-5	18.86	19.28	25.71	29.42
	5-10	17.85	18.20	24.75	28.54
	10-15	19.35	19.28	22.82	27.34
4	0-5	20.46	19.74	18.44	19.69
	5-10	20.78	20.23	20.66	22.48
	10-15	20.16	19.24	19.64	24.89
5	0-5	16.52	17.34	19.21	21.13
	5-10	17.48	19.87	22.55	20.59
	10-15	19.63	19.72	21.83	23.39
	LSD (0.05)[b]		1.99		

[a] An average of six measurements per treatment.

[b] LSD (0.05) for comparison within and between columns.

APPENDIX 7. Soil temperature in the outdoor study in 1980 and 1981.

Year	Sample Week	Soil Temperature[b] Treatment 1	Treatment 2	Treatment 3	Treatment 4
		----------(°C)----------			
1980	1[a]	22.6	22.3	22.2	22.2
	2	19.1	19.2	19.3	19.0
	3	20.8	20.6	20.2	19.3
	4	16.9	17.0	16.8	16.7
	5	16.7	16.3	16.7	16.0
	7	14.8	14.7	14.5	14.5
	LSD (0.05)		0.8		
	1[a]	23.6	23.4	23.5	23.1
	2	18.1	17.8	17.7	17.1
	3	18.3	18.3	18.0	17.8
	4	17.3	17.3	17.3	17.0
	5	16.8	16.9	16.8	16.4
	LSD (0.05)		0.7		

[a] Gutter placement.
[b] An average of three measurements in 1980, an average of six measurements in 1981, taken with a thermocouple psychrometer buried at a depth of 15 cm.

APPENDIX 8. 1980 Weather Data. [Lat. 49° 54'N; Long 97° 14'W; Elevation Altitude: 239.6 meters (ASL)]

JUNE

DATE	TEMPERATURE MAXIMUM °C	TEMPERATURE MINIMUM °C	REL. HUMIDITY MAXIMUM %	REL. HUMIDITY MINIMUM %	WIND TOTAL PRECIP. mm	WIND $\bar{X}$ SPEED km/h	WIND PREVAILING DIRECTION
1	21.9	8.8	70	30		22.8	ENE
2	24.2	4.8	77	20		15.0	NNE
3	27.5	5.6	73	19		8.3	SSW
4	22.9	10.5	94	40	8.8	18.0	SSW
5	24.1	10.5	95	28	Tr.	20.0	WNW
6	24.5	9.3	82	30		10.8	SE, SW, NW
7	25.5	11.5	20	41	Tr.	20.0	W
8	20.5	9.8	86	44	11.3	13.2	NW
9	20.2	5.7	95	39	3.1	14.1	NW
10	19.4	6.6	87	42	11.6	11.8	W, NW, NNW
11	23.2	8.0	85	37		15.0	W
12	26.3	8.6	76	35	Tr.	11.6	SSE
13	19.0	14.0	100	64	11.3	21.3	ENE
14	17.4	13.8	98	81	3.1	11.5	NW, NNW
15	15.1	7.1	98	69	11.6	24.9	NNW, W
16	25.5	4.7	95	32	0.2	14.9	SSW, W
17	22.0	10.9	95	50	5.0	31.7	S
18	16.9	8.2	94	37	5.6	34.5	NW
19	21.7	6.5	94	42	Tr.	14.2	S
20	23.2	8.6	93	37		7.5	Calm
21	22.3	5.8	95	41	3.7	13.8	ESE
22	20.4	10.8	95	47	Tr.	5.3	Calm
23	19.2	10.7	94	71	6.9	14.0	SSE
24	22.1	12.4	94	53	3.0	15.9	WNW
25	22.0	10.3	93	45		22.2	W
26	25.4	9.9	98	44		9.8	SSE
27	27.3	17.1	93	61	7.0	23.5	S
28	22.8	14.0	96	52	3.2	12.5	NE
29	23.6	10.5	96	40	7.4	9.0	NWN
30	22.8	13.2	85	60	8.6	27.1	S
31							
					Total		Prevailing
Mean	22.3	9.6	90	45	90.4	16.5	S
Normal	22.7	10.3	88	45	80.3	18.5	S

JULY

DATE	TEMPERATURE MAXIMUM °C	TEMPERATURE MINIMUM °C	REL. HUMIDITY MAXIMUM %	REL. HUMIDITY MINIMUM %	WIND TOTAL PRECIP. mm	WIND $\bar{X}$ SPEED km/h	WIND PREVAILING DIRECTION
1	28.3	17.8	79	49	0.4	36.5	S
2	24.2	16.7	85	54	0.4	19.6	SSW
3	27.4	13.1	96	40		7.5	NW
4	29.3	16.0	81	43		16.5	S, SW
5	31.4	17.7	84	34		15.0	S
6	34.0	17.1	67	43		26.4	S
7	32.8	22.2	76	57		32.6	S
8	26.7	14.7	75	29	0.2	28.8	WNW
9	30.2	12.8	64	24		17.0	WSW
10	29.6	14.0	81	30		10.5	ENE
11	27.1	14.9	95	60	8.7	8.7	Calm
12	30.5	16.1	98	27	Tr.	7.5	N, W
13	29.8	15.9	83	40		7.4	ENE
14	24.3	14.6	95	55	0.6	8.0	SSW
15	22.4	17.4	94	72	12.1	14.8	S
16	22.8	14.9	96	61	Tr.	11.1	WSW
17	26.3	12.0	98	43		9.7	WNW
18	28.5	14.8	96	41		4.8	NW
19	29.7	15.2	92	46	0.2	4.5	S
20	20.5	9.4	94	52		14.5	NNE
21	25.0	7.0	90	37		7.9	SSE, S
22	25.5	11.8	83	45		18.0	S
23	27.3	13.5	94	61	2.0	17.4	S
24	20.8	8.3	94	63	Tr.	18.5	W
25	21.6	5.6	93	33		16.7	NW
26	24.6	6.4	84	34		8.0	SW, W
27	26.5	9.7	86	37	2.2	12.3	SW
28	25.7	12.3	87	36		20.4	SSW
29	24.2	13.1	91	68	4.0	23.0	S
30	29.5	16.3	96	54	8.2	17.8	S
31	25.3	14.5	96	48		14.9	WNW
					Total		Prevailing
Mean	26.8	13.7	88	46	39.0	15.2	S
Normal	25.9	13.5	89	44	80.3	16.3	S

AUGUST

DATE	TEMPERATURE MAXIMUM °C	TEMPERATURE MINIMUM °C	REL. HUMIDITY MAXIMUM %	REL. HUMIDITY MINIMUM %	WIND TOTAL PRECIP. mm	WIND $\bar{X}$ SPEED km/h	WIND PREVAILING DIRECTION
1	25.3	9.0	100	44		5.7	Calm
2	26.0	15.2	92	49	2.0	7.9	ESE
3	23.4	13.2	98	71	0.2	4.0	Calm
4	28.6	12.0	100	47		5.6	SSE
5	21.4	17.2	81	81	56.6	12.4	N,NNW
6	25.5	15.4	96	43	10.0	23.5	NNW
7	29.2	12.3	96	48	Tr.	9.3	NW
8	22.6	11.3	96	53		18.0	N
9	23.3	9.6	95	43	0.2	13.7	NNE,
10	27.3	11.0	95	43		7.7	SSW, SW, WSW
11	32.2	16.0	92	26		10.9	WSW
12	26.3	13.0	94	36		11.3	ENE
13	32.3	14.4	90	39		12.8	S
14	24.6	11.5	89	42		15.2	N
15	21.5	7.8	95	23		13.0	NNE, NE
16	23.1	8.0	90	38		10.0	S
17	28.6	10.5	90	42	21.9	13.3	S
18	28.2	13.7	94	45	Tr.	13.1	S
19	28.9	15.7	79	43		22.2	S
20	28.0	16.7	83	55		15.2	SSE
21	25.9	18.6	82	55		19.2	S, SSE
22	27.9	14.8	94	56		6.7	S, SSE
23	27.7	19.0	89	58	Tr.	13.3	E
24	28.0	19.0	89	56	0.2	17.6	E, SE
25	26.3	17.9	89	58		10.6	E
26	27.6	15.2	92	30		15.8	NE
27	26.9	12.3	100	32		5.2	NE
28	27.3	13.0	81	32		15.8	S
29	27.5	12.9	92	38		18.1	S
30	30.7	16.2	92	42		25.3	S
31	22.2	8.5	95	76	12.5	24.0	NNW
					Total		Prevailing
Mean	26.6	13.6	92	46	103.6	13.4	S
Normal	25.0	12.2	92	47	73.7	17.1	S

APPENDIX 9. 1981 Weather Data. [Lat 49° 54'N; Long: 97° 14'W; Elevation Altitude: 239.6 metres (ASL)]

JUNE

DATE	TEMPERATURE MAXIMUM °C	TEMPERATURE MINIMUM °C	REL. HUMIDITY MAXIMUM %	REL. HUMIDITY MINIMUM %	WIND TOTAL PRECIP. mm	WIND $\bar{x}$ SPEED km/h	WIND PREVAILING DIRECTION
1	16.1	3.8	95	40		18.9	N
2	18.5	0.8	90	40		12.4	N
3	23.9	2.6	88	26		15.8	E
4	25.4	15.6	67	45	Tr.	33.8	SE
5	27.5	15.7	84	32	Tr.	17.2	S
6	20.9	5.8	68	45		27.6	N, W
7	17.2	5.8	69	35		28.6	NNE
8	22.7	7.1	77	26	Tr.	24.0	NW
9	25.0	9.8	82	40		13.6	NE
10	26.0	4.6	84	25		7.6	SE
11	32.3	14.7	53	26		27.7	S
12	25.3	16.0	96	47	2.2	25.5	S
13	23.8	10.8	93	35	Tr.	14.9	ENE
14	18.0	5.7	82	60	Tr.	22.8	NE
15	21.5	0.8	90	18		10.2	NE
16	27.7	6.0	79	18		11.9	W
17	19.9	10.3	82	39		24.4	NE
18	19.9	5.5	84	36		13.1	E, ENE
19	25.5	4.0	85	20		4.4	WNW
20	27.8	10.7	90	31	7.8	19.6	S, SSW, NW
21	27.0	12.0	98	34		8.9	NNW
22	34.4	15.7	85	16	0.2	19.4	W
23	33.7	17.1	70	36		12.7	W
24	31.0	20.2	81	25	0.6	28.5	W
25	25.2	11.2	85	35		26.8	WSW+
26	19.9	9.3	93	46	Tr.	20.3	E
27	20.1	12.1	96	60	19.8	31.5	ESE
28	17.2	12.3	96	85	13.4	25.5	NNW
29	22.0	11.6	93	47	Tr.	14.3	NW
30	26.0	11.6	89	48	0.6	20.2	SSW
31							
					Total		Prevailing
Mean	24.0	9.6	84	37	44.6	19.4	S
Normal	22.7	10.3	88	45	80.3	18.5	S

JULY

DATE	TEMPERATURE MAXIMUM °C	TEMPERATURE MINIMUM °C	REL. HUMIDITY MAXIMUM %	REL. HUMIDITY MINIMUM %	WIND TOTAL PRECIP. mm	WIND $\bar{x}$ SPEED km/h	WIND PREVAILING DIRECTION
1	22.6	8.2	90	33		11.4	NNW
2	30.4	11.7	70	26		15.0	WSW
3	28.0	13.8	81	35	1.2	17.8	NE, ENE
4	19.4	12.3	92	71	5.6	21.6	NE
5	25.1	9.1	98	41		7.0	Calm, S
6	28.6	16.6	87	44	Tr.	27.1	S
7	25.5	15.1	75	38	Tr.	24.5	WNW
8	28.6	10.5	91	31		8.7	W
9	33.5	19.0	74	31		13.3	SW
10	31.6	18.2	77	31		11.0	ENE, E, NW
11	29.0	17.6	68	50	2.8	17.3	S
12	29.4	15.7	77	29		14.8	W
13	34.8	17.5	79	38	Tr.	21.5	S
14	24.3	14.5	94	63	0.5	18.6	N
15	25.2	12.4	98	50	Tr.	8.9	N
16	26.5	14.9	96	51	Tr.	14.0	NNW
17	27.6	14.7	92	44	1.0	12.4	SSW
18	26.8	15.6	92	32	Tr.	20.7	WNW
19	25.0	13.5	88	40	Tr.	9.8	W
20	22.7	13.2	92	70	12.2	12.8	NNE
21	22.8	13.1	96	41	Tr.	12.6	N
22	27.2	12.6	89	34	Tr.	3.8	Calm
23	32.5	16.4	83	37		21.6	SSW
24	27.0	9.1	83	33		24.3	NNW
25	23.1	5.5	92	25		7.5	N, Calm
26	26.2	8.9	81	36	Tr.	17.8	SSW
27	28.3	14.3	86	28	Tr.	15.3	NW, WNW
28	27.0	13.7	89	29	Tr.	17.6	W, NW
29	31.8	12.4	81	25	Tr.	20.4	SSE, S
30	28.4	13.7	84	28	0.2	18.5	WNW
31	28.6	14.5	73	26	0.2	16.3	NW
					Total		Prevailing
Mean	27.3	13.5	85	28	23.7	15.6	W
Normal	25.9	13.5	89	43	80.3	16.3	S

AUGUST

DATE	TEMPERATURE MAXIMUM °C	TEMPERATURE MINIMUM °C	REL. HUMIDITY MAXIMUM %	REL. HUMIDITY MINIMUM %	WIND TOTAL PRECIP. mm	WIND $\bar{x}$ SPEED Km/h	WIND PREVAILING DIRECTION
1	25.8	12.7	85	37		22.0	NW
2	24.6	9.5	95	39		8.9	ENE
3	25.1	12.2	96	37	25.7	16.8	SE
4	20.4	12.0	96	53	3.6	31.5	SE
5	20.3	11.2	98	60	4.4	20.2	NW
6	21.6	10.6	96	62	4.3	6.5	Calm
7	23.5	14.3	96	50	11.5	9.6	NNE
8	23.3	12.8	98	51		14.8	NW
9	22.0	9.0	98	53		1.4	Calm
10	21.0	11.4	98	70	8.4	0.8	Calm
11	22.4	22.4	100	61	0.7	6.4	Calm
12	24.0	14.2	94	46	Tr.	8.5	WNW
13	23.0	11.4	98	59	1.6	9.8	NW
14	24.2	10.2	98	36		7.9	NNE, NNW
15	25.2	11.3	84	39		13.5	SE
16	17.8	12.3	98	60	10.7	23.1	SSE
17	17.3	12.7	98	78	5.7	9.3	W, WNW
18	27.0	9.4	96	51		16.2	SSE
19	30.7	14.9	98	50	Tr.	8.7	Calm
20	22.7	19.0	97	82	20.2	18.6	E
21	22.5	13.4	98	41	0.9	30.3	WNW, NW
22	22.1	11.4	76	41		25.2	W
23	23.5	12.5	87	43	0.3	6.6	WNW
24	28.9	12.1	93	50		9.5	S
25	21.1	9.8	89	46	Tr.	23.0	NW
26	18.5	6.0	87	43		13.9	WNW
27	21.4	3.5	94	37		7.3	Calm
28	18.6	12.8	96	73	1.3	23.5	S
29	20.4	10.9	98	64	3.7	12.5	SSW
30	20.4	10.9	96	40	6.8	14.8	WNW
31	19.5	6.8	89	50	0.2	6.4	S
					Total		Prevailing
Mean	22.5	11.3	94	52	109.8	13.8	Calm
Normal	25.0	12.2	92	48	73.7	17.1	S