EFFECT OF MOISTURE STRESS ON WILD OAT GROWTH AND DEVELOPMENT AND RESPONSE TO DICLOFOP METHYL

BY

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FOREWORD

This thesis has been written in manuscript style. Chapter III will be submitted for publication in the Canadian Journal of Plant Science. Chapter V will be submitted for publication in Weed Science, while Chapter IV will not be submitted for publication. For the sake of consistency, all manuscripts were prepared in accordance with the format specified by Weed Science.

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ABSTRACT

Akey, William Charles, M.Sc., The University of Manitoba, October 1982. Effect of Moisture Stress on Wild Oat Growth and Development and Response to Diclofop Methyl. Major Professor; Ian N. Morrison.

The growth and development of wild oats (Avena fatua L.) subjected to moisture stress was investigated both outdoors and in a growth room. Outdoors, wild oats grown in a clay loam soil received 2.5 or 0.6 cm water per week. In the growth room, wild oats were grown in a very fine sandy loam watered daily to a soil moisture content (SMC) of 20% (water potential -0.3 bars) or 10% (-6.5 bars). Significant reductions in growth occurred in wild oats subjected to moisture stress from emergence to maturity compared to unstressed controls. Maximum reductions were recorded in the leaf area, dry weight and number of viable tillers of 46, 32, 38%, respectively, outdoors and 55, 57 and 38%, respectively, in the growth room. Wild oat growth was reduced more by a period of water stress occurring after, rather than before, the four-leaf stage. Wild oats stressed during early stages of growth remained smaller than unstressed controls following alleviation of stress at the four-leaf stage.

Field and growth room studies were also undertaken to determine the influence of moisture stress on the control of wild oats with diclofop methyl {2-[4-(2,4 dichlorophenoxy) phenoxy] propionic acid}. Additional experiments were conducted in a growth room to determine the basis for the reduced effectiveness of the herbicide on

stressed wild oats. The field study was very inconclusive owing to the high degree of variability encountered in the results. In the growth room, control of wild oats brought to a SMC of 10% (-6.5 bars) prior to treatment, was slightly, but significantly, reduced compared to that at the 20% SMC(-0.3 bars). Maintaining the SMC at 10% for a further 5 days after spraying caused up to a 38% reduction in wild oat control. The retention, penetration, or metabolism of diclofop methyl were not significantly affected by moisture stress. However, moisture stress decreased the proportion of translocated ^{14}C-diclofop methyl recovered from the combined apex, third-leaf and tillers of wild oats. This may partially account for the reduced activity of this herbicide on stressed wild oats.

CHAPTER I

INTRODUCTION

Wild oats are by far the most serious annual grassy weed of cultivated fields in the prairie provinces of Canada (Sharma and Vanden Born, 1978). Wild oats have received considerable attention by research scientists and a large body of literature now exists on many aspects of their biology (Jones, 1976). Although wild oats prefer temperate to cool climates and moist soil conditions (Sharma and Vanden Born, 1978) their widespread distribution over much of the prairie provinces and continued existence despite the not infrequent hot and dry periods, would indicate that they are able to adapt to periods of limited water availability.

Few studies have considered the effects that water stress may have on the growth of wild oats. Pavlychenko and Harrington (1935) examined the development of the root systems of wheat and wild oats under dry farming conditions and concluded that wild oats was a serious competitor under those conditions. Sharma et al. (1977) reported reductions of up to 45% in the dry weight of wild oats grown at reduced soil moisture levels. The dormancy of seeds produced by wild oats was also found to be altered by conditions of low soil moisture (Sexsmith, 1969). Clearly, further studies on the influence of water stress on wild oat growth and development would improve our understanding of the biology of this species.

A number of soil- and foliar-applied herbicides are presently available for the control of wild oats. The postemergence herbicide, diclofop methyl, has proven to be particularly effective for the selective control of wild oats in cereal and oilseed crops (Chow and Dorrell, 1979; Todd and Stobbe, 1977). The response of a weed species to a herbicide is not a constant property but may be modified by changing environmental conditions or by the physiological state of the plant (Hammerton, 1967). Control of wild oats with diclofop methyl was reduced when they were grown at reduced soil moisture levels before or after treatment (Dortenzio and Norris, 1980). Under similar circumstances, reduced control of wild oats with flamprop-methyl [methyl-N-benzoyl-N-(3-chloro-4-fluro-phenyl)-DL-alanine] (Jeffcoat et al., 1977) and difenzoquat (1,2-dimethyl-3,5-diphenyl-1H-pyrazolium) (Miller et al., 1978) also occurred. An understanding of the mechanism by which water stress alters the response of wild oats to certain herbicides would benefit farmers through improved weed control recommendations and may in the future aid in the development of more effective weed control programs.

Studies were undertaken to determine: i) the effect of moderate moisture stress on the growth and development of wild oats; and ii) the basis for the reduced control of wild oats with diclofop methyl under conditions of moisture stress.

CHAPTER II

LITERATURE REVIEW

Introduction

In addition to influencing plant growth, environmental factors including temperature, relative humidity, and moisture stress are known to affect the response of both weeds and crop plants to herbicides (Hammerton, 1967; Muzik, 1976; Morrison and Cohen, 1980). While the effects of temperature and relative humidity on herbicide activity have been the subject of considerable research, the influence of moisture stress has received comparatively little attention. In the first part of this review attention is directed to the effects of moisture stress on plant growth and development; and in the second part the focus is shifted to the effects of moisture stress on herbicide performance.

Effects of Moisture Stress on Plant Growth and Development

Morphological Effects

Leaf Development. The development of water deficits in plants exposed to periods of limited water availability leads to a number of morphological changes (Begg and Turner, 1976). One of the most visible effects of water stress on plant morphology is its effect on leaf development, i.e. leaf initiation, enlargement, and senescence.

Nicholls and May (1963) examined the effects of water deficits on leaf primordium formation in barley (Hordeum vulgare L.) grown in growth cabinets. A reduction in soil water potential to about -5 bars reduced the number of leaf primordia forming spikelets instead of leaves. In a later study, Husain and Aspinall (1970) demonstrated that the formation of new leaf primordia on the apical meristem of barley was inhibited at soil water potentials of -1 bar and less. However, sensitivity of the apical meristem to water stress may vary among species. For example, Marc and Palmer (1976) found that water stress resulting in leaf water potentials of -20 to -30 bars, occurring 10 to 20 days after sowing, significantly reduced the number of leaves produced by the primary stem of sunflower (Helianthus annuus L.). This was considered to result from a decreased rate of leaf initation.

The final leaf area attained by a plant depends on both the rate and duration of cell division and cell elongation. Suppression of leaf enlargement begins at even mild water deficits. For example, Boyer (1968) found that leaf enlargement in sunflower, grown in soil at various moisture contents, ceased at leaf water potentials below - 3.5 bars. Similarly, leaf enlargement in soil-grown corn (Zea mays L.), soybean and sunflower plants was strongly inhibited when leaf water potentials dropped below -4 bars and stopped while turgor pressures were still positive (Boyer, 1970).

Of the two processes involved in leaf enlargement, cell division is generally regarded as being less sensitive to water stress than cell elongation (Slatyer, 1967; Hsiao, 1973). Elongation of intact young leaves of corn slowed when the soil water potential dropped

corresponding to a leaf water potential of -7 bars (Acevedo et al., 1971). However, when the stress was relieved, a transitory period of rapid growth completely made up for the reduced elongation during the stress period, indicating that cell division proceeded unabated during the stress period.

In some instances (Gardner and Nieman, 1964; Terry et al., 1971) the sensitivity of cell division has been shown to exceed that of cell elongation. In one of the few studies in which cell numbers were counted, McCree and Davis (1974) showed that a reduction of 30% in the final leaf area of sorghum [Sorghum bicolor (L.) Moench] grown under conditions of moderate moisture stress could be attributed solely to a reduction in the number of epidermal cells per leaf. Regardless of which of the processes of cell division or cell elongation is more sensitive, it is clearly evident that moisture stress reduces the potential leaf area that a plant may otherwise attain under well-watered conditions.

Water stress may also affect total leaf area by hastening the senescence of leaves (Karamanos, 1979). When wheat (Triticum aestiuum L.) and oat (Avena sativa L.) plants subjected to periods of moderate or severe stress at the tiller initiation stage were examined a few days after rewatering, virtually all of the leaves of the severely stressed plants and approximately half of the leaves of the moderately stressed plants were either completely dead or partially damaged (Joffe and Small, 1964). Kozlowski (1976) suggested that water stress alters the hormonal balance of leaves,

thus promoting senescence. An increase in abscisic acid levels and a decrease in the supply of cytokinins to the leaves are both known to occur in plants during periods of water stress (Aspinall, 1980) and may account for the observed increases in the rate of leaf senescence.

Both the aforementioned studies on leaf development and other studies which are discussed in later sections of this review, increasingly point to the fact that responses which have been measured in plants suddenly exposed to water stress under controlled environment conditions differ from those measured in field-grown plants (Boyer and McPherson, 1975; Begg and Turner, 1976; Brown et al., 1976). For example, Boyer (1970) and Acevedo et al. (1971) reported complete cessation of leaf elongation in corn at leaf water potentials of -7 to -9 bars, while a field study conducted by Watts (1974) showed that a decline in leaf water potential of -8 or -9 bars had little effect on leaf expansion in corn.

Part of the reason for the discrepencies in results obtained from controlled environment and field studies lies in the time period over which water stress develops in the plant. In the small containers commonly used in controlled environment studies the root density is high and the entire root system is subjected to a uniformly increasing moisture stress with little capacity for overnight recovery, while the roots of field-grown plants usually have access to larger volumes of soil so that water stress develops gradually over a longer period of time (Begg and Turner, 1976). The gradual development of water stress in the field may allow time for further root development and a greater possibility of overnight recovery

due to the availability of water lower in the soil profile (Begg and Turner, 1976).

Controlled environment studies which focus on the effects of water stress on plant growth cannot adequately predict plant growth responses to water stress in complex natural environments where numerous climatic and edaphic factors interact dynamically with each other and the plant (Kaufmann and Hall, 1974). Visible radiation, temperature, and humidity may all influence water loss from leaves and hence the development of plant water deficits through their effects on stomatal behaviour (Ketellapper, 1963; Kaufmann, 1981). Furthermore, changes in leaf initiation rates, leaf shape, leaf area, and stem growth are all known to occur in response to changes in temperature or light intensity in the absence of water stress (Schwabe, 1963); thereby adding further complexity to field studies.

Leaf Anatomy. For the leaves of many xerophytic species, an increase in the diffusive pathway from the intercellular spaces to the open air often is associated with a greater mesophyll surface area per unit leaf area (A^{mes}/A) (Lewis, 1972). A greater A^{mes}/A could result either from an increase in the number of layers of mesophyll cells, a decrease in mesophyll cell size, or both. Such changes could then lead to a greater internal surface area being available for the absorption of carbon dioxide per unit leaf surface area (Nobel, 1980).

Longstreth and Nobel (1979) examined the effects of increasing salinity of the growth medium on the anatomy of bean (Phaseolus

vulgaris L.) and cotton (Gossypium hirsutum L.) leaves. They found that mesophyll thickness increased with increasing salinity in both species due to an increase in the number of spongy mesophyll layers. However, the increase in A^{mes}/A did not lead to higher carbon dioxide uptake rates. In both species, depression of net carbon dioxide uptake rates occurred and this was largely attributed to a decrease in stomatal conductance. In contrast to these results, Nobel (1980) concluded that in cotton A^{mes}/A was unaffected as the soil water potential was reduced from -0.2 to -12 bars, although the leaf was 24% thinner when grown under the drier condition. The different results obtained in the two studies probably reflect the different methods used to induce the stress condition. In a second species, Plectranthus parviflorus (L'Herit.), Nobel (1980) found that A^{mes}/A increased about 40% due to an increase in the number of layers of mesophyll cells and a decrease in their size as soil water potentials declined. While cellular carbon dioxide conductance decreased nearly three-fold, stomatal water vapour conductance decreased more than four-fold, resulting in an approximate doubling of water use efficiency (ratio of photosynthesis to transpiration). However, it was concluded that the observed increases in water use efficiency were mainly due to changes in stomatal aperture rather than to changes in leaf anatomy. Therefore, while anatomical changes in leaves resulting in a greater A^{mes}/A do occur in some species subjected to water stress during leaf development, it appears that they may not be important insofar as water use efficiency is concerned.

The effect of water stress on cuticle development in leaves is not clear. Skoss (1955) observed that plants subjected to water stress produced thicker cuticles containing a greater proportion of waxes than those grown under more favourable conditions. In contrast, Amer and Williams (1958) noted that when Pelargonium zonale (Willd.) was subjected to moisture stress, cuticle thickness did not differ from that in plants grown under well-watered conditions. The relevant literature has been reviewed by Martin and Juniper (1970) and Hull et al. (1975). Recent studies using more modern techniques do not appear to have been undertaken. While controversy is evident in the literature, it appears that water stress may be positively correlated with increased cuticle thickness in some species.

The effect of water stress on the production of epicuticular wax is also uncertain. Studies by Weete et al. (1978) on cotton appear to indicate that wax synthesis is decreased during water stress and increased after rewatering. Incorporation of radioactive precursors into wax in cotton was decreased about 38% in stressed plants relative to controls, but was increased about 30% when the plants were held for at least six days at field capacity following the initial stress period. Contrary to this, Baker and Procopiou (1980) concluded that leaves of stressed plants synthesize far more wax than do unstressed plants.

The effects that moisture stress may have on the physical structure or chemical composition of cuticular or epicuticular waxes has yet to be systematically investigated.

Tiller Development. Van Der Paauw (1949) observed that drought occurring relatively early in the development of oats could reduce the number of secondary shoots produced. Later studies on wheat and oats (Joffe and Small, 1964) confirmed these observations. Both moderate and severe moisture stress at the tiller initiation stage significantly reduced the mean number of tillers produced in both species and the rate of tiller production in wheat. Increased tillering was evident following rewatering of the stressed plants, but the rate of tiller formation and the final number of tillers produced did not exceed those of the well-watered controls. Contrary to this, Chinoy (1961) found that retardation of tiller production in eight wheat varieties subjected to moisture stress at the tiller initiation or shooting stage was completely overcome after rewatering, and that the stressed plants produced more tillers than the well-watered controls. Chinoy's experiments were conducted outdoors under conditions of high temperature and low humidity which may have resulted in short periods of water deficit in the well-watered controls. This may account for the different results obtained in these two studies.

Aspinall et al. (1964) examined the growth and development of barley subjected to periods of soil moisture stress at various stages of development. Short periods of stress, sufficient to reduce the soil water content from field capacity to the permanent wilting point, initiated during vegetative growth, at anthesis, and during the grain-swelling phase, reduced tiller formation. However, following rewatering, the final tiller number was increased relative

to that of controls, with the increase being greater the earlier the stress was applied. The final number of grain bearing ears was not significantly affected indicating that either senescence of tillers or production of sterile tillers may have occurred. Begg and Turner (1976) cited data which showed that water stress applied to a wheat stand at the time of maximum tiller development resulted in an average rate of death of 11 tillers/m^2/day compared to 3 tillers/m^2/day in well-watered wheat. Aspinall et al. (1964) postulated that the maintenance of apical dominance by the major apicies may depend on their continued growth so that a temporary inhibition of growth during stress may release subordinate apicies from their control resulting in an increase in tiller production following rewatering.

Physiological Effects

Stomatal Aperture. The development of water deficits in plants is now well understood and has been extensively reviewed (Slatyer, 1967; Jarvis, 1975). In general, all plants undergoing active transpiration are experiencing some degree of water deficit. Plants extract water from the soil only when the water potential in the plant is lower than that in the soil and therefore water in the plant is seldom in equilibrium with water in the soil (Begg and Turner, 1976). While there is a steady decline in soil water potential as soil dries out, leaf water potential exhibits marked diurnal fluctuations as the evaporative demand varies throughout the day and night (Turner and Begg, 1981). The relationship between soil and leaf water potential is therefore an indirect one in which

the soil water potential sets the upper limit of recovery possible by the plant during the night (Slatyer, 1967).

It is now generally recognized that stomata do not respond directly to changes in leaf water potential until a critical threshold potential has been reached, after which stomata close over a narrow range of water potentials (Ritchie, 1981). Turner and Begg (1978) summarized the response of stomata to leaf water potential for a range of crop and pasture species and showed that under field conditions the threshold water potential for stomatal closure ranges from -8 bars in field beans to about -28 bars in cotton. In wheat the threshold value was about -14 bars. However, as Begg and Turner (1976) pointed out, there is no unique leaf water potential causing stomatal closure since the threshold leaf water potential varies with the position of the leaf in the canopy, the age of the plant, and previous growing conditions.

Jordan and Ritchie (1971) reported that stomatal diffusion resistance increased rapidly in container grown cotton plants when leaf water potentials were -16 bars or less. However, the stomatal diffusion resistance of field grown plants remained low for leaf water potentials as low as -27 bars. These results indicate a modification of the stomatal response to water stress which develops gradually over a prolonged period. More recent studies in wheat (Munns and Weir, 1981), sorghum, and sunflower (Jones and Turner, 1978; Jones et al., 1980) support these earlier results. Alterations in the relationship between leaf water potential and turgor potential, such that zero turgor and stomatal closure occur at a

lower leaf water potential are now believed to arise through adjustment of the osmotic potential (Jones and Turner, 1978). To date, the principal solutes involved in lowering the osmotic potential appear to be inorganic ions, sugars, and free amino acids (Jones and Turner, 1978; Jones et al., 1980).

Photosynthesis. Stomatal closure in response to water deficits not only reduces the transpiration rate but also the diffusion of carbon dioxide into the leaf. It is now generally accepted that the initial reduction in photosynthesis as plant moisture stress increases arises from a reduction in the conductance of carbon dioxide through the stomata (Hsiao, 1973). Consequently, changes in net photosynthesis with changes in leaf water potential follow very closely changes in stomatal conductance (El-Sharkawy and Hesketh, 1964) or transpiration rate (Boyer, 1970).

Aside from a reduction in carbon dioxide exchange, water stress is also known to have other effects on the photosynthetic process. Virgin (1965) reported that even small water deficits caused a strong inhibition of chlorophyll a formation in detached wheat leaves. Similarly, Duysen and Freeman (1974) reported that moderate water stress, sufficient to impair seedling growth, leaf unfolding, and leaf expansion in wheat, caused a reduction in total chlorophyll (a + b) and carotenoid accumulation. More recently, Duysen and Freeman (1975) demonstrated that water stress could cause alterations in the fine structure of chloroplasts.

Plaut (1971) observed an inhibition of carbon dioxide fixation by isolated chloroplasts at low osmotic potentials which was paralleled by decreased RUDP carboxylase activity but not by decreased photo-chemical reduction of NADP. Huffaker et al. (1970) reported, however, that mild water stress down to -11 bars did not affect barley seedling RUDP carboxylase activity. In wheat and barley plants subjected to more severe stress, Johnson et al. (1974) detected decreases in RUDP carboxylase activity of 30 to 50%. They concluded, however, that this was not limiting photosynthesis in the stressed leaves since a crude extract from the leaves showed substantial RUDP carboxylase activity even though no net photosynthesis was detectable. Boyer (1971) also provided evidence that the effect of water stress on chloroplast activity was more important than its effects on stomatal closure or carboxylating enzyme activity in limiting photosynthesis. A general consensus of opinion has yet to be reached on the physiological basis for reduced carbon dioxide fixation in water-stressed tissues.

Translocation. There is ample evidence that assimilate translocation in plants is reduced under moderate to severe moisture stress (Crafts and Crisp, 1971). In keeping with the mass flow hypothesis (Salisbury and Ross, 1978), water stress could influence translocation of photosynthetic assimilates by affecting the availability or utilization of assimilates, the loading and unloading of sieve elements, and/or the movement of assimilates in the phloem. The effects of water stress on assimilate availability, i.e., photosynthesis, have already been reviewed and will not be further discussed here.

Wardlaw (1967) clearly showed that in wheat the velocity of assimilate movement in the phloem was not reduced by a level of water stress that caused diffusion resistances indicative of stomatal closure. Rather, the effect of water stress was to delay and reduce the transfer of sugars from the assimilating tissue to the conducting tissue, thus indicating a reduction in loading into the vascular system. These results have been confirmed by Sung and Krieg (1979) in cotton and sorghum. In both species, photosynthetic rates declined as moisture stress increased prior to any measurable reduction in translocation rates. Measurement of the velocity of assimilate movement indicated that increasing the stress level had no measurable effect on the transport velocity. The rate of translocation was ultimately affected by longer periods of water stress and appeared to be closely related to the amount of photosynthate available for translocation.

As previously mentioned, another possible factor involved in the response of translocation to water stress is a reduced export of assimilates due to reduced demand. Wardlaw (1969) found that leaf expansion in Lolium temulentum was more sensitive to moisture stress than was photosynthesis of the source leaf. Inhibition of growth in the young expanding leaves, a primary sink for assimilates, was considered to be the major factor in reduced translocation from the source leaf. Watson and Wardlaw (1981) further explored this possibility in sorghum and wheat. Water potentials of leaves measured at the time of treatment with 30-second pulses of $^{14}CO_2$ ranged from slightly less than 0 bars in control plants to about -20 bars in severely stressed plants. In one experiment, mature

leaves adjacent to the treated leaf were removed to increase the demand for assimilates from the treated leaf. However, there was no indication that defoliation in any way enhanced movement of assimilates out of the treated leaf in either control or stressed plants. In a second experiment, translocation was blocked completely by steam-girdling the base of the treated leaf of non-stressed plants and the effect of this "decreased demand" on the labelling of leaf metabolites was measured. In both wheat and sorghum the entry of ^{14}C into sugars was reduced which could have resulted in a decreased rate of export out of the treated leaf and therefore an overall depression of the rate of translocation. However, because the effect of water stress on assimilate translocation was not altered by removal of competing photosynthetic tissue in the first experiment, it was concluded that reduced demand in response to water stress was not important in determining the rate of translocation.

Metabolism. Current evidence indicates that dark respiration is depressed whenever the plant water deficit is sufficiently great to cause stomatal closure (Begg and Turner, 1976). However, the effects of water stress on respiration has received less attention than its effect on photosynthesis and so is less clearly understood. Brix (1962) reported that respiration rates decreased steadily with decreasing soil water potentials in tomato (Lycopersicom esculentum Mill.) plants over the range of about -8 to -38 bars. Boyer (1970) similarly showed that dark respiration rates of shoots of soybean [Glycine max (L.) Merr.], sunflower, and corn decreased steadily in proportion to decreases in leaf water potential from -8 to -16

bars. Flowers and Hanson (1969) reported depressed respiration rates in soybean hypocotyls and isolated hypocotyl mitochondria cultured in increasing concentrations of sucrose. It was concluded that the primary effect of lowered water potential was from some effect on substrate penetration, electron transport or the coupled phosphorylation mechanism.

Todd (1972) reviewed the available literature on the effects of water stress on enzyme levels and activity. He listed 27 enzymes or enzyme systems which either increased or decreased in concentration in response to water stress. It was concluded that water deficits led to a release or activation of degradative enzymes. Mukherjee and Choudhuri (1981) recently reported on the activities of certain oxidative enzymes in the leaves of water-stressed cowpea (Vigna unguiculata L.) seedlings. While catalase activity decreased, the activities of all other oxidative enzymes (IAA-oxidase, ascorbic acid oxidase, peroxidase, and glycolate oxidase) increased to varying degrees over the stress period.

Early evidence suggested that protein synthesis was reduced in plants subjected to water stress (Shah and Loomis, 1965). This was later confirmed by the work of Ben-Zioni et al. (1967) who showed that the incorporation of amino acids into proteins in previously stressed tissue was reduced. Hsiao and Acevedo (1974) demonstrated that water stress caused a shift of ribosomes from the polymeric to the monomeric form about 30 minutes after the initiation of stress in corn seedlings. However, as Scott et al. (1979) pointed out, the effects of water stress on polyribosome content may only be important in young, expanding tissues. They found that large

reductions in polyribosome populations due to water stress occur only in growing tissues and appear to be related to reduced growth there. Thus polyribosome conversion may not be the sole factor involved in reduced protein synthesis in water-stressed tissues.

Influence of Moisture Stress on Herbicide Performance

General Observations - Field Studies

Susceptibility to a herbicide is not a constant property of a species but is dependent on both environmental and intrinsic factors (Hammerton, 1967). Several researchers have reported decreased effectiveness of postemergence herbicides applied before, during or after a period of reduced soil moisture levels. Friesen and Dew (1966) reported that tartary buckwheat [Fagopyrum tartaricum (L.) Gaertn.] subjected to moisture stress before, after, or before and after spraying was less affected by dicamba, 2,4-D, and picloram than well-watered control plants. Wiese and Rea (1962) reported a decrease in activity of 2,4-D on field bindweed (Convolvulus arvensis L.) under conditions of low soil moisture. An increase in the dosage of 2,4-D applied gave a greater level of control. Shahi (1975) cited data which showed that control of lambsquarters (Chenopodium album L.) with 2,4-D decreased in proportion to a reduction in the soil moisture content from field capacity to about 10 to 20% available soil moisture. Increasingly higher rates of application were required to give equivalent levels of control as soil moisture declined.

West et al. (1980) examined the effect of soil moisture stress on the toxicity of diclofop methyl to barnyardgrass [Echinochloa crus-galli (L.) Beauv.]. A trenching method was employed to expose the soil profile to the drying influence of the atmosphere for various periods of time. Control of slow-growing barnyardgrass plants (early planting) was significantly reduced by each reduction in soil moisture content. The level of control ranged from 97% in the high soil moisture treatment (-0.3 bars) to only 48% in the low soil moisture treatment (-3.4 bars). Control of fast-growing plants (late planting) was not affected by decreased soil moisture contents prior to treatment.

Dortenzio and Norris (1980) also reported reduced effectiveness of diclofop methyl on barnyardgrass subjected to moisture stress. Irrigation at various times after spraying was used to generate the various levels of moisture stress. Unfortunately, no information was provided on the soil or plant water status. Generally, control of barnyardgrass with diclofop methyl decreased as the time of irrigation after spraying was delayed. The activity of diclofop methyl in relation to soil moisture was influenced by the rate of application, with a higher dosage yielding only small variations in control in response to soil moisture reduction.

Interception and Retention

With foliar-applied herbicides, the amount of spray solution intercepted and retained on the leaves of weeds is important in determining the ultimate dosage of herbicide available to effect

toxic action (Holly, 1976). The quantity of spray intercepted by a plant is partly governed by the amount of leaf area and the way the leaf surface is oriented in relation to the more or less vertically descending spray droplets. Changes in the projected leaf area, i.e., the area exposed to vertically decending spray solutions as observed from directly above a plant (Kraatz and Andersen, 1980), may occur as a result of water stress induced changes in leaf shape or leaf angle. Leaf rolling, a common response to water stress in certain grasses, results in a marked reduction in the effective or projected leaf area and a more vertical leaf orientation (Begg, 1980). The rolling phenomenon has been shown to be closely related to changes in leaf water potential (O'toole and Cruz, 1980) and is attributed to a reduction in turgor of the bulliform cells on the adaxial surface of the leaf causing the upper leaf surface to be rolled inside (Esau, 1977). For example, Begg (1980) found that leaf rolling in sorghum was very sensitive to the onset and recovery from stress. The effective leaf area of severely stressed sorghum plants was reduced by approximately 68% compared to the effective leaf area of unstressed plants.

While water stress is usually not a factor under investigation in studies on the effects of changes in total leaf area, projected leaf area, and leaf angle or orientation on herbicide retention, it can, as previously outlined, be the causal agent of these changes and should theoretically produce a similar end result. Davies et al. (1967) investigated the effect of total and projected leaf area and leaf angle on the retention of ioxynil by three dissimilar species.

Total leaf area was greatest in mustard (Sinapis arvensis L.), intermediate in barley and least in pea (Pisum sativum L.). Projected leaf area, on the other hand, decreased in the following order: mustard, pea, and barley. Ioxynil retention was closely correlated with projected leaf area but not total leaf area. To investigate the effect of leaf angle on retention, these workers developed an apparatus which allowed leaves to be held at specified angles to the spray direction. Changing the leaf angle from 10° to 70° from the vertical caused an average three- to four-fold increase in ioxynil retention by barley. This was explained on the basis of a greater likelihood of a vertically falling droplet being deflected from a leaf if the angle between the droplet path and the leaf surface is small. A similar study was conducted by Hibbit (1969) on wild oats and flax. Projected leaf areas of wild oats and flax (Linum usitatissimum L.) increased with plant age. Spray retention similarly increased with plant age and appeared to be directly related to increases in projected leaf area. The effect of leaf angle on spray retention was also measured but, unlike the previous study by Davies et al. (1967), leaf strips with the abaxial surface exposed were used instead of whole leaves. The volume of spray solution retained by wild oat leaf strips was decreased by 50% as the angle from the horizontal was increased from 0 to 45° and was decreased by 95% when the leaf strips were vertical.

The amount of spray solution retained by a weed species following foliar application will also be affected by the wettability of the exposed surfaces. The wettability of a leaf by a liquid is arbitrarily determined by measuring the advancing contact angle.

By definition, a contact angle of 0° characterizes a completely wettable surface, while contact angles greater than 0° (up to a maximum of 180°) indicate a degree of unwettability (Martin and Juniper, 1970). It is now generally recognized that both the chemical nature and physical structure of epicuticular waxes markedly influence the contact angle of impinging droplets and the wettability of leaves (Hull, 1970). Water repellency is greatest when the wax has a rough surface in the form of projecting rods or a crystalline or semi-crystalline structure (Silva Fernandes, 1965). Waxes with significant quantities of long-chain ketones and paraffins were the most difficult to wet, regardless of the quantity of wax present. Martin and Juniper (1970) cited evidence that waxes with large amounts of alkanes, esters, ketones, and secondary alcohols are the most difficult to wet.

Early work by Fogg (1947) indicates that water stress may have a significant effect on leaf wettability and therefore herbicide retention. He noted that wilting of the leaves of wild mustard and wheat lowered their wettability compared to when the leaves were turgid. This was ascribed to an increase in the surface roughness and contact angles resulting from wrinkling of the leaf cuticle in response to loss of turgor in the underlying epidermal cells. The results of Riepma (1960) support those of Fogg (1947). A decrease in water supply to the roots of flax, chickweed [Stellaria media (L.) Vill.], and bean plants resulted in increased contact angles and decreased wettability.

Riepma (1960) also demonstrated that the quantity of epicuticular wax can be important in determining retention. Addition of

trichloroacetic acid to the soil before peas were sown caused a decrease in epicuticular wax production and a subsequent decrease in contact angle of the leaves. However, Bukovac (1976) concluded that the amount of wax present on leaf surfaces probably contributes little to wettability provided that a level sufficient to adequately cover the cutin matrix is present.

While it is known that water stress influences leaf wettability and herbicide retention, from the limited amount of experimental evidence available, it is difficult to specify which of the three factors of wax thickness, chemical composition or physical structure are altered or the relative importance of these alterations in determining the final volume of herbicide retained.

Penetration and Absorption

Once a herbicide has contacted and been retained on the leaf surface, it must then penetrate the cuticle in order to reach and be taken up by the underlying epidermal cells. A disturbing amount of confusion exists in the literature regarding the effects of water stress on herbicide penetration and absorption. There is some evidence that water stress can result in increased cuticle thickness and wax impregnation (Skoss, 1955). Following an extensive review of the literature, Hull (1970) observed that an inverse relationship apparently exists between overall cuticle thickness and herbicide absorption. Martin and Juniper (1970) reviewed some of the same literature and concluded that cuticle thickness was probably not a prime factor in controlling differences in permeability among species.

Van Overbeek (1956) suggested that swelling of the relatively polar cutin by water would spread the wax components further apart, thereby enhancing cuticular permeability to aqueous solutions. It was concluded that a similar effect would be achieved if the epidermal cells and the underlying tissues were highly turgid. An early study by Hauser (1955) appeared to support this theory, in that increasing soil moisture stress apparently decreased the uptake of growth regulator type herbicides. Certain more recent studies also lend support to this theory while others do not. For example, Basler et al. (1961) found that while relative turgidity of bean leaves decreased significantly with increasing water stress, the absorption of 2,4-D was not affected. On the one hand, Pallas and Williams (1962) found no significant change in the amount of 2,4-D absorbed by the leaves of beans as soil water stress increased. On the other hand, the absorption of ^{32}P was increased with increasing stress, suggesting that different mechanisms may exist for absorption of widely different compounds.

Merkle and Davis (1967) subjected bean plants to moderate and severe moisture stress by withholding water for various periods of time. The absorption of 2,4,5-T and picloram was unaffected by the stress treatments. Davis et al. (1968) examined the effects of increasing moisture stress over the range of soil water potentials of -0.5 to -20.8 bars on the absorption of 2,4,5-T and picloram in the two woody species, mesquite (Prosopis glandulosa Torr.) and winged elm (Ulmus alata Michx.). Increased soil water stress did not affect the absorption of 2,4,5-T or picloram in winged elm but did decrease absorption of picloram in mesquite by about 70% at the

lowest soil water potential. In field bindweed it was reported that absorption of 2,4-D was decreased by 50% in plants grown at a soil water content which resulted in severe wilting (Goodin, 1969). However, picloram absorption was not significantly affected.

It is difficult to get a clear picture of the significance of water stress to absorption of phenoxy type herbicides from the foregoing studies due to differences in the species used, herbicides applied, and the levels of water stress to which the plants were subjected. Recent studies with non-phenoxy type herbicides are also conflicting. For instance, Dortenzio and Norris (1980) showed that diclofop methyl absorption was not altered when applied to wild oat plants preconditioned at field capacity or at a moisture level slightly above the permanent wilting point. In contrast to this, McWhorter et al. (1980) reported that glyphosate absorption was significantly depressed in johnsongrass [Sorghum halepense (L.) Pers.] seedlings preconditioned by growing in soil at a water content just above the permanent wilting point as compared to controls grown at field capacity. Glyphosate absorption was not significantly altered in soybean by the stress treatment.

Ahmadi et al. (1980) examined the effect of water stress on glyphosate absorption in barnyardgrass. Prior to treatment, plants were grown in soil at water contents ranging from 10 to 40%, corresponding to soil water potentials of -37 to -1/8 bars. Glyphosate absorption was significantly depressed in 15 cm. high plants grown at 10, 20 and 30% soil water contents compared to absorption at the 40% soil water content and in the 7.5 cm. high plants at the 10%

soil water content only. Apparently, plant growth stage at the time of treatment can alter the influence that moisture stress has on the response of some species to herbicide treatment.

Translocation

With the exception of those herbicides which exert their toxic action at or near the point of application, all others must be translocated from the point of application to the site of toxic action. Studies which have focused on herbicide translocation in relation to water stress appear to be limited to those herbicides which are symplastically translocated. Since apoplastic transport of herbicides is primarily governed by the rate of transpiration, stomatal closure in response to developing water deficits should result in reduced transport via this route.

There is no doubt that water stress inhibits translocation of herbicides, but the physiological basis for such inhibition is rarely investigated in herbicide studies. If it is accepted that foliar-applied herbicides move in the phloem along with photosynthetic assimilates, then symplastic transport of herbicides should be influenced by the effects that water stress has on translocation.

The translocation of 2,4-D in bean plants subjected to various degrees of water stress was investigated by measuring the amount of radiolabelled 2,4-D translocated during a five-hour period (Basler et al., 1961). Plants with relative water contents below 80% (soil water content about 80% of field capacity) translocated only trace

amounts of 2,4-D, while plants with relative water contents above this value showed sharp increases in translocation. Furthermore, following rewatering, plants required several hours to regain the ability to translocate significant amounts of 2,4-D even though they had regained full turgor within one or two hours. Pallas and Williams (1962) also found decreased translocation of 2,4-D and ^{32}P with increasing soil moisture deficits over the range of soil water potentials from -1/3 to -4 bars. The movement of both 2,4-D and ^{32}P followed the route of the assimilate stream as indicated by autoradiograms. Water stress has also been shown to reduce the translocation of picloram in field bindweed (Goodin, 1969), beans (Merkle and Davis, 1967), and in the woody species, mesquite and winged elm (Davis et al., 1968).

The translocation of non-phenoxy type herbicides also appears to be adversely affected by water stress. Chase and Appleby (1979) measured the translocation of glyphosate in purple nutsedge (Cyperus rotundus L.) subjected to water stress. They found that twice as much glyphosate was translocated in plants with a leaf water potential of -2 bars as compared to those with a leaf water potential of -11 bars at the time of treatment. Similarly, Ahmadi et al. (1980) reported decreased translocation of glyphosate in Johnsongrass seedlings grown in soil at a moisture content of 10% (-37 bars) three days before and three days after treatment.

Jeffcoat et al. (1977) investigated the effect of water stress on the translocation of the wild oat herbicide, flamprop-methyl, in oat plants grown in nutrient solution. Autoradiograms demonstrated

that moisture stress reduced the translocation of the free acid form of the herbicide, flamprop (the active metabolite).

Phytotoxic Action and Metabolism

The mechanisms of toxic action of herbicides are varied. The toxic action of most herbicides depends on interference with basic physiological or biochemical processes within the plant. The metabolism of herbicides in plants involves a series of enzymatic reactions. The influence of water stress on the metabolism of herbicides remains virtually uninvestigated. At the time of this reivew only two studies were found which dealt with the influence of water stress on the metabolism of foliar applied herbicides. Jeffcoat and Harries (1975) subjected oats and barley to water stress by supplying them with only enough water to maintain them just above wilting and examined the effect of the imposed stress on the metabolism of flamprop-isopropyl. Barley tolerance to the herbicide was not altered by the stress, while the oats showed increased susceptibility. Water stress was found not to have any marked influence on the metabolism of flamprop-isopropyl in either oats or barley over a period of 14 days after treatments and the increased susceptibility of the oats was attributed to a reduced growth rate rather than to an increased rate of hydrolysis of the herbicide. In a second study, Jeffcoat et al. (1977) examined the effect of water stress on the metabolism of flamprop-methyl by oats. The toxic action of flamprop-methyl like that of flamprop-isopropyl is dependent on its de-esterification to the active acid,

flamprop. In contrast to the results of Jeffcoat and Harries (1975), oat plants were found to be most sensitive to flamprop-methyl when not under water stress. The increased sensitivity was linked to the fact that water stress applied for two weeks after treatment with the herbicide decreased the production of the free acid, flamprop.

Inasmuch as the earlier reviewed changes in respiration rates, enzyme activities, and protein synthesis in response to water stress will in turn have diverse and far reaching effects on biochemical and physiological processes occuring in cells, it seems reasonable to conclude that they could significantly affect the action or metabolism of any foreign molecules including herbicides introduced into those cells.

CHAPTER III

The Effect of Moisture Stress on the Growth and Development of Wild Oats (*Avena fatua*)

INTRODUCTION

Wild oats (*Avena fatua* L.) continue to be the most troublesome annual grassy weed of cultivated land in the prairie provinces of Canada (Sharma and Vanden Born, 1978). While a great number of studies have been published on various aspects of the biology and control of wild oats including an interpretive review of world literature (Jones, 1976), reports describing the influence of environmnental factors on the growth and development of wild oats are limited. On a world wide basis limited availability of water is the single most important environmental factor limiting plant growth (Begg and Turner, 1976). Thus studies on the influence of water deficits on growth and development are essential for a complete understanding of the biology of wild oats and may further the development of effective control measures.

Under dryland farming conditions, competition between wild oats and crops may be intensified due to the limited availability of soil moisture. Pavlychenko and Harrington (1935) found that wild oats had developed a more extensive root system than wheat (*Triticum aestivum* L.) by 22 days after emergence under dry farming conditions and concluded that wild oats was a serious competitive weed under those conditions. Sharma *et al*. (1977) reported that wild oats grown at reduced soil moisture levels yielded lower dry weights than those grown at field capacity.

Both the temperature and soil moisture conditions under which wild oats were grown affected the dormancy of seeds produced (Sexsmith, 1969). It was suggested that hot and dry conditions might cause a shift in the proportions of strongly dormant to weakly dormant strains in favour of the more dormant strains. Other studies have shown the importance of adequate soil moisture to the germination and emergence of wild oats (Koch, 1968; Quail and Carter, 1968; Sharma et al. 1976).

The objective of the studies reported here was to examine in some detail the effect of a soil moisture deficit on the water status, growth, and development of wild oats both outdoors and under growth room conditions.

MATERIALS AND METHODS

Outdoor study, growth conditions. During the summer of 1981, an experiment was conducted outdoors in two specially constructed enclosures 5.5 m long by 1.8 m wide by 0.8 m high (Plate 1). Each enclosure was subdivided into four equal sections which constituted individual plots. The enclosures, constructed with a slight slope (5%) from back to front, were placed on the ground, levelled, and treated with wood preserver. To prevent a loss of soil moisture to the air and exchange of soil moisture between adjacent plots, the enclosures were lined inside with sheets of 6 mil clear plastic.

In the fall of 1980, the enclosures were filled with Altona clay loam soil (39% sand; 32% silt; 29% clay; pH 7.7) which was allowed to settle during the winter. The following spring, the exterior surfaces

Plate 1. Wooden enclosures used for growing wild oats in the outdoor study.

of the enclosures were covered with white enamel paint. Semicircular hoops, constructed with 3 m lengths of electrical conduit, were positioned in the plots perpendicular to the long axis of the enclosures. The hoops were used to support a sheet of 6 mil clear plastic which was placed over each enclosure during extended periods of rainfall. The ends of each enclosure were left uncovered to ensure air movement over the plots.

On May 28, 1981, seeds of wild oats were planted by hand to a depth of 2.5 cm in 1.8 m long rows (75 seeds/row) spaced 15 cm apart. When the wild oats reached the two- to three-leaf stage (June 17), gutters were placed between all rows to further control the amount of rainfall reaching the plots. The gutters consisted of 2 m by 16 cm strips of asphalt felt roofing paper formed and held in semicircular channels by short lengths of plastic coated copper wire. Ten gauge steel wire hoops were used at the ends of each gutter to hold it securely between the rows. Sections of galvanized steel rain gutter, 1.3 m long, were used to direct runoff from the plots into 45 l galvanized steel wash tubs. A plastic covering was used to prevent evaporation from the wash tubs.

The experimental design was a randomized complete block with four replicates and two treatments. The two treatments, stressed and unstressed, were generated by weekly addition of 0.6 cm water or 2.5 cm water, respectively, to the plots.

Total weekly rainfall was measured by a rain gauge stationed adjacent to the enclosures. To determine the quantity of water required to be added to each plot per week, the following equation was used:

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

where x = volume of water (l) required to be added to a particular plot; a = volume of water (l) calculated to be required for each of the treatments; b = total weekly rainfall (cm); c = plot area (cm^2); and d = volume of water (l) accumulated per week in each wash tub.

Outdoor study, soil-water relations. Soil water potentials were measured on a weekly basis using a dewpoint microvoltmeter[1] and screen-cage psychrometers[2] buried at a depth of 20 cm in the centre of each plot. Additionally, the average soil moisture content (SMC) of the top 20 cm of soil was determined gravimetrically each week for each plot from three random samples per plot. A moisture release curve (Appendix Figure 1) was used to convert SMC to soil water potential. Both the soil water potential and SMC were measured at the end of each 7 day period just prior to the weekly addition of water to the plots.

Outdoor study, plant-water relations. Average stomatal diffusion resistance and transpiration rate of wild oats were also determined from a random sample of four plants per plot using an auto diffusion porometer[3]. An average leaf water potential was determined on leaf sections removed from the middle of the most recently fully expanded leaf using sample chambers[4] and a dew-point microvoltmeter. Both the porometer and leaf

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

[2] Model 74-13, J.R.D. MERRILL SPECIALTY EQUIPMENT, Logan, Utah

[3] Model LI-1600, LI-COR, INC., Lincoln, Nebraska

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

water potential measurements were taken at the end of each 7 day period just prior to the weekly addition of water to the plots.

Outdoor study, plant growth and development. At weekly intervals, beginning when the wild oats were at the three-to four-leaf stage, a sample of four plants per plot was harvested and leaf areas, numbers of viable tillers, heights and dry weights were recorded. Protein contents were determined by the Kjeldahl method on a 1 g sample of tissue from the harvested plants. A factor of 6.25 was used to convert nitrogen content to percent protein.

On three dates: July 8, July 15, and July 23, corresponding to the jointing, flag leaf, and heading stages, respectively, a sample of 10 plants per treatment was harvested for epicuticular wax determinations using a procedure described by Ebercon et al. (1977). This is a colorimetric method based on the color change produced due to reaction of wax with acidic $K_2Cr_2O_7$ reagent. A calibration curve (Appendix Figure 2) relating quantity of epicuticular wax present in solution to absorbance at 590 nm was developed with wax removed from leaves of wild oats and used to determine the quantity of epicuticular wax present per unit leaf area.

For anatomical studies on leaf morphology, a sample of four plants was removed from each treatment on the same dates as the samples for epicuticular wax determinations. The following leaves were used: the fifth leaf for plants at the jointing stage; the first leaf below the flag leaf for plants at the flag-leaf stage; and the flag leaf for plants at heading. Blades of the appropriate leaves were cut from the

plants and the area, width and length were measured. Transverse sections, 1 to 2 mm long were placed in 5% phosphate buffered glutaraldehyde, pH 6.8, and kept under vacuum for 20 h. Following this, the tissues were washed in four changes of 0.025 M phosphate buffer, post-fixed in 2% OsO_4 for 1 h; and subsequently washed in two changes of the same buffer and three changes of distilled water. The tissues were then dehydrated in a graded ethanol series and subsequently infiltrated with a mixture of 100% ethanol and Spurr's resin (1:1 v/v) for 24 h. The tissues were subsequently infiltrated with three changes of Spurr's resin over 24 h and polymerized for 20 h at 70 C. Transverse sections of the material were then cut on a microtome with glass knives, affixed to glass slides by gently heating on a hot plate, and stained with toluidine blue O (TBO) pH 9.0 for 1 min. A portion of each section from the center of the midvein to the center of the first major vein on one side of the midvein was photographed. Black and white prints were made from the negatives with a final magnification of 330x. Total cross-sectional area, area occupied by mesophyll cells, and area occupied by intercellular spaces were determined by cutting and weighing the corresponding images depicted in the photographs.

Growth room study, growth conditions. Four litre plastic food containers were filled with approximately 4 kg air-dried Almasippi very fine sandy loam (79% sand; 12% clay; 9% silt; 4% OM; pH 7.7) amended with: 200 ppm N as NH_4NO_3; 50 ppm P as $Ca(H_2PO_4)_2.H_2O$; and 160 ppm K and 65 ppm S as K_2SO_4. Pots were weighed and sufficient water was added to bring the SMC to 20%. Seeds of wild oats were placed on the soil surface and

covered with a 1 cm layer of soil at the same SMC. Pots were then placed in a growth room equipped with Gro-Lux WS Sylvania fluorescent lights yielding a photosynthetic photon flux density (PPFD) of 293 $\mu Em^{-2}s^{-1}$ over a 16 h photoperiod. Temperature was held constant at 21 C during the light period and 16 C during the dark period. The relative humidity was maintained at 55 to 60%. Pots were weighed and watered once daily as required to maintain the SMC at 20%. Upon emergence, seedlings of wild oats were thinned to six per pot (Trial 1) or 5 per pot (Trial 2).

The experimental design was a randomized complete block with three replicates and four treatments. At the outset of the experiment, each treatment consisted of four pots of wild oats, one of which was harvested at each of four sampling times. The individual treatments consisted of pots of plants maintaned at a SMC of: i) 20% for the entire experiment; ii) 20% until emergence and then allowed to decline without watering to 10% for the duration of the experiment; iii) 20% until the four-leaf stage and then allowed to decline to 10% for the duration of the experiment; and iv) 20% until emergence, allowed to decline to 10% until the four-leaf stage and then rewatered to 20%. The 20 and 10% SMC correspond to soil water potentials of -0.3 and -6.5 bars, respectively, as determined from a moisture release curve (Appendix Figure 3). Hereinafter, the four treatments are referred to as: i) high; ii) low; iii) high-low; and iv) low-high, respectively.

The experiment was repeated twice. Growth responses of the wild oats were very similar in Trial 1 and Trial 2 and data from the combined experiments is presented here. A change in the timing of the light and

dark periods in the growth room between the two trials caused differences in the plant water status between trials at the time of measurement. While the trends in leaf water potential, stomatal diffusion resistance, and transpiration rate were similar in both trials, the results from Trial 2 were less variable and are reported here. Refer to Appendix Table 1, and Appendix Figures 4 and 5, for the results from Trial 1.

Growth room study, plant-water relations. At weekly intervals when the SMC was 20% in the high and high-low treatments, and 10% in the low and low-high treatments, average values of stomatal diffusion resistance and transpiration rate were determined on a random sample of three plants from one of the four pots in each treatment. Leaf water potentials were also determined as previously described for the outdoor experiment.

Growth room study, plant growth. At the two-leaf, four-leaf, and jointing stages and at maturity, the wild oats from one pot from each treatment were harvested and leaf areas, heights, number of viable tillers, and dry weights of the shoots were recorded. Protein contents were determined as previously described for the outdoor study.

RESULTS AND DISCUSSION

Outdoor study, soil-water relations. The contribution of rainfall to the water content of the soil in the enclosures is presented in Table 1. To ensure development of a uniform stand of wild oats, no attempt was made to restrict the amount of rainfall intercepted by the plots prior to emergence. Following emergence, a large clear plastic sheet was

Table 1. Weekly rainfall received after seeding of wild oats.

Weeks after seeding	Rainfall		
	Total[a]	Potential on plots[b]	Actual on plots[c]
	cm		
1	1.8	1.8	1.8
2	0.0	0.0	0.0
3[d]	2.8	2.8	1.1
4	3.0	1.6	0.6
5	3.3	2.9	0.8
6	0.0	0.0	0.0
7	1.0	1.0	0.5
8	0.2	0.0	0.0
9	0.2	0.2	0.1
10	5.4	5.4	2.7

[a] Measured by standard raingauge.

[b] After removal of a portion of the total rainfall by the plastic sheet used to cover the enclosures.

[c] After removal of a portion of the "potential" rainfall by the gutters between the rows.

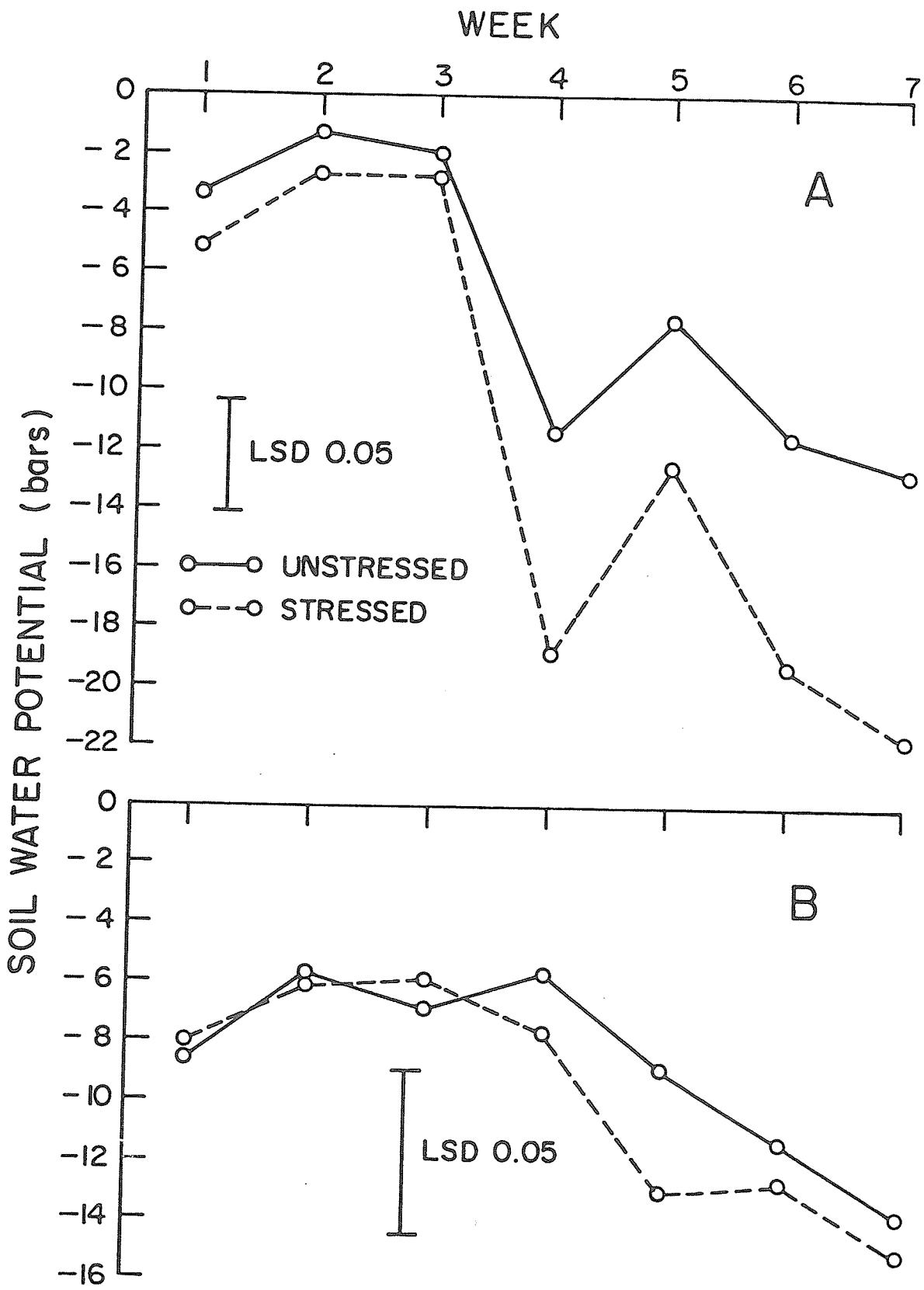
[d] Gutters in place between the rows of all plots.

placed over the enclosures during heavy or extended rainfall. However, total elimination of all rainfall from the plots with the plastic cover was not feasible. Consequently, at 3, 5, and 10 weeks after seeding, the amount of rainfall intercepted by the plots exceeded the amount of water (0.6 cm/week) required to maintain the stressed treatment at the desired SMC.

The gutters, which were placed between the rows when the wild oats reached the two- to three-leaf stage, removed approximately 50 to 70% of the rain falling on the plots when the enclosures were not covered. The efficiency of the gutters did not decrease measurably over the course of the experiment. However, the gutters appeared to be more efficient during short periods of heavy rainfall than during extended periods of light rainfall.

Soil water potentials derived from the average gravimetric SMC of the top 20 cm of soil did not decline significantly until 3 weeks after the wild oats reached the three- to four-leaf stage (Figure 1A). The water potential of the soil in those plots associated with the stressed treatment was reduced to a significantly lower level than in those associated with the unstressed treatment for the duration of the experiment, reaching a minimum of about -22 and -13 bars, respectively. The water potential of the soil measured with psychrometers at a depth of 20 cm did not differ significantly between the stressed and unstressed treatment plots (Figure 1B). However, the soil water potential did decline significantly over the course of the experiment reaching a minimum of about -15 bars in the stressed treatment plots compared to about -14 bars in the unstressed treatment plots. Apparently, the amount of water added to the unstressed

Figure 1. Soil water potential: (A) derived from the average gravimetric water content of the top 20 cm of soil and a moisture release curve and (B) measured by screen cage psychrometers buried at a depth of 20 cm near the center of the plots. Soil sampling was initiated when wild oats reached the three- to four-leaf stage.


WEEK
1
2
3
4
5
6
7
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
A
LSD 0.05
UNSTRESSED
STRESSED
SOIL WATER POTENTIAL (bars)
B
LSD 0.05

treatment plots (2.5 cm/week) did not maintain the desired high soil water content for the entire week since the soil water potential measured at the end of each week just prior to watering declined in unstressed treatment plots as well as the stressed treatment plots. Therefore, it is probable that the wild oats in the unstressed treatment suffered varying degrees of water deficit during periods of high evaporative demand between weekly waterings.

Outdoor study, plant-water relations. Leaf water potentials, measured at the end of each week just prior to the addition of water to the plots, generally decreased over the duration of the experiment in both the stressed and unstressed plants (Table 2). Changes in the leaf water potential were reasonably well correlated with changes in the soil water potential averaged over the top 20 cm of soil or measured at a depth of 20 cm (Table 3). Beginning at week 5, the leaf water potential of wild oats appeared to be lower in the unstressed plants than in the stressed plants (Table 2). There is no ready explanation for these apparently anomalous results since soil water potentials measured over the same period were not lower in the unstressed treatment plots than in the stressed treatment plots (Figure 1), and the wild oats in both treatments should have experienced the same conditions of evaporative demand. Moreover, a t-test of the weekly leaf water potential measurements showed that the differences between treatments were not significant (Table 2). However, the small sample size used and the high degree of variability of the means may have precluded the demonstration of significant differences between treatments.

Changes in the stomatal diffusion resistance and transpiration rate

Table 2. Effect of moisture stress on the water potential of the most recently fully expanded leaf of wild oats[a].

Week	Treatment	Leaf water potential[b] Mean	Sx
		(bars)	
1	Unstressed	-3.7	1.4
	Stressed	-6.6	4.4
2	Unstressed	-4.2	2.5
	Stressed	-5.4	1.3
3	Unstressed	-7.3	4.2
	Stressed	-8.5	1.5
4	Unstressed	-8.9	1.1
	Stressed	-14.1	4.4
5	Unstressed	-10.7	3.0
	Stressed	-8.0	2.0
6	Unstressed	-16.0	4.6
	Stressed	-14.1	1.1
7	Unstressed	-28.6	5.3
	Stressed	-18.9	6.4

[a] Sampling started at the three- to four-leaf stage.

[b] Mean and standard error.

of the wild oats were more strongly correlated with changes in the soil water potential averaged over the top 20 cm of soil as opposed to the soil water potential measured at the 20 cm depth (Table 3). This was not unexpected since, initially at least, the highest concentration of roots would be near the soil surface. Salim and Todd (1965) reported that the transpiration rate of barley (Hordeum vulgare L.), wheat, and oats (Avena sativa L.) was a linear function of the SMC from near the permanent wilting point to within 70 to 80% of the available soil moisture.

Simple correlation coefficients between the leaf water potential and either stomatal diffusion resistance or transpiration rate were not significant (Table 3). While leaf water potentials generally declined steadily, stomatal diffusion resistance decreased over the first three weeks of sampling in both stressed and unstressed plants and did not begin to increase until the soil water potential (Figure 1A) fell below -2 or -3 bars and the leaf water potential (Table 2) fell below -9 or -15 bars in the unstressed and stressed plants, repectively (Figure 2A). Transpiration rates followed a similar but inverse pattern (Figure 2B). The sharp decrease in stomatal diffusion resistance and smaller increase in transpiration rate at week 5 (Figure 2) was due to rain which fell on the plots (7 weeks after seeding) during the seven day period previous to sampling (Table 1).

The stomatal diffusion resistance of wild oats was not greatly increased by the imposed moisture stress (Figure 2A). Jordan and Ritchie (1971) found that stomatal diffusion resistance of field grown cotton (Gossypium hirsutum L.) remained low for water potentials down to -27 bars. In most species there is a threshold level of leaf water potential above which

Table 3. Simple correlations among variables associated with the water status of the soil and of wild oats.

Variable[a]	Unit	Mean	N	Sd	SWP-2	LWP	DR	Tr
SWP-1	bars	- 9.5	56	7.3	0.35**	0.67**	-0.44**	0.52**
SWP-2	bars	- 9.4	54	5.4	-	0.71**	-0.13 N.S.	0.31*
LWP	bars	-11.1	14	6.8	-	-	-0.21 N.S.	0.41 N.S.
DR	scm^{-1}	3.2	56	1.6	-	-	-	-0.77**
Tr	$\mu g\ cm^{-1}s^{-1}$	4.7	56	2.4	-	-	-	-

[a]Explanation of symbols: SWP-1 = soil water potential determined from the average gravimetric soil water content over a 0 to 20 cm depth and a moisture release curve, SWP-2 = soil water potential measured with psychrometers buried at a depth of 20 cm at the centre of the plots, LWP = leaf water potential, DR = stomatal diffusion resistance, Tr = transpiration.

[b]Values followed by * or ** are significant at the 5% or 1% level, respectively.

stomatal diffusion resistance and stomatal opening remain relatively constant (Hsiao, 1973). However, the threshold leaf water potential at which zero turgor and stomatal closure occur may be lowered in some species due to an accumulation of osmotic solutes in response to water stress which develops gradually over an extended period of time (Jones et al. 1980; Munns and Weir, 1981). Except for the initial sample at week 1, there were no significant differences in stomatal diffusion resistance between the stressed and unstressed wild oats (Figure 2A). Similarly, there were no significant differences in transpiration rate between treatments after week 3 (Figure 2B). The lack of significant differences in stomatal diffusion resistance and transpiration rate between treatments may have been due to an adjustment of the osmotic potential in the leaves of the stressed wild oats so that stomatal closure would occur at increasingly lower leaf water potentials.

Outdoor study, plant growth and development. While differences in soil or plant water status between treatments were small at the time of measurement, they were sufficient to cause significant differences in the growth of the wild oats. By the third week of sampling, the number of viable tillers was significantly less in the water-stressed plants than in the unstressed plants (Figure 3A). Tiller initiation was decreased in wheat and oat plants subjected to moderate or severe water stress at the tiller initiation stage (Joffe and Small, 1964) and Begg and Turner (1976) cited evidence of increased tiller senescence in wheat subjected to water stress. It was not clear in this study whether decreased tiller initiation or increased tiller senescence was primarily responsible for the observed

Figure 2. The effect of moisture stress on the (A) stomatal diffusion resistance and (B) transpiration rate of the most recently fully expanded leaf of wild oats over a period of 7 weeks beginning at the three- to four-leaf stage.

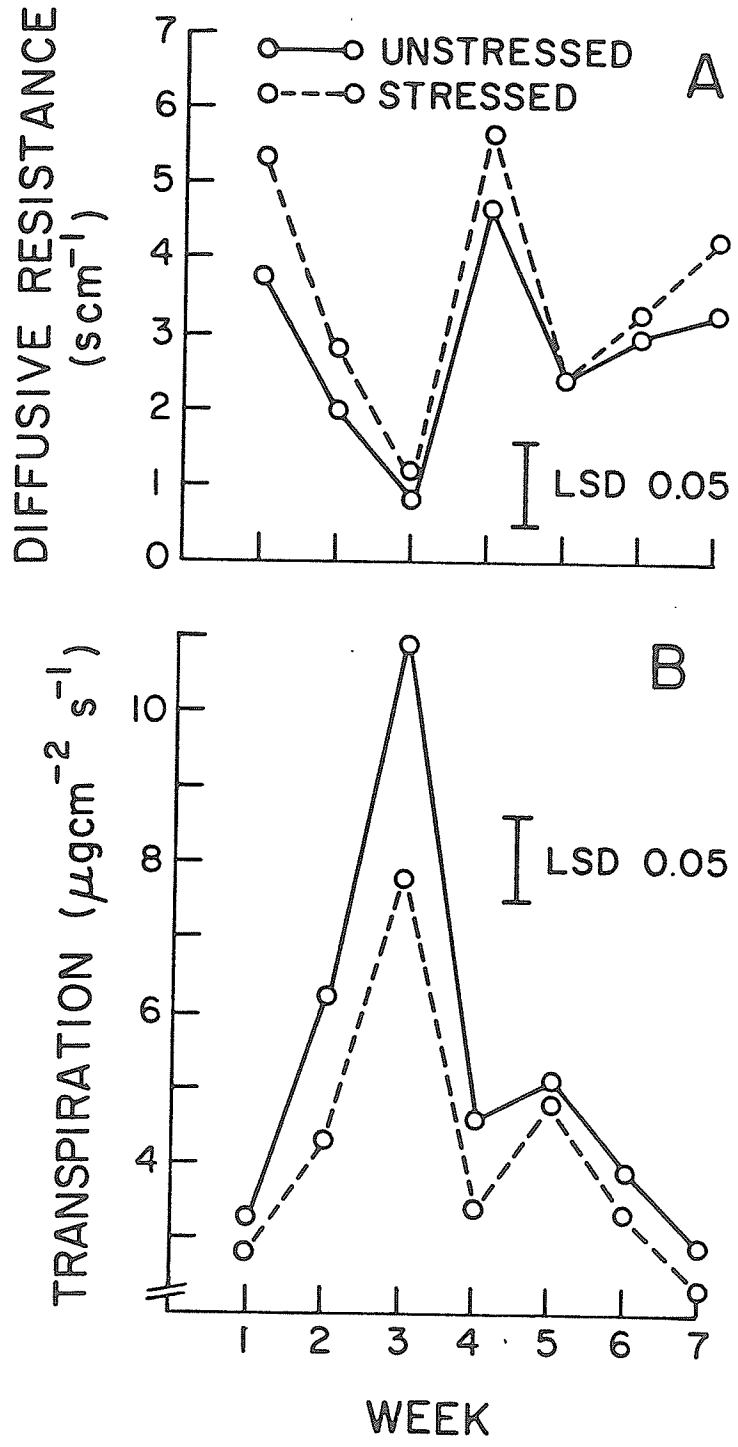
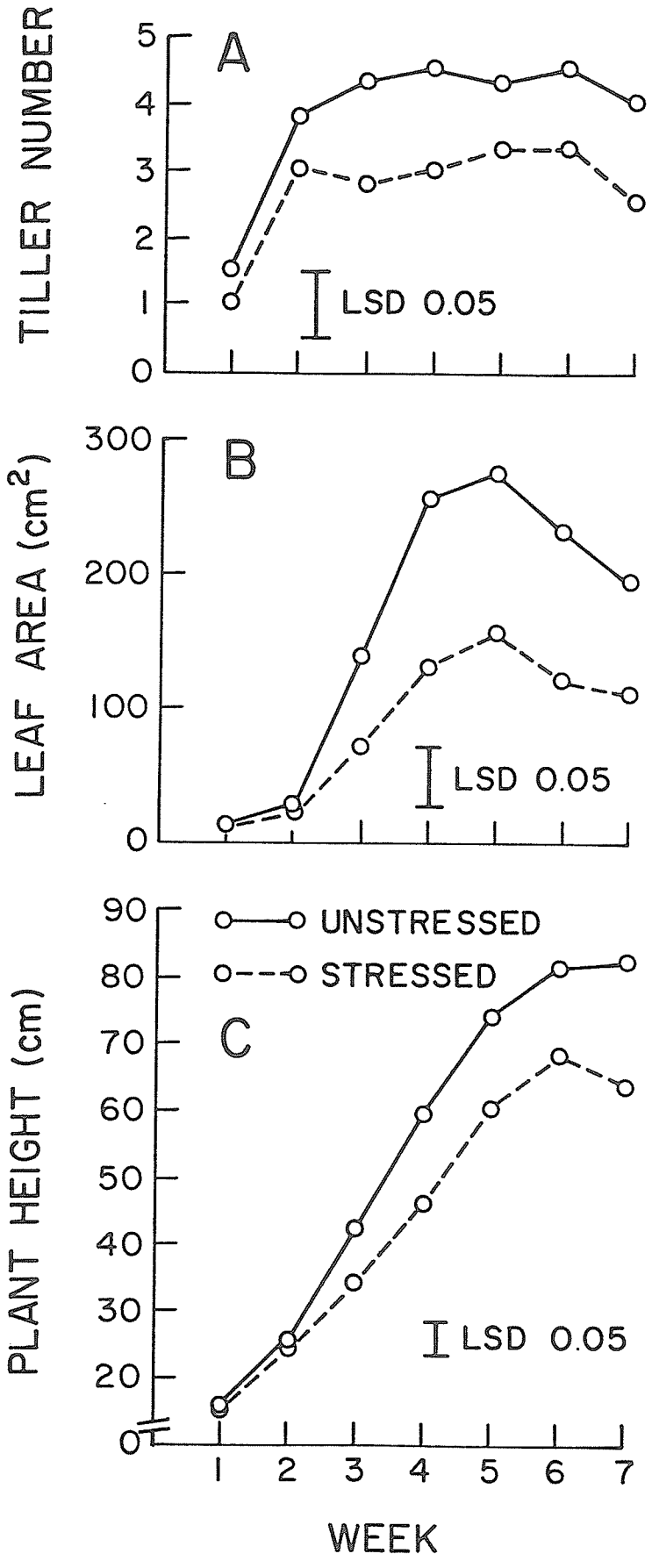

DIFFUSIVE RESISTANCE (s cm⁻¹)
UNSTRESSED
STRESSED
A
LSD 0.05
TRANSPIRATION (μg cm⁻² s⁻¹)
B
LSD 0.05
WEEK

Figure 3. The effect of moisture stress on (A) the number of viable tillers, (B) leaf area, and (C) height of wild oats over a period of 7 weeks beginning at the three- to four-leaf stage.


TILLER NUMBER
A
LSD 0.05
LEAF AREA (cm²)
B
LSD 0.05
PLANT HEIGHT (cm)
UNSTRESSED
STRESSED
C
LSD 0.05
WEEK

reduction in the final number of viable tillers in wild oats subjected to water stress. Tiller initiation continued throughout the course of the study in both treatments and tiller senescence was also evident, but no attempt was made to separately quantify these responses.

A reduction in leaf area in response to decreased soil water availability is often attributed to reduced leaf enlargement (Acevedo et al. 1971; Boyer, 1970). However, total leaf area may also be reduced through a decrease in the number of leaves formed due to an inhibition of leaf primordia formation (Nicholls and May, 1963; Husain and Aspinall, 1970). The leaf area of the stressed wild oats was markedly lower than that of the unstressed wild oats after week 3 (Figure 3B). The maximum leaf area per plant occurred at week 5 in both treatments, being approximately twice as great in the unstressed plants as in the stressed plants. The decrease in leaf area after the fifth week of sampling was likely due to a combination of both tiller and leaf senescence.

Although the height of the wild oats increased in both treatments over the course of the experiment, beginning at week 3 shoot height was significantly less in the stressed plants than in the unstressed plants (Figure 3C). By the end of the experiment, the stressed plants were about 17 to 23% shorter than the unstressed plants. Water stress at the shooting stage has also been reported to retard stem elongation in wheat (Chinoy, 1961). Initially, the difference in the height of wild oats between treatments was likely due to a reduction in leaf elongation in the stressed plants and later to a reduction of both leaf and shoot elongation.

A decrease in the number of viable tillers, leaf area, and height of water-stressed wild oats could conceivably influence its ability to compete

against a less water-stress sensitive crop species. Carlson and Hill (1982) found that the proportion of wild oats in a wild oats-wheat stand was closely related to competition-linked yield losses in spring wheat. A permanent reduction in the number of tillers could ultimately mean a reduction in the number of seed bearing stems and possibly the number of seeds being returned to the soil, while a reduction in leaf area would reduce the amount of photosynthetic tissue and hence the amount of photosynthetic assimilate available for both vegetative growth and seed production. A decrease in shoot height might further reduce the ability of wild oats to compete for available light.

The protein content per gram of shoots of wild oats declined more or less linearly over the course of the study for both treatments (Figure 4A), presumably due to a gradually increasing dilution by cellulose and other structural carbohydrates. Hsiao (1973) listed protein synthesis as being very sensitive to water stress, with inhibition occurring in most species at tissue water potentials of -0.5 to -5 bars. However, it is clear from the results in Figure 4A that, except at week 1, the protein content of wild oats was not significantly lower in the stressed wild oats than in the unstressed wild oats. In contrast, the dry weight (four plants/sample) of the stressed wild oats was significantly lower than that of the unstressed wild oats beginning at week 4 (Figure 4B). The observed differences in dry weight between treatments probably reflected the earlier noted differences in leaf area, shoot height, and number of viable tillers.

The effect of water stress on the production of epicuticular wax in wild oats was measured at three growth stages (Table 4). The amount of surface wax present on the leaves of the wild oats was greater at heading

Figure 4. The effect of moisture stress on the (A) protein content and (B) dry weight per sample of wild oats harvested over a period of 7 weeks beginning at the three- to four-leaf stage. Each sample consisted of four plants.

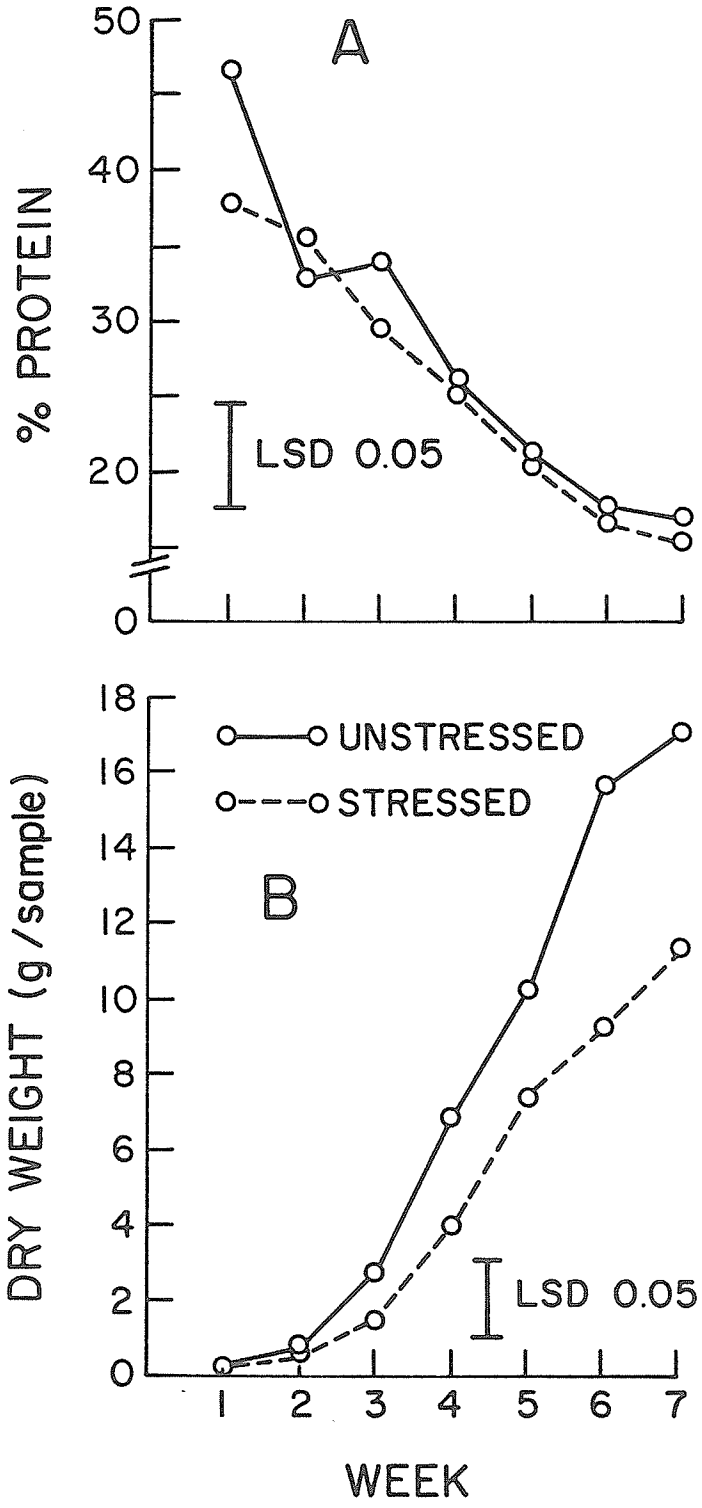

A
% PROTEIN
50
40
30
20
0
LSD 0.05
B
DRY WEIGHT (g/sample)
18
16
14
12
10
8
6
4
2
0
UNSTRESSED
STRESSED
LSD 0.05
1
2
3
4
5
6
7
WEEK

Table 4. Effect of moisture stress on the development of epicuticular wax in wild oats at three growth stages.

Treatment	Wax Development[a]		
	Jointing	Flag	Heading
	μg/cm^2		
Unstressed	7.55a	7.80a	11.02b
Stressed	7.81a	7.75a	17.83c

[a]Means in rows or columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

than at jointing or the flag-leaf stage in both treatments. However, the leaves of wild oats subjected to water stress produced about 60% more epicuticular wax by heading than the leaves of wild oats grown under well-watered conditions. There were no significant differences in wax production between treatments at jointing or the flag-leaf stage. These results are in general agreement with the conclusion of Baker and Procopiou (1980) who observed that epicuticular wax sythesis is stimulated in plants subjected to water stress. This does not seem to be a general occurrence, however, as Weete et al. (1978) reported that wax synthesis was inhibited about 38% in cotton subjected to water stress compared to well-watered controls.

The effects of moisture stress on the anatomy of the leaves of wild oats was also measured on material sampled on the same dates as the leaves for epicuticular wax determinations were sampled (Table 5). Neither the area occupied by intercellular space, nor the area occupied by mesophyll cells, nor the total cross-sectional area of the leaves was significantly affected by moisture stress at any of the growth stages examined, according to an F-test. The ratios of mesophyll surface area to total area also did not differ significantly between treatments (data not shown). However, because the entire procedure for obtaining the data was exceedingly time consuming, a sample of only three transverse sections was used to compute each mean. The sample size and variability encountered between samples (C.V.'s of about 11 to 22%) may have masked any significant differences between treatments. Generally, the trend was one of reduced mesophyll area and reduced intercellular space in the leaves of the stressed wild oats compared to the leaves of the well-watered wild

Table 5. The effect of moisture stress on the anatomy of wild oat leaves at three growth stages.

Growth stage	Leaf sampled	Treatment	Area[a]		
			Intercellular spaces	Mesophyll	Total
			(μm^2)		
Jointing	Fifth	High	10.9	21.8	38.4
		Low	10.9	16.5	33.2
Flag-leaf	Two below The flag	High	14.0	22.7	42.4
		Low	9.2	19.6	34.2
Heading	Flag	High	5.9	11.9	22.2
		Low	4.8	9.7	18.7

[a]Measured from photographs (330x) of transverse sections. Mean of three samples.

oats. The reductions in mesophyll area and intercellular space were likely due to a reduction in either leaf thickness, leaf width or both since the total area of the cross sections was also reduced while the ratios of mesophyll area and intercellular space to total area did not differ greatly between treatments. Nobel (1980) found that water stress induced increases in the ratio of mesophyll surface area per unit leaf surface area of certain species, but concluded that the water use efficiency (ratio of photosynthesis to transpiration) was not improved by the greater internal surface area exposed for CO_2 uptake.

Growth room study, plant-water relations. To complement and expand on the outdoor study, an experiment was conducted under controlled conditions in the growth room. In addition to treatments comparable to the stressed and unstressed treatments included in the outdoor experiment, two additional treatments were added to provide information on the effects of either alleviating or imposing water stress at the four-leaf stage on the growth of wild oats.

The first time the experiment was conducted visual wilting was evident in the high SMC treatment at the time of watering near the end of the experiment. Therefore, the number of seedlings of wild oats per pot was reduced from six to five when the experiment was repeated. Despite the decreased number of plants per pot, the growth responses of the wild oats to the various SMC regimes were very similar in both trials and data from the combined trials are presented here. However, a change in the timing (but not the duration) of the light period in the growth room between Trial 1 and Trial 2 resulted in the lights being on

for a longer period of time in Trial 2 before stomatal diffusion resistances, transpiration rates and leaf water potentials were measured. Consequently, higher stomatal diffusion resistances and lower transpiration rates and leaf water potentials were recorded for the wild oats grown at a reduced SMC in Trial 2 compared to Trial 1. Therefore, although the trends in these measurements over the course of the experiment were similar in both Trials, only the results from Trial 2 which were less variable than those from Trial 1 are presented here. See Appendix Table 1 and Appendix Figures 4 and 5 for the results from Trial 1.

The weekly leaf water potentials of wild oats grown under the various SMC regimes are presented in Table 6. Leaf water potentials were measured 2 h after watering of the pots was completed and, therefore, these values probably represent neither the lowest nor the highest leaf water potentials that occurred, since total recovery of the leaf water potential would likely not occur in 2 h. In the high SMC treatment the leaf water potential remained fairly constant over the course of the experiment except at weeks 4 and 5 when it decreased to a much lower value before returning to its former level. There is no obvious explanation for the sudden drop in the leaf water potential at these sampling times. In the low SMC treatment the leaf water potential did not drop much below that in the high treatment until near the end of the experiment when it reached a minimum of about -17 bars, compared to -5 bars in the high SMC treatment.

Following the return of the SMC from 10 to 20% at week 2, the leaf water potential in the low-high treatment increased from about -17 bars to about -2 bars by week 3. On the other hand, when water was withheld

Table 6. Effect of various SMC regimes on the[a] water potential of the most recently fully expanded leaf of wild oats[a].

Week	Leaf water potential[b]			
	High	High-low	Low	Low-High
	bars			
1	- 6.0	- 9.5	- 8.5	-10.6
2[c]	- 5.4	- 7.4	- 7.7	-16.8
3	- 5.0	-14.2	- 7.9	- 2.3
4	- 9.9	-24.0	- 8.3	- 4.9
5	-15.1	-31.6	-15.1	- 2.3
6	- 8.7	-33.4	- 7.9	- 5.7
7	- 7.6	-31.6	-15.1	- 4.5
8	- 4.9	-23.2	-16.6	- 3.7

[a] Sampling started at the two-leaf stage.

[b] Non-replicated samples.

[c] Low-high treatment rewatered after sampling; water withheld from high-low treatment after sampling.

from the high-low treatment after week 2 until the SMC decreased to 10%, the leaf water potential decreased to a level considerably below that of the plants in the low treatment. The wild oats in the low treatment, which were subjected to water stress at the time of emergence, were visibly smaller than those in the high-low treatment at week 2 and may also have had a smaller root system. Therefore, the plants in the low treatment would not have placed as great a demand on the limited soil water available in the pots as those in the high-low treatment and thus would not have experienced the same level of water deficit nor the same low leaf water potentials.

There were no large differences in stomatal diffusion resistance among the treatments prior to week 3 (Figure 5). Beyond week 3, the stomatal diffusion resistance increased similarly in the low and high-low treatments until about week 6 when it appeared to be levelling off. From week 2 to week 3 the stomatal diffusion resistance of wild oats in the low-high treatment decreased about 60% following an increase of the SMC from 10 to 20% at week 2. Subsequently, there were no significant differences in stomatal diffusion resistance between the high and low-high treatments indicating a complete recovery of stomatal diffusion in the wild oats previously grown at a SMC of 10%. However, since the stomatal diffusion resistance was significantly higher in the wild oats in the low and high-low treatments after week 2 than in the high and low-high treatments, the water deficits which developed in the low and high-low treatments were sufficient to cause at least partial stomatal closure.

Prior to week 3, there were no differences in transpiration rate

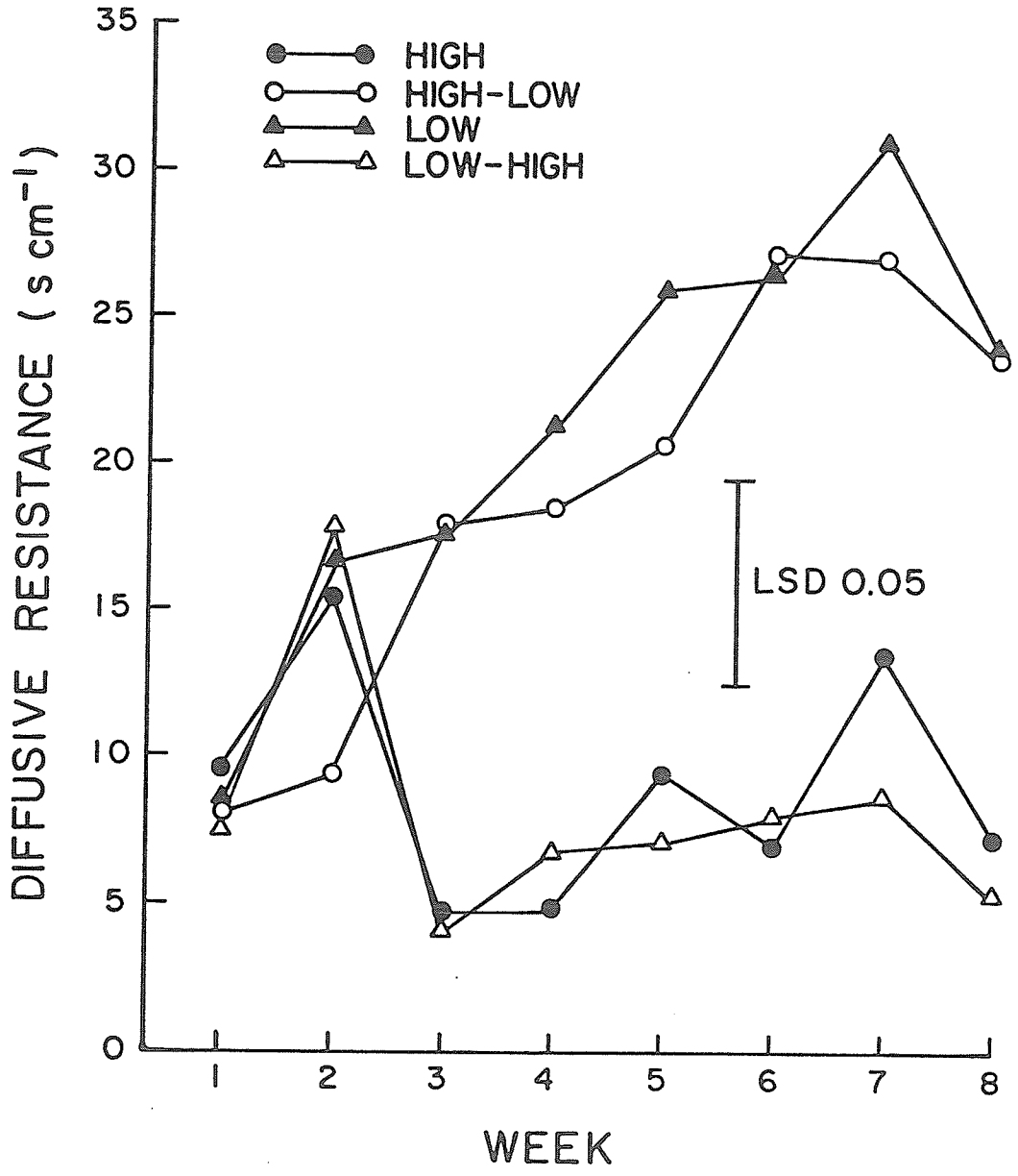


Figure 5. Effect of various SMC regimes on the stomatal diffusion resistance of wild oats from the two-leaf stage to maturity. At the four-leaf stage (week 2), the SMC in the low-high treatment was increased from 10 to 20% for the duration of the experiment and water was withheld from the high-low treatment until the SMC decreased to 10%.

among the four treatments (Figure 6). It is not clear why the transpiration rate of wild oats in the high and high-low treatments at week 1 and week 2 was significantly lower than that of wild oats in the high treatment at week 3 since the SMC was the same. Beginning at week 3, the transpiration rate of wild oats in the high treatment was generally significantly greater than that of wild oats in the low treatment except near the end of the experiment when the transpiration rate appeared to fluctuate more strongly from week to week in the high treatment.

The transpiration rate of wild oats in the low-high treatment decreased from week 1 to week 2 but increased markedly following an increase of the SMC from 10 to 20% at week 2 such that there were no differences in transpiration rates between the high and low-high treatments for the duration of the experiment. In contrast, decreasing the SMC from 20 to 10% in the high-low treatment at week 2 caused a reduction in the transpiration rate so that beginning at week 3 there were no significant differences in the transpiration rate of the wild oats in the low and high-low treatments.

In general, stomatal diffusion resistance and transpiration rates of wild oats in the high and low treatments of the growth room study did not closely match those measured in the unstressed and stressed treatments of the outdoor study. Stomatal diffusion resistances (Figure 5) were higher and transpiration rates (Figure 6) lower in the wild oats in the low treatment of the growth room study compared to the corresponding stressed treatment of the outdoor study (Figure 2). Begg and Turner (1976) assembled considerable evidence indicating that the pattern of development of water stress in plants may differ in the two environments

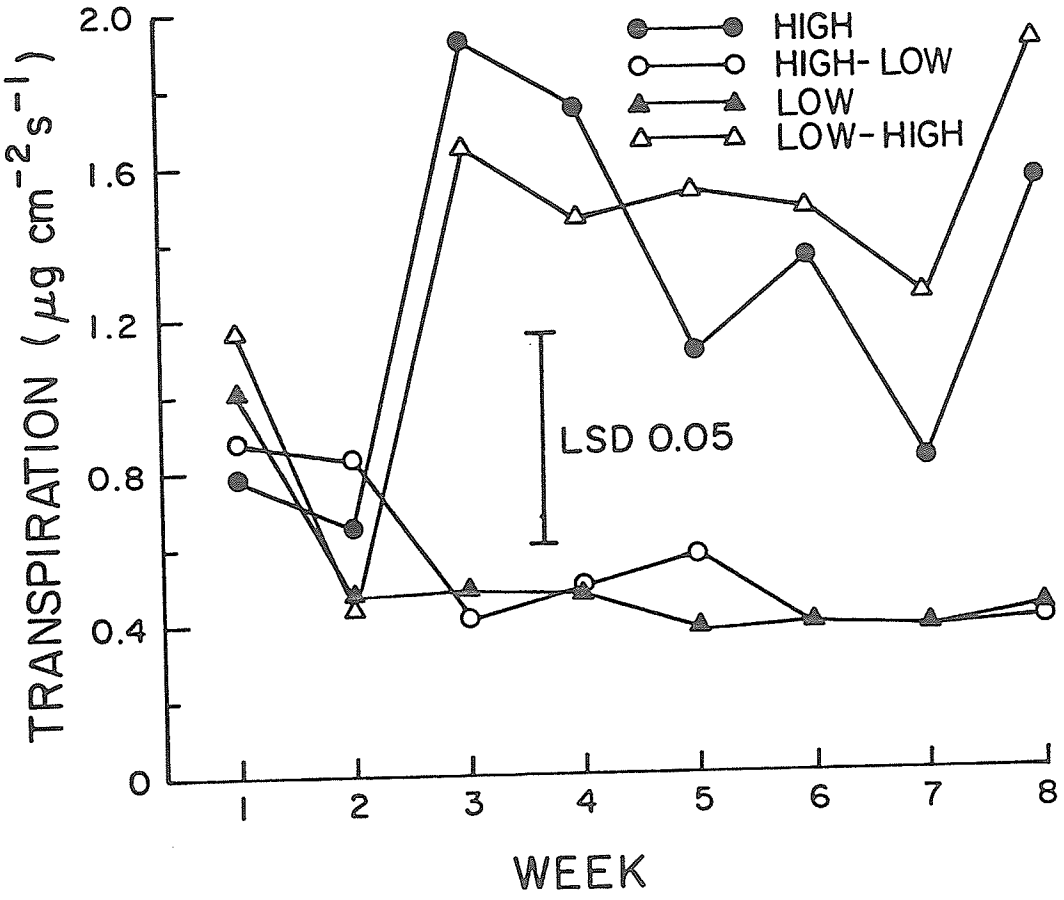
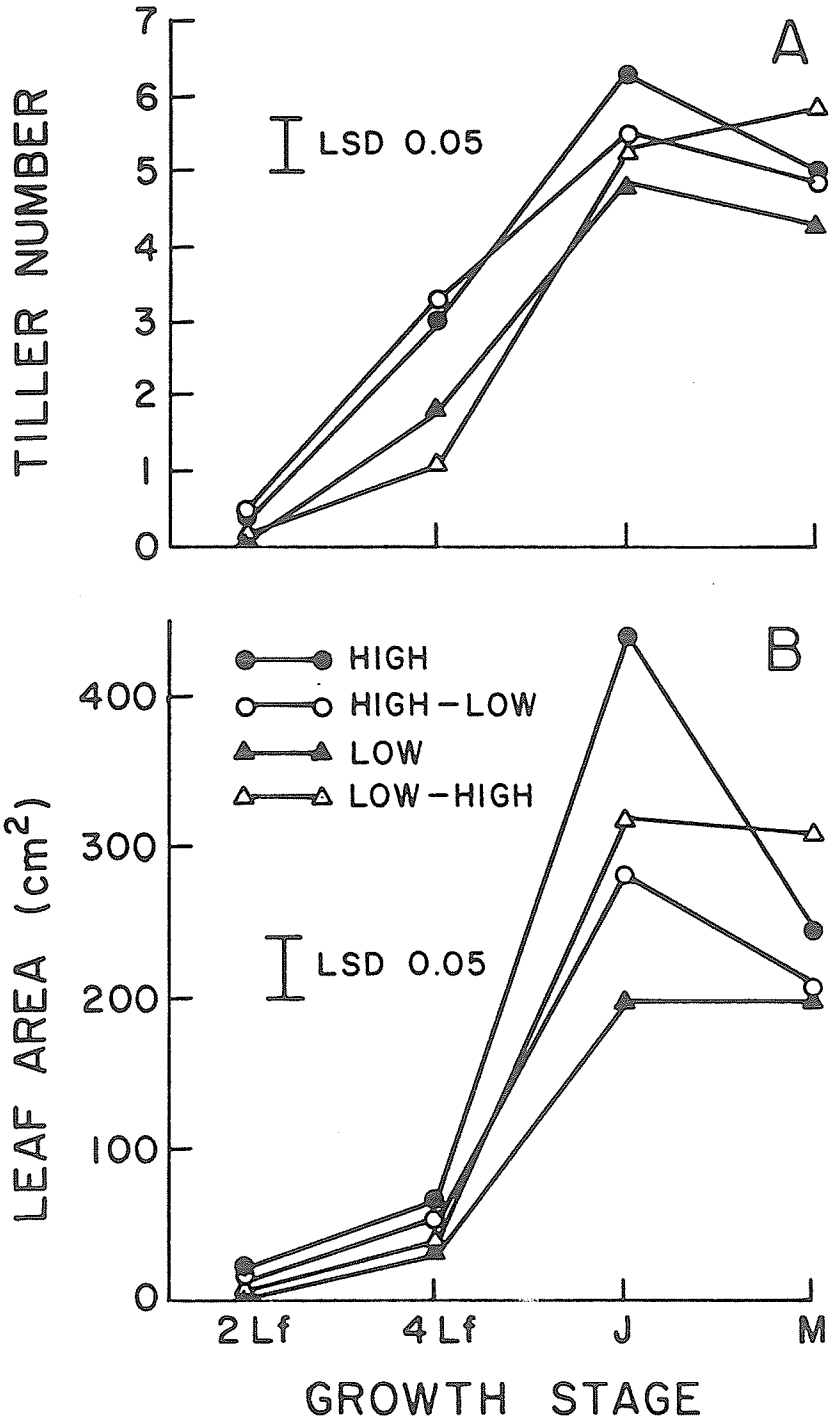


Figure 6. Effect of various SMC regimes on the transpiration rate of wild oats from the two-leaf stage to maturity. At the four-leaf stage (week 2) the SMC in the low-high treatment was increased from 10 to 20% for the duration of the experiment and water was withheld from the high-low treatment until the SMC decreased to 10%.

such that the quantitative response to the water stress in growth room studies may not always be repeated in the field. The rapid and relatively even drying of the entire soil mass in the growth room study would have afforded little opportunity for adaptation to the water stress in wild oats through osmotic adjustment. Moreover, the more gradual development of the water stress in the outdoor study and the larger volume of soil may have permitted the expansion of roots deeper into the soil profile where water would have been more accessible than near the surface (Begg and Turner, 1976). Therefore, in the outdoor study wild oats may have experienced less severe water stress than in the growth room study as indicated by the stomatal diffusion resistance and transpiration rates recorded.

Growth room study, plant growth. Similar to the results of the outdoor study, subjecting wild oats to water stress at emergence under growth room conditions reduced the number of viable tillers per plant (Figure 7A). At the four-leaf stage the number of viable tillers per plant in the low treatment was about 40% less than in the high treatment. However, at jointing the difference in the number of viable tillers per plant between the high and low treatments decreased to about 25% due to a large increase in the rate of tiller formation in the stressed wild oats between the four-leaf and jointing stages. At maturity, the number of viable tillers per plant in the high treatment was not significantly greater than in the low treatment due to a slightly greater rate of tiller senescence in the high treatment from jointing to maturity. In the outdoor study, however, a greater rate of tiller senescence occurred

Figure 7. Effect of various SMC regimes on the (A) number of viable tillers and (B) leaf area of wild oats the at four growth stages. At the four-leaf stage (week 2), the SMC in the low-high treatment was increased from 10 to 20% for the duration of the experiment and water was withheld from the high-low treatment until the SMC decreased to 10%.


A
TILLER NUMBER
0
1
2
3
4
5
6
7
LSD 0.05
B
LEAF AREA (cm²)
0
100
200
300
400
HIGH
HIGH-LOW
LOW
LOW-HIGH
LSD 0.05
2 Lf
4 Lf
J
M
GROWTH STAGE

in the stressed wild oats so that at the end of the experiment, the number of viable tillers in the stressed wild oats was significantly lower than in the unstressed wild oats (Figure 3A).

Initiation of water stress at the four-leaf stage resulted in a significant reduction in the number of viable tillers per plant in the high-low treatment compared to that of well-watered wild oats in the high treatment at jointing but not at maturity (Figure 7A). An increase in the SMC from 10 to 20% in the low-high treatment at the four-leaf stage resulted in a rapid recovery of the previously retarded rate of tiller production in the wild oats so that, at maturity, the number of viable tillers per plant exceeded that in the high treatment by about 15%. These results are in agreement with the findings of Chinoy (1961) who worked with wheat and Aspinall et al. (1964) who worked with barley. In both of these studies, a brief period of water stress at the tiller initiation phase followed by a period of no stress resulted in a rapid increase in tiller formation and a larger final tiller number in the initially stressed plants than in the well-watered controls. In contrast, Joffe and Small (1964) reported that the final tiller number in wheat and oats subjected to water stress at the tiller initiation stage remained below that of the well-watered controls following alleviation of the stress. A loss of apical dominance by the major apices during a period of water stress may release the subordinate apices from their control thus causing an increase in tiller production after rewatering (Aspinall et al. 1964). Therefore, seed production in wild oats may not be adversely affected if the period of water stress ends at the four-leaf stage or earlier.

The pattern of changes in leaf area of wild oats in response to changes in the water status of the soil is shown in Figure 7B. Unlike tiller number, leaf area of wild oats was not significantly reduced by water stress initiated at emergence until jointing, although the leaf area was slightly greater in the high and high-low treatments than in the low and low-high treatments. At jointing, the leaf area of wild oats in the low treatment was reduced to less than half of that of wild oats in the high treatment, whereas at maturity the differences in leaf area between the two treatments was reduced to about 18% due to a marked senescence of the leaves in the high treatment which was not paralleled in the low treatment.

Water stress is generally believed to hasten the senescence of leaves (Kozlowski, 1976). However, the rate of leaf senescence in wild oats in the high treatment between jointing and maturity was clearly much greater than in any of the other treatments. In the oudoor study, the rate of leaf senescence after week 5 was also slower in the water-stressed wild oats than in the unstressed wild oats (Figure 2B). Thus, in wild oats the process of leaf senescence may be delayed rather than hastened by water stress. However, because the wild oats in the well-watered high treatment were larger than those in the low treatment especially near the end of the experiment, they placed a strong demand on the limited water available in the pots and quite probably experienced a considerable degree of water stress between the daily waterings. This water stress occurring relatively late in the development of wild oats which had not previously been subjected to water stress may have resulted in the observed greater rate of leaf senescence in the high treatment

compared to in the low treatment.

The short period of water stress from emergence to the four-leaf stage in the low-high treatment reduced the leaf area of wild oats at jointing compared to the high treatment but not by as much as in the low treatment (Figure 7B). At maturity, the leaf area of wild oats in the low-high treatment exceeded that of wild oats in the high treatment due to the extensive leaf senescence in wild oats in the high treatment. Subjecting wild oats to water stress at the four-leaf stage caused a sharp decline in leaf enlargement so that, at jointing, the leaf area was 35% less in the high-low treatment than in the high treatment. At maturity, the leaf area in the high-low treatment was not significantly different from that of wild oats in the low treatment due to leaf senescence from jointing to maturity. Therefore, maximum leaf area in wild oats was recorded at jointing in this study and any changes in leaf area which occurred after jointing appeared to be due to leaf senescence, either natural or water stress-induced.

The protein content of wild oats remained constant until the four-leaf stage after which time it decreased in all treatments over the duration of the experiment (Figure 8). Prior to jointing there were no significant differences in protein content among the four treatments. At jointing, the protein content of wild oats was significantly lower in the high treatment than in the low and low-high treatments. At maturity the protein content of wild oats was also significantly lower in the high treatment than in the low and high-low treatments. The observed differences in protein content of wild oats among treatments at jointing and at maturity while significant were small and were consequently attributed to a greater dilution of the protein by cellulose and other structural carbohydrates

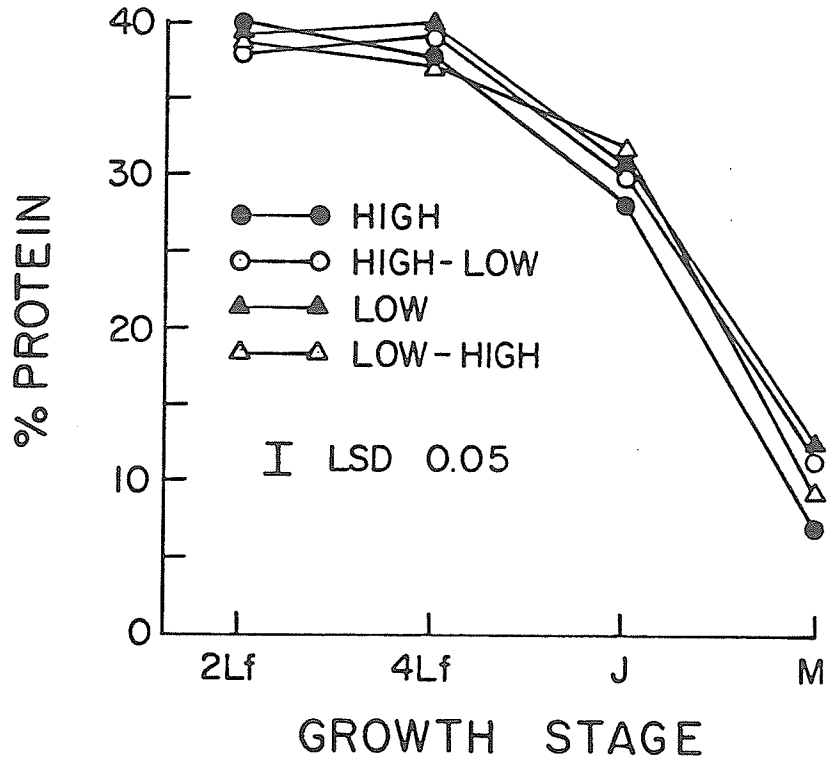


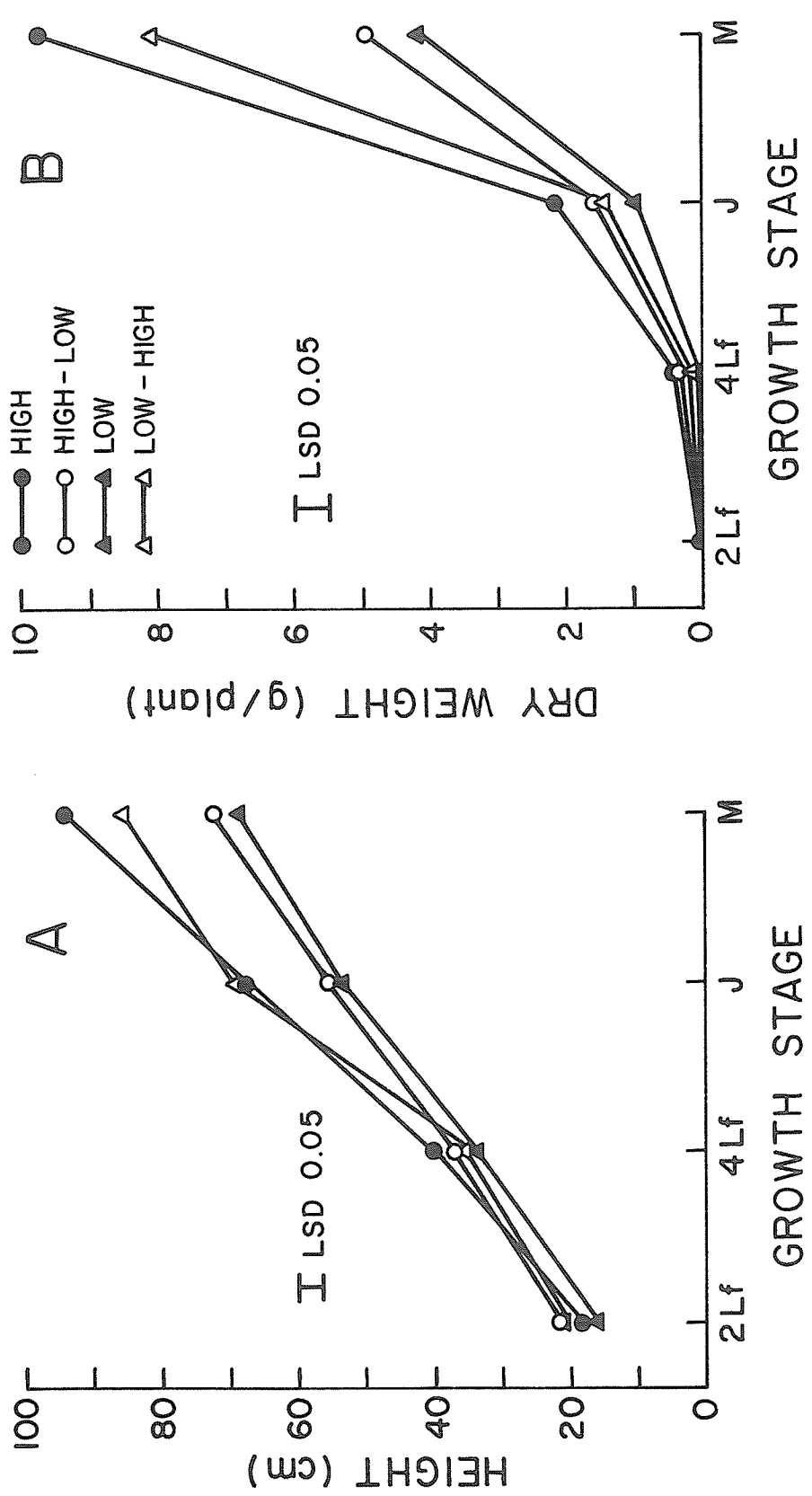
Figure 8. Effect of various SMC regimes on the protein content of wild oat shoots at four growth stages. At the four-leaf stage (week 2), the SMC of the low-high treatment was increased from 10 to 20% and water was withheld from the high-low treatment until the SMC decreased to 10%.

in the larger plants of the high and low-high treatments rather than to any effect of water stress on protein synthesis or degradation.

As in the outdoor study, shoot elongation in wild oats under growth room conditions was also significantly reduced by water stress (Figure 9A). Although the height of wild oats continued to increase from emergence to maturity, the rate of elongation was retarded in the stressed treatments resulting in plants which were 23 to 27% shorter at maturity in the high-low and low treatments, respectively, compared to the height of plants in the high treatment.

Shoot elongation of wild oats in the high-low treatment was nearly identical to that in the low treatment following a decrease in the SMC from 20 to 10% at the four-leaf stage. This was not unexpected since the water stress was imposed before the major portion of shoot elongation took place and continued until maturity when shoot elongation ceased. Increasing the SMC from 10 to 20% at the four-leaf stage resulted in a temporary sharp increase in the rate of elongation until jointing after which the elongation rate declined so that, at maturity, the wild oats in the low-high treatment were about 10% shorter than those in the high treatment. Contrary to these results, Joffe and Small (1964) found that stem height reductions in wheat and oats subjected to water stress at the tiller initiation stage were completely overcome after rewatering. However, a period of severe water stress at the shooting stage, similar to the high-low treatment in the experiment reported here, did cause a permanent reduction in the height of oats at maturity while an equivalent period of moderate water stress did not.

Figure 9. Effect of various SMC regimes on the (A) height and (B) dry weight of wild oats at four growth stages. At the four-leaf stage (week 2), the SMC in the low-high treatment was increased from 10 to 20% for the duration of the experiment and water was withheld from the high-low treatment until the SMC decreased to 10%.


A
B
HEIGHT (cm)
DRY WEIGHT (g/plant)
GROWTH STAGE
GROWTH STAGE
2Lf
4Lf
J
M
LSD 0.05
LSD 0.05
HIGH
HIGH-LOW
LOW
LOW-HIGH
0
20
40
60
80
100
0
2
4
6
8
10

The response curves of dry weight over the course of the experiment as influenced by the various SMC regimes are shown in Figure 9B. There were no significant differences in dry weight of wild oats among the treatments prior to jointing. The dry weight of wild oats in the low treatment was about one half that of wild oats in the high treatment at jointing and about 57% less by maturity. This was a greater reduction in dry matter production than occurred in the outdoor study where the dry weight of stressed wild oats at maturity was only about 33% less than that of the unstressed wild oats. This further emphasizes the differences in response of plants to water stress that can occur between field and growth room studies. Sharma et al. (1977) reported dry weight reductions of 20% and 45% in wild oats grown in soil with moisture contents cycled between 50 and 100% field capacity and 25 and 100% field capacity, respectively, compared to when the SMC was cycled between 75 and 100% field capacity.

The reduction in dry matter accumulation of wild oats from the four-leaf stage to jointing in the high-low treatment compared to the high treatment was approximately equivalent to the increase in dry matter accumulation over the same period in the low-high treatment. Following a continued reduction in the rate of dry matter accumulation, the dry weight of wild oats in the high-low treatment at maturity was only about 15% greater than that of wild oats in the low treatment. However, the rate of dry matter accumulation of wild oats in the low-high treatment from jointing to maturity was almost equal to that of wild oats in the high treatment so that, at maturity, the brief period of water stress from emergence to the four-leaf stage was almost com-

pletely overcome and resulted in a reduction of less than 20% in the final dry weight of wild oat shoots relative to the high treatment.

About 80 to 90% of the dry matter accumulation in plants is ultimately derived from photosynthesis (Karamanos, 1979). As was earlier shown, water stress initiated either at emergence or at the four-leaf stage resulted in approximately an 80% increase in the stomatal diffusion resistance (Figure 5) and a 60% reduction in the transpiration rate (Figure 6) of wild oats by the conclusion of the experiment. Net assimilation rates were not measured so it cannot be directly concluded from these results that photosynthesis was inhibited. However, it is certain that at least partial stomatal closure occurred and changes in net photosynthesis are known to follow fairly closely changes in stomatal conductance (El-Sharkawy and Hesketh, 1964) or transpiration rate (Boyer, 1970). Furthermore, photosynthesis is not only affected by stomatal aperture which regulates CO_2 uptake (Hsiao, 1973) but also by the quantity of assimilating area available for light interception. It is now generally accepted that leaf expansion is more sensitive to water stress than is CO_2 assimilation and, consequently, dry matter production can be reduced even if the level of plant water deficit is not severe enough to cause stomatal closure and restrict CO_2 uptake (Hsiao and Acevedo, 1974). In view of the fact that dry matter accumulation in the unstressed wild oats increased from jointing to maturity (Figure 9A) even though leaf senescence during the same period resulted in a loss of about 45% of the assimilating area (Figure 7B), it seems reasonable to conclude that the reductions in dry matter accumulation in the stressed wild oats were primarily due to an inhibition of photosynthesis through stomatal closure.

In the outdoor study, differences in stomatal diffusion resistance and transpiration rates of wild oats between the stressed and unstressed treatments were small (Figure 2), but the dry weight was still reduced by about 30% in the stressed wild oats compared to the unstressed wild oats (Figure 4B). Thus, it is likely that in the outdoor study, dry weight reduction in wild oats subjected to water stress was due to decreased photosynthesis through a reduction of the assimilating area (Figure 3B).

For the most part, the effect of water stress on the growth and development of wild oats under growth room conditions was very similar to its effect in the outdoor study despite the differences in soil types and levels of water stress. The larger volume of soil, higher light intensities and fluctuating evaporative demand in the outdoor study no doubt more closely approximated a normal field situation.

Wild oats generally appeared to be quite sensitive to water stress, with the observed reductions in leaf area, tiller number, and plant height resulting in a considerable decrease in the dry weight both in the growth room and outdoors. It remains to be determined how these responses might affect the competitive ability of wild oats in a crop and whether water stress significantly affects the reproductive capacity of the species.

CHAPTER IV

The Effect of Soil Moisture on the Control of Wild Oats (*Avena fatua*) with Diclofop Methyl

INTRODUCTION

Under ideal conditions a postemergence application of diclofop methyl (2-[4-(2,4-dichlorophenoxy)phenoxy]propionic acid) effectively controls many annual grassy weeds including wild oats (*Avena fatua* L.) and green foxtail [*Setaria viridis* (L.) Beauv.] (Todd and Stobbe, 1977). In the prairie provinces of Canada, the weather varies considerably from year to year, and in hot and dry years less than adequate control of wild oats with diclofop methyl has sometimes been observed.

That a period of reduced soil moisture levels before, during or after spraying influences the activity of many foliar-applied phenoxy type herbicides is well known from both field and growth room studies (Wiese and Rea, 1962; Friesen and Dew, 1966; Shahi, 1975). Similar information on the behaviour of more recently developed non-phenoxy type herbicides is limited, especially under field conditions. Control of slow-growing barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] (early planting) with diclofop methyl was significantly reduced by each reduction in soil moisture content prior to treatment (West *et al.*, 1980). Control of fast-growing plants (late planting) was not affected by decreased soil moisture contents prior to treatment. Dortenzio and Norris (1980) observed that control of barnyardgrass with diclofop methyl decreased as

the time of irrigation after spraying was delayed. Under growth chamber conditions, the control of wild oats with diclofop methyl was decreased by about 50% when the soil moisture content was decreased from just below field capacity to slightly above the permanent wilting point (Dortenzio and Norris, 1980). The present study was undertaken to determine the effect of water stress on the control of wild oats with diclofop methyl under field conditions.

MATERIALS AND METHODS

During the summer of 1980, a field study was conducted near Carman, Manitoba on Almasippi very fine sandy loam (79% sand; 9% silt; 12% clay; 4% OM; pH 7.4). On May 28, plots were fertilized with 85 kg/ha urea ammonium phosphate (27-27-0) and seeded with wheat (Triticum aestivum L. CV. 'Neepawa') (115 kg/ha) and wild oats (75 seeds/m^2) in rows spaced 15 cm apart. The wheat was planted to a depth of 5 cm with a commercial seeder and the wild oats were planted by hand to a depth of 2.5 cm. Plots were 1.5 m by 2 m with approximately a 5% slope parallel to the direction of the rows.

The experimental design was a randomized complete block with four replicates and eight treatments. The treatments consisted of four soil moisture regimes: irrigated; normal; moderate stress; and strong stress; each of which was either treated with herbicide or left as an unsprayed check.

To generate moisture level differences among the treatments, gutters constructed of asphalt felt roofing paper (as described in Chapter III) were placed between rows when wild oats reached the two- to three-leaf stage. For the treatments designated as normal and irrigated, gutters were further modified by the removal of 10 circular sections 6 cm in diameter from each gutter to allow movement of water into the underlying soil. For the moderate stress treatment, modified and unmodified gutters were alternated between the rows. Unmodified gutters only were placed between the rows in the strong stress treatment.

An overhead sprinkler system was used to apply 2.2 cm water per week to the irrigated treatment. Addition of water to the irrigated treatment was based on the mean weekly rainfall data for May and June over a 37 year period from 1938 to 1975. To compensate for the abnormally dry conditions prior to and after seeding, 2.5 cm of water was applied to all plots 1 week after seeding. Subsequently, 1.9 cm of water was added to all plots 2, 3, and 4 weeks after seeding. Irrigated treatments continued to receive an additional 2.2 cm of water per week until seven weeks after seeding.

Two weeks after seeding, ceramic cup psychrometers[1] were buried in plots at depths of 20 cm and 40 cm. An automatic data logging system[2] was used to measure soil water potentials at 4:00 a.m. and 4:00 p.m.

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[1]WESCOR, INC., Logan, Utah.

[2]MDL-590, S-B Systems, Manhattan, Kansas.

When wild oats reached the three- to four-leaf stage, a sample equivalent to one row was taken diagonally across the plots excluding the outside two rows of each plot. A count of wild oats was also taken in a 1/4 m^2 quadrant of each plot. One half of all plots were then treated with a solution of a commercially formulated emulsifiable concentrate (E.C.) of diclofop methyl [119 g/l active ingredient (a.i.)] at 0.7 kg/ha a.i. using 80015 Tee Jet nozzles mounted on a bicycle sprayer.

Fifteen days after spraying, gutters were removed from all plots and a second sample of wheat and wild oats was taken perpendicular to the first sample. A count of wild oat plants was again taken on all plots as previously described.

Seven weeks after spraying, when wild oats reached maturity, the inner eight rows and inner 1 m lengths of all plots were harvested by hand. Wheat and wild oats were separated, counted and placed in a drying room. The wheat was subsequently threshed for grain yield.

RESULTS AND DISCUSSION

Measurements made on a sample of wild oats and wheat removed from the plots at the time of treatment with diclofop methyl (0.7 kg/ha) are presented in Table 7. Large differences occurred among the treatments in the number of wheat and wild oat plants comprising each sample. Therefore, dry weights of both wheat and wild oats were corrected for differences in stand using covariance in order to get a better measure of the effect of the various gutter treatments on the growth of the two species. Dry weights in subsequent samples were not adjusted in this manner.

Table 7. Effect of gutter treatments on the growth of wild oats and wheat at the time of herbicide treatment.[a]

Treatment	Wild oats			Wheat
	Count[b]	Dry weight[c] per sample	Leaf area per plant	Dry weight[c] per sample
		(g)	(cm^2)	(g)
Irrigated	8.3a	0.53a	13.1a	36.5a
Normal	7.0a	0.47a	15.9a	37.7a
Moderate stress	8.1a	0.38a	12.3a	41.6a
Strong stress	8.1a	0.48a	16.2a	29.0a

[a]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

[b]Based on a random 1/4 m^2 sample.

[c]Corrected for differences in stand using covariance.

No significant differences were evident among the treatments for any of the parameters used to assess the growth of wheat and wild oats (Table 7). Leaf expansion is generally accepted to be one of the most moisture stress sensitive growth processes (Hsiao, 1973). Due to the absence of significant differences in the leaf area of wild oats among the treatments, it appeared that the gutters were not effective in altering soil moisture levels up to the time of herbicide treatment. An undetected malfunction in the data logging system, which developed during the course of the experiment, precluded the measurement of soil water potentials. Therefore, quantitative information on soil moisture levels among treatments was not available.

Abnormally low rainfall prior to and after seeding slowed the emergence of wild oats and resulted in uneven stands. A period of 4 weeks elapsed between the time of seeding and when wild oats reached the two- to three-leaf stage. However, wheat stands were well developed at that time. To avoid shading of the wild oat plants, gutters were not placed between the rows until wild oats reached the two- to three-leaf stage. Therefore, only a short period of time elapsed between the placing of the gutters and herbicide treatment at the three- to four-leaf stage. This may in part account for the lack of significant differences in growth among treatments at the time of spraying. Moreover, although the irrigated treatments were watered over a period of several hours with the gutters removed, a certain amount of runoff from the plots occurred due to the slow rate of infiltration of water into the dry soil. Consequently, the amount of

water actually taken up by the irrigated treatments was somewhat less than the amount applied.

A second sample of wheat and wild oats was removed from all plots 15 days after treatment with diclofop methyl (Table 8). Wild oat counts and leaf area or wheat dry weight values did not differ significantly among or between the sprayed and unsprayed gutter treatments. Similarly, there were no significant differences in the height of wild oat plants among the sprayed treatments or among the unsprayed treatments. The significant height reduction in the sprayed normal treatment as compared to the unsprayed irrigated and strong stress treatments was not consistent with expected results assuming that the gutter treatments were effective in reducing soil moisture levels.

With respect to dry weight of wild oats, differences were apparent between corresponding sprayed and unsprayed treatments, but these differences were not always significant. Generally, control of wild oats, as indicated by the differences in dry weight between the sprayed treatments and equivalent unsprayed controls, decreased as soil moisture levels decreased from the irrigated to the strong stress treatments. However, the smallest level of control did not occur in the sprayed strong stress treatment but rather in the sprayed moderate stress treatment. The unmodified gutters between the rows of the strong stress treatment may have reduced evapotranspiration sufficiently to prevent development of the desired soil moisture deficit. West et al. (1980) similarly reported decreased activity of diclofop methyl on barnyardgrass

Table 8. Effect of gutter treatments on the growth of wheat and control of wild oats 15 days after treatment with diclofop methyl (0.7 kg/ha a.i.)[a].

Treatment	Wild oats				Wheat
	Count[b]	Dry Weight per sample	Leaf area per plant	Height per plant	Dry Weight per sample
		(g)	(cm^2)	(cm)	(g)
Irrigated	7.5a	5.54a	66.4a	58.8a	92.6a
Normal	5.0a	2.54bcd	40.0a	43.3ab	108.8a
Moderate stress	7.5a	3.42abc	46.4a	49.9ab	75.1a
Strong stress	7.5a	4.05ab	47.7a	60.6a	133.3a
Irrigated-sp[c]	6.3a	1.69cd	39.0a	44.6ab	98.4a
Normal-sp	5.8a	1.28cd	23.1a	33.3b	120.4a
Moderate stress-sp	4.5a	2.47cd	42.6a	51.3ab	101.9a
Strong stres-sp	5.3a	1.01d	40.5a	37.2ab	98.6a

[a]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

[b]Based on a random 1/4 m^2 sample.

[c]Herbicide treated.

under field conditions as soil moisture levels were decreased. Dortenzio and Norris (1980) found that control of barnyardgrass in the field was greatest when diclofop methyl application was followed by daily irrigation during a period when no rain fell.

In general, wild oat stand and dry weight and wheat culm number measured at final harvest (Table 9), decreased among the unsprayed treatments from the irrigated to the strong stress treatment. However, the decreases were not always statistically significant. Wheat grain yield, on the other hand, did not appear to follow any consistent pattern among the sprayed or unsprayed treatments. Gutters were removed from all plots two weeks after herbicide treatment. Irrigated plots continued to receive additional water until final harvest but all other plots received only natural rainfall. A total of only 4.9 cm of rain fell from the time the gutters were removed until final harvest (Table 10) so that, except for the irrigated plots, all others were likely experiencing a water deficit at the time of final harvest.

Control of wild oats with diclofop methyl at final harvest, as indicated by the reduction in stand and dry weight among the sprayed treatments compared to the corresponding unsprayed controls, generally decreased from the irrigated to the strong stress treatment. Control of wild oats was greatest in the sprayed irrigated treatment (56.8% and 89.4% reductions in stand and dry weight, respectively) and least in the sprayed strong stress treatment (21.2% and 22.4% reductions in stand and dry weight, respectively). Control of wild oats in the sprayed normal and moderate stress treatments was intermediate.

Table 9. Effect of gutter treatments on the growth of wheat and control of wild oats seven weeks after treatment with diclofop methyl (0.7 kg/ha a.i.)[a].

Treatment	Wild oats		Wheat	
	Stand per plot	Dry Weight per plot	Culm number per plot	Grain yield per plot
		(g)		(g)
Irrigated	44.0a	104.5a	455.0a	226.1ab
Normal	34.0ab	66.6ab	417.3ab	242.2a
Moderate stress	29.3abc	76.3ab	368.3c	184.6bc
Strong stress	28.3abc	55.0bc	370.3c	212.7abc
Irrigated-sp[b]	19.0bc	11.1d	453.3a	205.8abc
Normal-sp	22.5bc	18.9cd	385.0bc	217.7abc
Moderate stress-sp	14.8c	15.5cd	430.8a	236.1a
Strong stress-sp	22.3bc	37.2bcd	343.0c	173.2c

[a]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

[b]Herbicide treated.

Table 10. Record of precipitation received at Carman research station, Carman, Manitoba, 1980.

Date		
Month	Day	Rainfall
		(cm)
May	28[a]	0.20
	31	0.15
June	4	0.33
	12	0.08
	13	0.10
	17	0.08
	23[b]	0.15
	27	0.15
	28	0.08
	29	1.17
	30	4.50
July	4	1.02
	7[c]	0.48
	11	0.51
	13	0.61
	14	0.23
	16	0.86
	17	0.08
	21[d]	0.25
	31	0.10
August	3	1.70
	4	0.05
	5	0.33
	10	0.30
	11	0.05
	14	0.05
	18	0.99
	20	0.69
	21	0.61
	28[e]	0.13

[a]Plots seeded.
[b]Gutters placed between rows.
[c]Plots treated with diclofop methyl.
[d]Gutters removed.
[e]Final harvest.

Wheat culm number in the sprayed treatments appeared to respond favourably to the increased level of control of wild oats. Wheat culm number increased in the same order as control of wild oats among the sprayed treatments, i.e., strong stress < normal < moderate < irrigated and this may be related to decreased competition from the wild oats present. Why the control of wild oats was greater in the moderate stress treatment than in the normal treatment is not known. Wheat grain yield, however, appeared to vary independently from the control of wild oats. Wheat and wild oats were both harvested when the wild oats reached maturity. However, the wheat was not fully mature at that time and had to be artificially dried prior to threshing. The grain yields reported here, then, may not be representative of values which would have been attained if the wheat was fully mature at harvest time.

On the whole, the results from this experiment were extremely inconsistent and very inconclusive. A great deal of variability in the individual plot values for all parameters measured, coupled with the aforementioned problems of equipment failure, and abnormally dry conditions made it impossible to draw any conclusions from this study regarding the effect of soil moisture stress on the control of wild oats with diclofop methyl.

CHAPTER V

Effect of Soil Moisture on the Response of Wild Oats (*Avena fatua*) to Diclofop Methyl

INTRODUCTION

The postemergence herbicide diclofop methyl {2-[4-(2,4-dichlorophenoxy)phenoxy] propionic acid} has proven to be effective for the control of wild oats (*Avena fatua* L.) and other annual grassy weeds both in cereal and broadleaf crops (Chow and Dorrell, 1979; Todd and Stobbe, 1977). The growth of wild oats has been shown to be adversely affected by low soil moisture conditions (Sharma *et al.*, 1977). Application of diclofop methyl and certain other postemergence herbicides to wild oats under these conditions may result in less than adequate control (Jeffcoat *et al.*, 1977; Miller *et al.*, 1978). Dortenzio and Norris (1980) reported a loss in activity of diclofop methyl on wild oats and three other annual grasses when the soil moisture content was reduced from near field capacity to near the permanent wilting point. Under field conditions, early-season barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] plants were more completely controlled with diclofop methyl as the soil moisture level was increased (Ahmadi *et al.*, 1980). The primary causes for the observed reduction in activity of diclofop methyl in plants subjected to periods of limited water availability have not been reported. The objectives of the studies reported here were: i) to determine the degree to which a moderate soil moisture deficit reduces the control of wild oats with diclofop methyl; and ii) to study the effect of moisture

stress on the retention, uptake, translocation and metabolism of diclofop methyl by wild oats.

MATERIALS AND METHODS

General procedures. Four litre plastic food containers were filled with approximately 4 kg of air-dried Almasippi very fine sandy loam (79% sand; 12% clay; 9% silt; 4% OM; pH 7.7) ammended with: 200 ppm N as NH_4NO_3; 50 ppm P as $Ca(H_2PO_4)_2 \cdot H_2O$; and 65 ppm S and 160 ppm K as K_2SO_4. All pots were weighed and sufficient water was added to bring the soil moisture content (SMC) to 20%. Seeds of wild oats were placed on the soil surface and covered with 1 cm of soil at the same moisture content. Pots were placed in a growth room equipped with Gro-Lux Sylvania fluorescent lights yielding a PPFD of 220 to 297$\mu Em^{-2}S^{-1}$ over a 16 h photoperiod. Temperature was maintained at 22.5 C during the light period and 16 C during the dark period. Relative humidity was between 55 and 60%. Unless otherwise noted, plants were thinned to 12 per pot at emergence.

After an initial period of growth the SMC was either held constant at 20% or reduced to 15 or 10% by withholding water and then rewatered to 20% after various periods of time. The 20, 15, and 10% SMC's correspond to soil water potentials of -0.3, -0.8, and -6.5 bars, respectively, as determined from a moisture release curve (Appendix Figure 3). All pots were weighed and watered daily as required to maintain the appropriate SMC.

The wild oats were typically at the two- to three-leaf stage before

the desired moisture content was reached in all pots. At that time, a sample of six plants was harvested from each pot and heights, leaf areas, and average dry weights were recorded. The water potential of the most recently fully expanded leaf of untreated check plants was also determined at that time and at various times after herbicide treatment in some experiments, using leaf sample chambers[1] and a dewpoint microvoltmeter.[2]

The remaining six plants per pot were treated with solutions of commercially formulated emulsifiable concentrates (E.C.) of diclofop methyl [190 g/l active ingredient (a.i.)], bromoxynil octanoate (3,5-dibromo-4-hydroxy benzonitrile octanoate) (227 g/l a.i.) or diclofop methyl plus bromoxynil octanoate using a stainless steel Tee Jet 80015 nozzle (275.8 kPa) mounted on a greenhouse cabinet sprayer. The concentration of diclofop methyl in the spray solutions was equivalent to 0.5 kg/ha a.i. applied in 107 l/ha water, while the bromoxynil octanoate concentration was equivalent to 0.25 kg/ha a.i. applied in the same amount of water.

Unless otherwise noted, all the wild oats were harvested 14 days after spraying. Height and average dry weight were recorded at that time. To evaluate the control of wild oats with the herbicides or herbicide mixture, values determined at the time of treatment were subtracted from final harvest values to yield post-treatment gain in height or dry weight. Resulting figures were expressed as the percentage of an untreated check at each moisture level.

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

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

All experiments were repeated at least two times unless otherwise noted. Data from the experiments were combined for statistical analysis.

Post-spraying stress study. When the desired SMC was attained in all pots, one pot at each SMC was sprayed with a solution of diclofop methyl (0.5 kg/ha a.i.). A second pot at each SMC served as an unsprayed control. Five days after spraying, the 10% SMC treatment was rewatered to 20% SMC. The experimental design was a randomized complete block with four replications of each treatment.

Extended stress study. At 2, 4, 6, 8 or 10 days after spraying of wild oats wih diclofop methyl (0.5 kg/ha a.i.), the 10% SMC treatment was rewatered to 20% SMC. One pot at each SMC and days-of-stress after spraying combination served as an unsprayed check. To allow for more complete recovery of the wild oats maintained at a SMC of 10% for 10 days, the period of time between spraying and final harvest was extended from 14 to 20 days in this study. The experimental design was a randomized complete block with four replications of each treatment.

Pre-spraying stress study. Following spraying with diclofop methyl (0.5 kg/ha a.i.), pots of wild oats at a SMC of 10% were either rewatered immediately to 20% or after a further 5 days of water stress. One pot at each SMC and days-of-stress after spraying combination served as an unsprayed check. The experimental design was a randomized complete block with four replications of each treatment.

Tank-mixture study. Five days after spraying with diclofop methyl (0.5 kg/ha a.i.), bromoxynil octanoate (0.25 kg/ha a.i.), or diclofop methyl

plus bromoxynil octanoate, pots at a SMC of 10% were rewatered to a SMC of 20%. One pot at each SMC and herbicide treatment combination served as an unsprayed check. The experimental design was a randomized complete block with four replications of each treatment.

Retention study. Wild oats at the two- to three-leaf stage were sprayed with a solution of diclofop methyl (0.5 kg/ha a.i.) to which a fluorescent dye[3] (0.3 g/100 ml) was added. Immediately after spraying, plants were cut at soil level and placed in 455 ml preserving jars containing 40 ml of the diclofop methyl solution without dye. The jars were then capped and shaken vigorously for 5 seconds to remove the dye from the wild oats. Plants were then removed from the jars and reserved for dry weight determinations. A fluorometer[4] was used to measure fluorescence of the plant washes. A calibration curve (Appendix Figure 6), relating the amount of dye present in solution to fluorescence, was used to determine the quantity of dye present in the plant washes. The filters used in the fluorometer were a 7-60 primary filter with a cut-off of 365 nm and a secondary 2A-15 filter with a cut-off of 520 nm. Light was supplied by a general purpose #110-850 lamp.

The experimental design was a randomized complete block with eight replications of each treatment.

Penetration study. Soil and plant materials were prepared as described under general procedures except that seedlings of wild oats were thinned to four per pot at emergence. No sample of wild oats was harvested at

[3]Fire Orange Red E.4 E Series Pigment, Swada (London) Limited.

[4]Model III, G.K. Turner Associates, Palo Alto, California.

the time of treatment for leaf area, height, and dry weight measurements.

Diclofop methyl, uniformly ring-labelled with ^{14}C in the dioxyphenoxy ring (sp. ac. 18.2 μCi/mg), was formulated with sufficient solvent blank, unlabelled technical diclofop methyl, and water to make a solution equivalent to 0.5 kg/ha. An aliquot of 10 1 of the radioactive emulsion containing 0.01 μci/μl was applied as a 3 cm long band near the middle of the adaxial surface of the second leaf. The band was contained by 1 mm wide strips of lanolin paste.

One plant from each pot was harvested after 6, 12, 24, or 48 h. The treated zone was cut from the treated leaf and the surface activity removed by washing with 5 ml of 30% ethanol. The leaf washes were collected in plastic mini-vials and evaporated to dryness under an air stream. Five ml of scintillation cocktails[5] was added to each vial and the radioactivity was quantified with a liquid scintillation counter. All samples were corrected for quench by the external standard-channels ratio method and for background. Radioactivity within the plants was recovered by combusting them in a sample oxidizer[6] and capturing the evolved $^{14}CO_2$ in 5 ml of a CO_2 trapping agent (CO_2mMET)[7] plus 13 ml phase combining system (PCS)[8] and xylene (2:1 v/v). The radioactivity was then quantified with a liquid scintillation counter and quench and background corrections were made.

Penetration of the radiolabelled herbicide was expressed as a percentage of the total radioactivity recovered from the leaf washes and

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[5]Aquassure, New England Nuclear, 49 Albany St., Boston, Mass.

[6]Model 306 Packard Tri-Carb Sample Oxidizer.

[7]Amersham Corporation, 505 Iroquois Shore Rd., Oakville, Ont.

[8]Amersham Corporation, 505 Iroquois Shore Rd., Oakville, Ont.

plant samples. The experimental design was a randomized complete block with five replications of each treatment.

Translocation study. Preparation of soil and plant material was carried out as described under general procedures except that seedlings of wild oats were thinned to five per pot at emergence. A sample was not harvested for growth measurements at the time of treatment. A completely randomized design was used in which each of the five plants per pot was considered to be a replicate.

An emulsion of radiolabelled ^{14}C-diclofop methyl was formulated as for the penetration study. A 10µl aliquot of the emulsion containing 0.05 µci was applied as a 3 cm band near the middle of the adaxial surface of the second leaf. The band was contained by 1 mm strips of lanolin paste. All plants were harvested 72 h after treatment and divided into the following sections: treated zone of the treated leaf, leaf blade above the treated zone; leaf blade below the treated zone; sheath of the treated leaf; third leaf plus tillers; and apex plus younger leaves.

Leaf surface activity was removed from the treated zone by washing with 5 ml of 30% ethanol. Leaf washes were collected in plastic mini-vials and evaporated to dryness under an airstream. Radioactivity in the leaf washes was assayed by adding 5 ml of scintillation cocktail to each vial and counting on a liquid scintillation counter. Radioactivity in the various plant parts was determined by combusting the samples in a sample oxidizer, capturing the evolved $^{14}CO_2$, and counting on a liquid scintillation counter as previously described for the penetration study.

Translocation of the radiolabelled herbicide was calculated as a percentage of the total activity recovered from the combined plant sections.

Metabolism study. Methods as described under general procedures were used to prepare soil and plant material except that seedlings of wild oats were thinned to four per pot at emergence.

An emulsion of radiolabelled ^{14}C-diclofop methyl was formulated as for the penetration study. A 10 µl aliquot of the emulsion containing 0.25 µci was applied as a 3 cm band near the middle of the adaxial surface of the second leaf. The band was contained by 1 mm wide strips of lanolin paste.

Following treatment, the treated zone was cut from the treated leaf and the surface activity was removed by washing with 5 ml of 30% ethanol. The plants were then frozen for subsequent extraction. The leaf washes, collected in plastic mini-vials, were evaporated to dryness under an air stream and then resuspended in 0.1 ml 95% ethanol.

Radioactivity in the plants was determined by a method similar to that described by Todd and Stobbe (1980). Individual plants were extracted in 1 ml 80% aqueous acetonitrile using a glass tissue grinder. The extract plus four 1 ml aqueous acetonitrile-rinses of the apparatus were centrifuged at 12000 x g for 10 minutes and the supernatant was decanted. Resuspension of the pellet in 4 ml aqueous acetonitrile followed by centrifugation was repeated a further two times with all of the supernatants being combined in a liquid scintillation vial. The combined supernatants were evaporated to dryness under an airstream and

then resuspended in 0.5 ml aqueous acetonitrile and 95% ethanol (1:1 v/v).

Diclofop methyl and its metabolites in the leaf washes and plant extracts were separated by thin layer chromatography (TLC). Aliquots of 6 l and 12 l of the resuspended leaf washes and plant extracts, respectively, were spotted on plastic backed silica gel TLC plates[9]. The leaf wash sample TLC plates were subsequently developed to a height of 10 cm in benzene, methanol, and acetic acid (85:10:5 v/v/v). Due to difficulties encountered in separating two of the metabolites of diclofop methyl using this solvent system, the plant extract sample TLC plates were developed to a height of 15 cm in chloroform, acetic acid, and hexane (70:20:10 v/v/v).

Sections of the TLC plates corresponding to co-chromatographed reference standards of diclofop methyl and its metabolites as viewed under uv-light were scraped off and placed in plastic mini-vials. Three ml of scintillation cocktail followed by 0.8 ml water were added to each vial to form a gel in which the scrapings were suspended. Sections of the TLC plates not corresponding to reference standards were also removed and similarly suspended. Radioactivity in the samples was determined by liquid scintillation methods.

Radioactivity in the remainder of the leaf wash samples was quantified by liquid scintillation methods following the addition of 3 ml of scintillation cocktail to each vial. The remainder of the plant extract samples were bleached to minimize chlorophyll quenching by the addition

[9]Bakerflex Silica Gel IBF2.

of 0.5 ml 10% benzoyl peroxide in toluene (w/v) according to the method of Walter and Purcell (1966). Radioactivity in the samples was then quantified by liquid scintillation methods following the addition of 10 ml of scintillation cocktail to each vial.

RESULTS AND DISCUSSION

Post-spraying stress study. A period of approximately 7 to 10 days of withholding water was required to reduce the SMC from 20 to 15 or 10%. Plant water deficits which developed during the drying down phase resulted in significant reductions in the growth of wild oats in the 15 and 10% SMC treatments relative to the 20% SMC treatment (Table 11). The growth of wild oats did not differ significantly between the 15 and 10% SMC treatments.

It is not clear why the leaf water potential of wild oats at the 10% SMC was higher than the corresponding soil water potential (-6.5 bars) since plants can only extract water from the soil when their water potential is lower than that of the soil (Begg and Turner, 1976). Preliminary studies showed that uneven drying of the soil occurred when the SMC was lowered from 20 to 10% so that the moisture content near the bottom of the pot was higher than 10% while that near the top was lower than 10%. If the root density was greater near the bottom of the pot where moisture extraction from the soil was presumably easier, then the leaf water potential would not necessarily have to be lower than -6.5 bars for transpiration to continue. On the other hand, the sample size employed in the determination of leaf water potentials was small and may

Table 11. Effect of moisture stress developed during the drying down phase on leaf water potential and growth of wild oats prior to herbicide treatment.

Soil moisture content	Leaf water potential[b]	Growth parameter[a]		
		Height	Leaf area	Dry weight[c]
(%)	(bars)	(cm)	(cm^2)	(g/pot)
20	-3.1 ± 1.7	38.1a	37.2a	0.84a
15	-2.6 ± 1.2	32.5b	24.9b	0.64b
10	-4.5 ± 1.6	32.0b	22.7b	0.63b

[a]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

[b]Mean and standard error.

[c]Six plants per pot.

not have been adequate to give an accurate estimate of the true leaf water potential. Furthermore, evapotranspiration from the pots of wild oats between the daily waterings reduced the SMC below the desired 20, 15, and 10% levels. Preliminary experiments indicated that, at the time of herbicide treatment, the soil water potentials in the 20 and 10% SMC treatments dropped below the desired levels of -0.3 and -6.5 bars to about -0.4 and -13.3 bars, respectively, between each watering. At the end of the experiment, i.e., 14 days after herbicide treatment, when all pots were at a SMC of 20%, the soil water potential was about -0.6 bars at the time of daily watering.

Maintaining the SMC at 10% for a further 5 days after spraying with diclofop methyl resulted in a 38% reduction in the control of wild oats as compared to that at a SMC of 20% (Table 12). The control of wild oats at the 15% SMC was not significantly different from that at the 20% SMC. West et al. (1980) reported a 50% reduction in the control of barnyardgrass with diclofop methyl when the SMC decreased from 20 to 7%. Dortenzio and Norris (1980) also found decreased control of wild oats and three other grasses with diclofop methyl when the plants were grown at a reduced SMC.

Extended stress study. Having established that the activity of diclofop methyl was influenced by the water content of the soil, an experiment was then conducted to determine the period of moisture stress required after spraying to signficiantly reduce the control of wild oats. Water stress which developed when the SMC was reduced from 20 to 10% caused a significant reduction in the leaf area of wild oats but not the height

Table 12. Effect of a five day period of moisture stress after treatment on the control of wild oats with diclofop methyl (0.5 kg/ha a.i.).

Soil moisture content	Control[a,b]	
	Height	Dry Weight
%		
20	94.1a	89.3a
15	89.1a	83.8a
10	58.7b	54.8b

[a]Percent reduction of post- treatment gain in height or dry weight of untreated check at each moisture level.

[b]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

or dry weight (Table 13). Because the length of the drying down phase varied from experiment to experiment, the wild oats varied somewhat in their development (two- to three-leaf stage) and response to the water stress which developed prior to spraying (Table 11 and 13). The leaf water potential of the unsprayed stressed wild oats, while quite variable, did not decrease greatly as the period of water stress after spraying was increased (Table 14).

Maintaining the SMC at 10% for 2 days after spraying before rewatering to 20%, resulted in a small but significant decrease in the control of wild oats on a dry weight basis compared to when the SMC was held constant at 20% (Table 15). Extending the period of water stress to 4, 6, 8, or 10 days after spraying generally resulted in progressively smaller reductions in the post treatment dry weight gain of wild oats. Post treatment increase in the height of wild oats was quite variable in this and other experiments and was not shown to be significantly affected until the period of water stress after spraying was extended to 8 days (Table 15). Dortenzio and Norris (1980) similarly found that control of wild oats with diclofop methyl was decreased if the period of water stress was ended 2 or 4 days after spraying. On the other hand, barnyardgrass control with diclofop methyl was not reduced if the period of water stress was ended within 4 days after spraying. Therefore, species apparently differ in their response to diclofop methyl when subjected to water stress.

Pre-spraying stress study. Since the control of wild oats with diclofop methyl was significantly reduced even when the period of water stress

Table 13. Effect of moisture stress developed during the drying down phase on the growth of wild oats prior to herbicide treatment.

Soil moisture content	Growth parameter[a]		
	Height	Leaf area	Dry weight[b]
(%)	(cm)	(cm^2)	(g/pot)
20	28.6	20.16	0.47
10	28.9 N.S.	16.80*	0.44 N.S.

[a]Means in columns separated by an asterisk are significantly different at the 5% level according to an F test.

[b]Six plants per pot.

Table 14. Water potential of the most recently fully expanded leaf of unsprayed wild oats (10% SMC) at various times after herbicide treatment.

Stress period after spraying	Leaf water potential[a]
(days)	(bars)
0	- 8.4 ± 0.6
2	- 6.7 ± 2.3
4	- 8.4 ± 2.3
6	-12.7 ± 2.9
8	- 9.6 ± 1.6
10	- 8.7 ± 2.8

[a]Mean and standard error.

Table 15. Effect of varying the period of moisture stress after herbicide treatment on the control of wild oats with diclofop methyl (0.5 kg/ha a.i.).

Stress period after spraying	Soil moisture content	Control[a,b]	
		Height	Dry weight
(days)	%		
0	20	82.5a	88.9a
2	10	81.2a	81.0b
4	10	72.2ab	77.1b
6	10	74.3ab	77.2b
8	10	61.0b	68.5c
10	10	65.1b	68.3c

[a]Percent reduction in post-treatment gain in height or dry weight of the untreated control at each stress period after spraying.

[b]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

was ended 2 days after spraying (Table 15), an experiment was necessary to determine if the soil water deficit which developed during the drying down phase was sufficient to alter the response of wild oats to diclofop methyl. As shown in Table 16, seedlings of wild oats were significantly smaller at the time of spraying when the SMC was decreased from 20 to 10% prior to spraying as opposed to being maintained at 20%.

Although the SMC was increased from 10 to 20% at the time of spraying, the control of wild oats with diclofop methyl, as measured by reduction of the post-treatment dry weight gain, was significantly lower than the control attained when the SMC was maintained at 20% before spraying (Table 17). Wild oat control was reduced to a greater extent when the SMC was maintained at 10% for a further 5 days after spraying as opposed to being rewatered to 20% at the time of spraying. While the activity of diclofop methyl on wild oats was obviously quite sensitive to mild water stress, the rapid recovery to near normal activity when the water stress was alleviated at the time of spraying indicated that water stress may have interfered with a sensitive physiological process requisite to the activity of diclofop methyl. These results confirm a previous report that the SMC prior to spraying affected the subsequent control of wild oats with diclofop methyl (Dortenzio and Norris, 1980).

Tank-mixture study. At present, bromoxynil is the only herbicide recommended as a tank-mixture with diclofop methyl for the control of wild oats and broadleaf weeds in barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.), and flax (*Linum usitatissimum* L.) in Manitoba. The herbicidal activity of diclofop methyl is antagonized severely by growth-

Table 16. Effect of moisture stress developed during the drying down phase on leaf water potential and growth of wild oats prior to herbicide treatment.

Soil moisture content	Leaf water potential[b]	Growth parameter[a]		
		Height	Leaf area	Dry weight[c]
(%)	(bars)	(cm)	(cm^2)	(g/pot)
20	-4.2 ± 1.3	23.0	11.1	0.37
10	-8.6 ± 2.3	22.1*	9.2*	0.33*

[a]Means in columns separated by on asterisk are significantly different at the 5% level according to an F test.

[b]Mean and standard error.

[c]Six plants per pot.

Table 17. Effect of relieving, at various times after treatment, moisture stress developed during the drying down phase on the control of wild oats with diclofop methyl (0.5 kg/ha a.i.).

Stress period after spraying	Soil moisture content	Control[a,b]	
		Height	Dry weight
(days)		%	
0	20	86.9a	87.8a
0	10	82.4a	81.9b
5	10	71.6b	67.4c

[a]Percent reduction in post-treatment gain in height or dry weight of untreated check at each moisture level.

[b]Means followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

regulator type herbicides such as 2,4-D[(2,4-dichlorophenoxy)acetic acid)], MCPA{[(4-choro-o-tolyl)oxy]acetic acid}, and dicamba (3,6-dichloro-o-anisic acid)(O'Sullivan et al., 1977; Quershi and Vanden Born, 1979; Todd and Stobbe, 1980). Bromoxynil, a non-hormonal, contact type herbicide did not interact antagonistically with diclofop methyl in a tank-mixture if the rate of bromoxynil did not exceed 0.56 kg/ha (O'Sullivan et al., 1977).

During years when rainfall was low, reports were sometimes received of less than adequate control of wild oats when bromoxynil was used in a tank-mixture with diclofop methyl.[10] Therefore, an experiment was conducted to determine whether bromoxynil interfered with the action of diclofop methyl when the two herbicides were applied as a tank-mixture to wild oats subjected to water stress.

The growth of wild oats was decreased significantly when the SMC was reduced from 20 to 10% prior to spraying as compared to being maintained at 20% (Table 18). Extending the period of reduced SMC for a further 5 days after spraying significantly reduced the control of wild oats with diclofop methyl applied alone or as a tank-mixture with bromoxynil (Table 19). However, there were no significant differences in the control of wild oats achieved with diclofop methyl alone or mixed with bromoxynil within each soil moisture content. A tank-mixture of the two herbicides actually appeared to slightly improve the control of wild oats at both SMC's as compared to the control attained with diclofop methyl alone, although the improvement in control was not significant. Bromo-

[10]Morrison, I. N. 1981. Personal communication.

TABLE 18. Effect of moisture stress developed during the drying down phase on leaf water potential and growth of wild oats prior to herbicide treatment.

Soil moisture content	Leaf water potential[b]	Growth parameter[a]		
		Height	Leaf area	Dry weight[c]
(%)	(bars)	(cm)	(cm^2)	(g/pot)
20	-2.3 ± 1.1	28.8	24.03	0.59
10	-6.2 ± 0.8	26.2*	18.04*	0.49*

[a]Means in columns separated by an asterisk are significantly different at the 5% level according to an F test.

[b]Mean and standard error.

[c]Six plants per pot.

Table 19. Effect of a five day period of moisture stress after treatment on the control of wild oats with diclofop methyl (0.5 kg/ha a.i.) or bromoxynil (0.25 kg/ha a.i.) alone or as a tank-mixture.

Treatment	Soil moisture content	Control[a]	
		Height	Dry weight
		%	
Diclofop methyl	20	88.0a	88.4a
	10	74.6b	76.2b
Diclofop methyl + bromoxynil	20	89.3a	90.9a
	10	81.0ab	80.6b
Bromoxynil	20	10.8c	19.7c
	10	1.5c	10.8d

[a]Percent reduction in post-treatment gain in height or dry weight of untreated control at each moisture level.

xynil applied alone caused reductions of about 20 and 10% in the control of stressed and unstressed wild oats, respectively, on a dry weight basis (Table 19). A similar result is evident in the data of O'Sullivan et al. (1971). Under growth room conditions, then, bromoxynil did not antagonize the herbicidal action of diclofop methyl when wild oats were subjected to mild water stress.

Retention study. The retention of spray solutions by wild oats is partly governed by the amount of leaf area and the way the leaf surface is oriented to the spray droplets (Hibbit, 1969; Sharma et al., 1978). The effect of water stress on leaf area or leaf angle of wild oats has not, to our knowledge, been previously reported.

The leaf area of wild oats was reduced about 22% when the SMC was decreased from 20 to 10% prior to spraying as compared to being held constant at 20% (Table 20). A reduction in the SMC from 20 to 15% prior to spraying did not affect the leaf area of wild oats. The dry weight of wild oats was also not affected by the pre-spraying SMC. While the leaf area was significantly reduced by the water stress prior to spraying, the retention of a diclofop methyl spray solution was not significantly affected (Table 20). While the overall trend was one of increasingly reduced spray retention as the SMC prior to spraying was reduced from 20 down to 10%, differential retention could not account for the observed decreased activity of diclofop methyl on wild oats subjected to water stress.

Penetration study. The influence of water stress on the absorption of foliar-applied herbicides is not clear. Some studies have shown that

Table 20. Effect of moisture stress developed during the drying down phase on the growth of wild oats and retention of diclofop methyl (0.5 kg/ha a.i.).[a]

Soil moisture content	Growth parameter		Spray retention		
	Leaf area	Dry weight[b]			
(%)	(cm^2)	(g/pot)	(µl/plant)	(µl/g)	(µl/cm^2)
20	18.86a	0.41a	1.76a	26.44a	0.10a
15	18.02a	0.39a	1.43a	22.29a	0.08a
10	14.80b	0.38a	1.35a	21.49a	0.09a

[a]Means in columns followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

[b]Six plants per pot.

water stress does not affect the absorption of phenoxy type herbicides such as 2,4-D, 2,4,5-T[(2,4,5-trichlorophenoxy)acetic acid], and picloram (4-amino-3,5,6-trichloropicolinic acid) (Basler et al., 1961; Pallas and Williams, 1962; Merkle and Davis, 1967), while other studies have shown that water stress significantly reduces the absorption of picloram and 2,4-D(Davis et al., 1968; Goodin, 1969). Among the non-phenoxy type herbicides, water stress reduced the absorption of glyphosate [N-(phosphonomethyl)glycine](Ahmadi et al., 1980; McWhorter et al., 1980) but not diclofop methyl (Dortenzio and Norris, 1980).

The time course of penetration of ^{14}C-diclofop methyl into wild oats is presented in Table 21. Uptake was rapid during the first 6 h and then continued at a slower rate for the duration of the study reaching a maximum of 70% of the total recovered dpm, in wild oat preconditioned by growing at a SMC of either 20 or 10%. Penetration was significantly less into wild oats grown at a SMC of 10% as opposed to 20% at 6 h but not at 12, 24, or 48 h following application. However, it is unlikely that the short term slower rate of penetration of ^{14}C-diclofop methyl into the stressed as compared to the unstressed wild oats could entirely account for the observed differences in control between the two treatments.

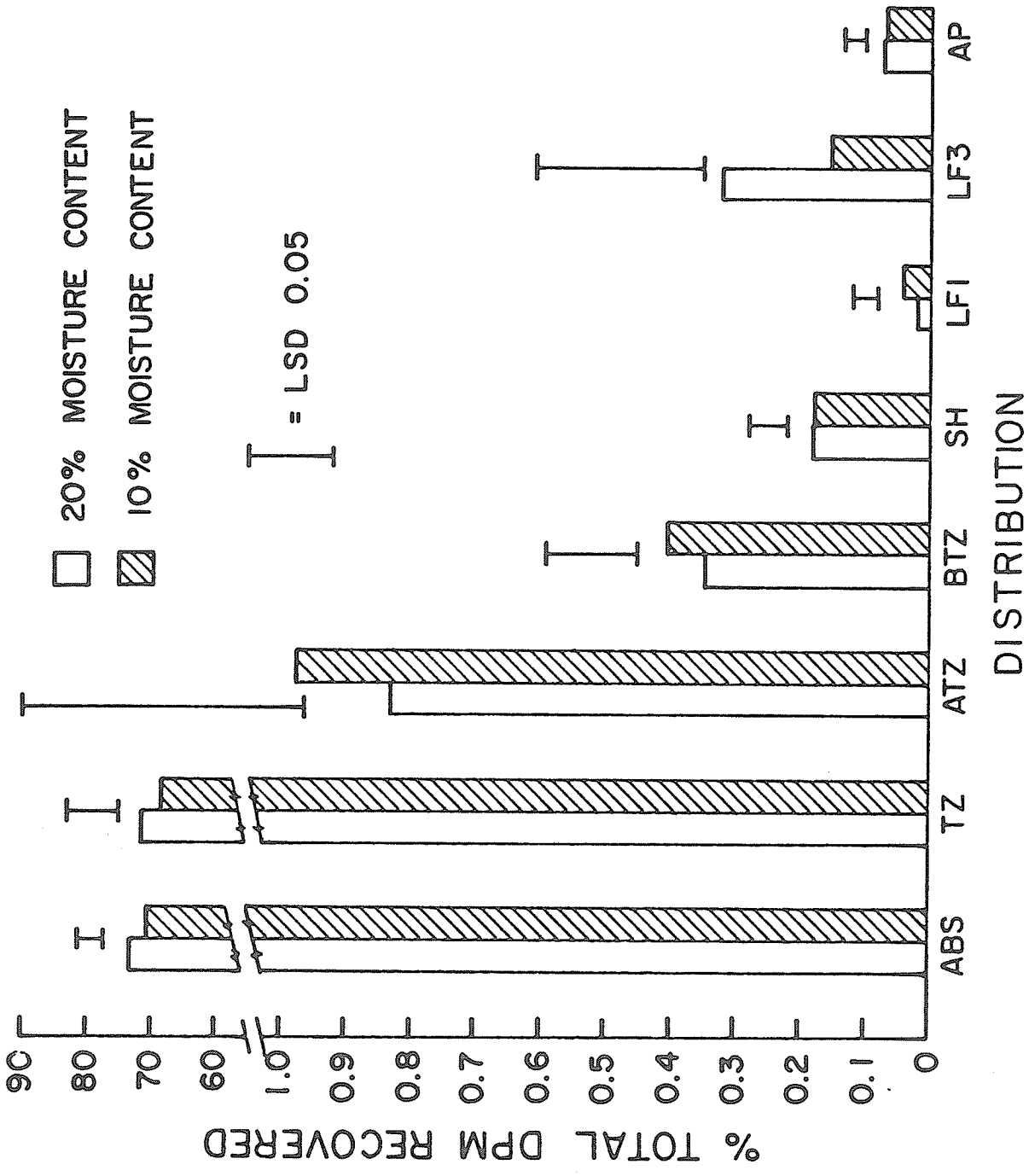
Translocation study. It is generally accepted that the movement of foliar-applied herbicides takes place in the phloem along with photosynthates (Robertson and Kirkwood, 1970), although the actual mechanism of translocation in the phloem has not been fully resolved (Morrison and Cohen, 1980). Since there is ample evidence that the translocation of

Table 21. Effect of moisture stress developed during the drying down phase on the penetration of ^{14}C-diclofop methyl applied to the second leaf of wild oats.

Time	Soil moisture content	Total ^{14}C-activity recovered[a]
(h)	%	
6	20	45.0
	10	38.4*
12	20	52.9
	10	47.5 N.S.
24	20	63.2
	10	58.8 N.S.
48	20	71.2
	10	70.2 N.S.

[a]Expressed as a percentage of the total radioactivity recovered per plant. For each sampling time, means in columns separated by an asterisk are significantly different at the 5% level according to an F-test.

Figure 10. Effect of moisture stress on the distribution of radioactivity in wild oats 72 h after leaf-spot application of ^{14}C-diclofop methyl. ABS = total radioactivity absorbed; TZ = treated zone of the treated leaf; ATZ = leaf blade above the treated zone; BTZ = leaf blade below the treated zone; SH = sheath of the treated leaf; LFI = first leaf; LF3 = third leaf plus tillers; AP = shoot apex and younger leaves.

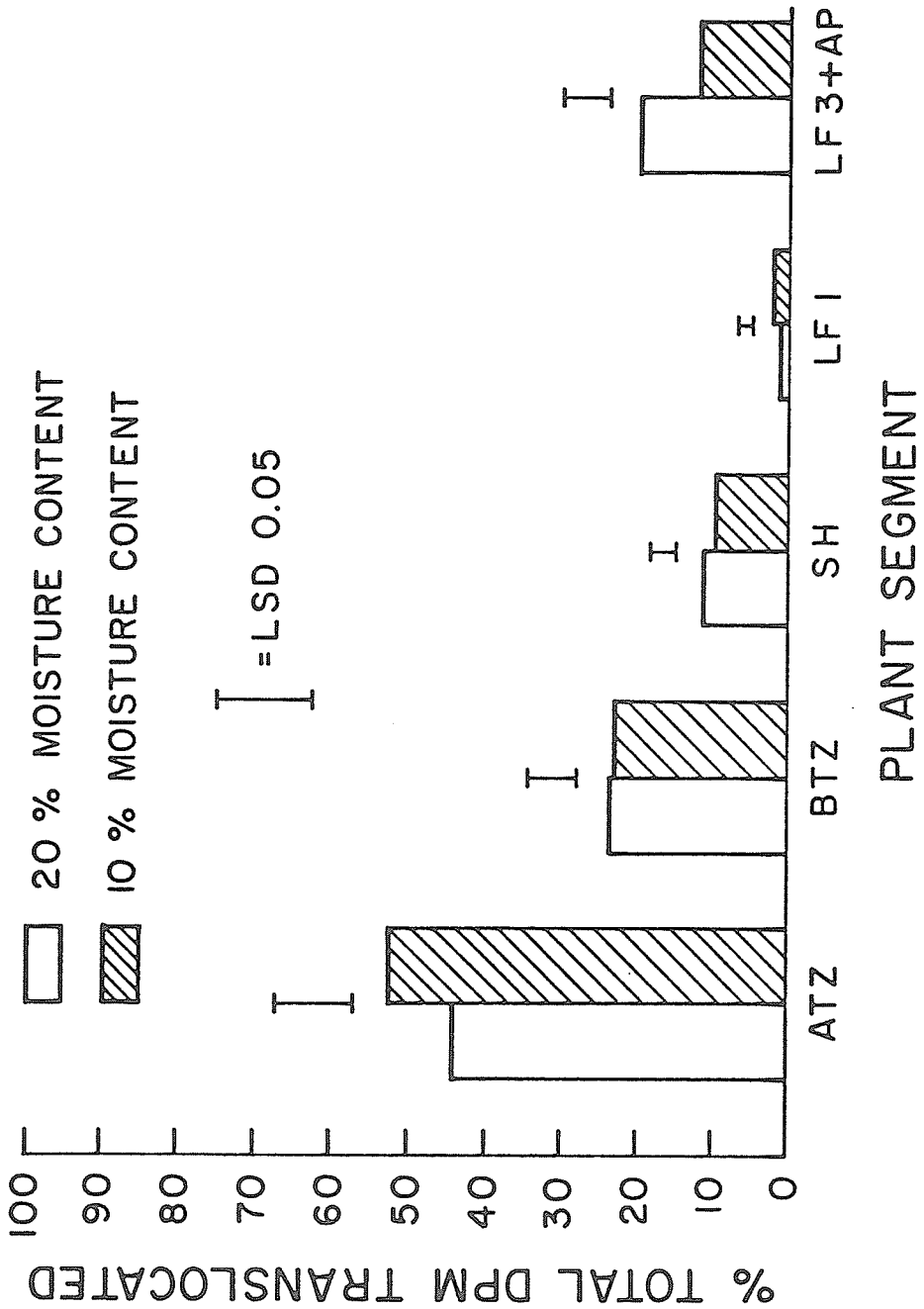

20% MOISTURE CONTENT
10% MOISTURE CONTENT
= LSD 0.05
% TOTAL DPM RECOVERED
90
80
70
60
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
ABS
TZ
ATZ
BTZ
SH
LF1
LF3
AP
DISTRIBUTION

photosynthetic assimilates in plants is reduced under conditions of moderate to severe moisture stress (Crafts and Crisp, 1971), it is likely that herbicide transport would also be reduced by moisture stress. There is now no doubt that this is true and several reports have clearly demonstrated that water stress can inhibit the translocation of both phenoxy and non-phenoxy type herbicides (Merkle and Davis, 1967; Davis et al., 1968; Jeffcoat et al., 1977; Ahmadi et al., 1980).

Both the rate and amount of diclofop methyl translocation following folair application is low (Kocher, 1981). The distribution of radioactivity recovered from the shoots of wild oats 72 h after application of ^{14}C-diclofop methyl is presented in Figure 10. Reducing the SMC from 20 to 10% prior to treatment did not affect the absorption of ^{14}C-diclofop methyl or the distribution of radioactivity within the shoot as compared to when the SMC was held constant at 20%. However, the very limited translocation of the ^{14}C-activity and the highly variable nature of the data may have precluded the demonstration of significant differences between the stressed and unstressed treatments. The total radioactivity translocated out of the treatment zone amounted to only about 1.8% of the total recovered activity in both the stressed and unstressed plants. Todd and Stobbe (1980) similarly reported very limited translocation of ^{14}C-diclofop methyl out of the treatment zone of wild oats after 72 h.

The proportion of ^{14}C-activity in the various plant segments expressed as a percentage of the total activity translocated out of the treatment zone is shown in Figure 11. A significantly greater amount of ^{14}C-activity was present in the combined expanding third leaf, tillers, apex, and younger leaves of the unstressed wild oats than in the stressed

Figure 11. Effect of moisture stress on the distribution of radioactivity translocated out of the treatment zone 72 h after leaf-spot application of ^{14}C-diclofop methyl to wild oats. ATZ = leaf blade above the treated zone; BTZ = leaf blade below the treated zone; TZ = treated zone; SH = sheath of the treated leaf; LFI = first leaf; LF3 + AP = third leaf, tillers, fourth leaf, and shoot apex.


20 % MOISTURE CONTENT
10 % MOISTURE CONTENT
= LSD 0.05
% TOTAL DPM TRANSLOCATED
0
10
20
30
40
50
60
70
80
90
100
ATZ
BTZ
SH
LF 1
LF 3+AP
PLANT SEGMENT

wild oats 72 h after application of ^{14}C-diclofop methyl. Successful control of wild oats with diclofop methyl is dependent on the inhibition of growth of the shoot apex and new leaves (Hoerauf and Shimabukuro, 1979). Therefore, the differences in the distribution of the ^{14}C-activity translocated out of the treatment zone indicated that differential translocation may have contributed to the observed reduction in the control of wild oats grown at a SMC of 10% rather than 20% prior to and after spraying with diclofop methyl.

Metabolism study. Few studies have examined the effects of moisture stress on the metabolism of foliar-applied herbicides. Jeffcoat and Harries (1975) found that metabolism of flamprop-isopropyl [isopropyl-N-benzoyl-N-(3-chloro-4-fluorophenyl)-DL-alanine] in oats (Avena sativa L.) and barley was not affected when the plants were subjected to moisture stress after treatment. A more recent study showed that reduced control of oats subjected to water stress was linked to a reduction in the de-esterification of flamprop methyl [methyl-N-benzoyl-N-(3-chloro-4-fluro-phenyl)-DL-alanine] to form the active acid, flamprop (Jeffcoat et al., 1977). The fact that de-esterification to form the phytotoxic free acid diclofop is the first step in the metabolism of diclofop methyl in wild oat (Kocher, 1981), coupled with the fact that diclofop applied alone can inhibit meristematic activity in wild oats (Hoerauf and Shimabukuro, 1979), indicates that interference with de-esterification in wild oats grown at reduced soil moisture levels might likewise result in a reduced level of control.

The time course of the metabolism of ^{14}C-diclofop methyl in wild

oats is presented in Table 22. Due to problems encountered in the separation of the metabolites in the leaf washes, the analysis of the metabolites in the plant extracts only is presented here. The results are expressed as percentages of the total ^{14}C recovered from the TLC plates at each sampling time and within each SMC treatment and do not include radioactivity from leaf washes. The two compounds, hydroxy diclofop {2-[4-(2,4-dichloro-3,5,7-hydroxy)phenoxy] proprionic acid} and phenoxy phenol [4-(2,4-dichlorophenoxy)phenol] are not considered to be important components in the metabolism of diclofop methyl by wild oats.[11] The percentage radioactivity as diclofop methyl decreased while the percentage as diclofop increased over the course of the experiment so that after 2 days diclofop methyl accounted for about 70% and diclofop for about 12% of the ^{14}C-activity in both the stressed and unstressed wild oats. The major portion of the remaining activity consisted of non-mobile polar compounds which, while not identified positively, were believed to be ester-conjugates of diclofop (Shimabukuro et al., 1979). Conjugate production appeared to increase substantially over the course of the experiment (Table 22).

With the exception of diclofop methyl at 24 h after treatment, moisture stress did not significantly affect the proportion of metabolites formed in wild oats. There is no explanation at present for the sudden significant decrease in the percentage of diclofop methyl in the wild oats grown at a SMC of 10% at 24 h after treatment and at no other

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[11] Todd, B.G. 1979. Metabolism and selectivity of diclofop-methyl in wheat, barley, wild oat and green foxtail. PhD. Thesis, University of Manitoba, 187 pp.

Table 22. Effect of moisture stress on the metabolite composition of extracts of shoots of wild oats at various times after treatment with ^{14}C-diclofop methyl.

Time	Soil moisture content	Distribution of ^{14}C on thin layer chromatogram				
		Diclofop methyl	Hydroxy diclofop[c]	Diclofop	Phenoxy phenol[d]	Other[e]
(h)		%				
6	20	90.1	0.2	7.0	1.1	1.6
	10	83.7 N.S.	0.5 N.S.	11.7 N.S.	1.6 N.S.	2.6 N.S.
12	20	84.9	0.3	11.9	0.8	2.2
	10	78.1 N.S.	0.5 N.S.	15.0 N.S.	2.2 N.S.	4.2 N.S.
24	20	74.9	0.4	13.9	1.4	9.5
	10	60.1*	0.5 N.S.	20.5 N.S.	1.1 N.S.	12.1 N.S.
48	20	69.2	0.6	12.9	2.3	15.2
	10	69.5 N.S.	0.4 N.S.	11.1 N.S.	0.5 N.S.	18.4 N.S.

[a]Percent of total ^{14}C on chromatogram at each sampling time and within each SMC.

[b]For each sampling time, means for individual metabolites separated by an asterisk are significantly different at the 5% level according to an F-test.

[c]2-[2,4-dichloro-3,5,6-hydroxy)phenoxy] propionic acid.

[d]4-(2,4-dichlorophenoxy)phenol.

[e]Remaining activity on chromatogram.

time. While the difference in metabolism of diclofop methyl in the stressed and unstressed wild oats were not significant, a more or less consistent trend of more rapid de-esterification of diclofop methyl to diclofop and more rapid conversion of the diclofop to non-phytotoxic ester conjugates appeared to take place in the wild oats grown at a SMC of 10% as compared to 20%. Coupled with the small and non-significant differences in spray retention (Table 20), penetration (Table 21) and translocation (Figure 10 and 11), the small differences in metabolism (Table 22) may have been sufficient to result in the reduced control of wild oats with diclofop methyl when the plants were subjected to water stress.

CHAPTER VI

GENERAL DISCUSSION

In view of the fact that soil moisture is often a limiting factor to plant growth in the prairie provinces of Canada and recognizing the severe detrimental effect of wild oats on the production of cereal and oilseed crops, the studies reported in this thesis should be of benefit to farmers as well as weed biologists.

For the most part, the specially constructed wooden enclosures proved to be very useful in the investigation of the effects of moisture stress on the growth and development of wild oats outdoors. While they represented a reasonably close approximation of field conditions, they allowed for better control of soil moisture levels. In general, wild oats grown outdoors in the wooden enclosures or in plastic containers in the growth room responded similarly to reduced soil moisture levels. However, the small differences in stomatal diffusion resistances and transpiration rates that occurred between the stressed and unstressed plants outdoors and the fairly steady decline in the water potential of the top 20 cm of soil in both treatments indicated that the wild oats in the unstressed treatment may not have received sufficient water to maintain a well-watered condition. As well, because of the relatively slow development of a water deficit in the stressed treatment and large volume of soil, wild oats in the stressed treatment may have undergone some form of

adaptation to the stress such as osmotic adjustment or the development of more extensive root systems to take advantage of water deeper in the soil profile.

While the height, leaf area, dry weight and number of viable tillers were significantly reduced in the stressed as compared to unstressed wild oats in both environments, greater reductions were recorded in the growth room. Furthermore, the lower transpiration rates and higher stomatal diffusion resistances in the stressed wild oats in the growth room as compared to outdoors indicated that wild oats in the growth room were more strongly stressed. The small soil mass in the plastic containers used in the growth room would likely have dried almost evenly throughout and at a more rapid rate between waterings. Moreover, an examination of the moisture release curves of the different soil types used outdoors and in the growth room indicated that the Almasippi very fine sandy loam requires only a small change in water content below 10% to result in large decreases in the soil water potential and hence water availability. Near the end of the experiment in the growth room, between the daily waterings wild oats undoubtedly reduced the soil moisture content below 10% in the low soil moisture treatment. The slower drying Altona clay loam soil used in the outdoor study might have been more suitable for the growth room studies.

Since the response of wild oats to moderate moisture stress was both rapid and pronounced, further studies to examine the significance of the observed reductions in growth on the competitive ability of wild oats intermixed with a crop under arid or semi-arid

conditions would be of considerable interest and value. Such studies might entail a determination of the ability of wild oats to adapt to water deficits through an examination of the root system, the water use efficiency, and the component potentials which comprise the total water potential. The effect of the observed marked decrease in the number of viable tillers in wild oats subjected to moisture stress on the survival and distribution of the species might also be examined.

Changes which occurred in the growth and development of wild oats under low soil moisture conditions may be important in the control of wild oats with foliar-applied herbicides including diclofop methyl. Rewatering of previously stressed wild oats at the four-leaf stage resulted in a rapid increase in the number of viable tillers produced. Such an increase occurring after spraying with diclofop methyl or other herbicides might mean an increase in the number of seed-bearing culms escaping control and continued competition of the treated wild oats with the crop.

Aside from the effects that decreased leaf area have on photosynthesis and dry matter production, changes in the amount of leaf area exposed to vertically descending spray solutions (projected leaf area) are known to affect the retention of herbicides by wild oats (Davies et al., 1967; Hibbit, 1969; Sharma et al., 1978). However, while the total leaf area of wild oats was significantly reduced by water stress prior to spraying, the retention of a diclofop methyl solution was not significantly affected. The quantity of spray solution retained by a weed species following

foliar application will also be affected by the wettability of the leaves. Riepma (1960) demonstrated that the quantity of epicuticular wax on a leaf surface affected its wettability and spray retention. The leaves of wild oats subjected to moisture stress from emergence to maturity outdoors produced significantly more surface wax than those of unstressed plants, but not until heading. However, Weete et al. (1978) reported a 30% increase in surface wax synthesis in cotton following rewatering of plants previously subjected to water stress. A similar increase in wax production might occur in stressed wild oats after alleviation of the stress and might significantly alter the retention of diclofop methyl or other herbicides in the field. Verification of this hypothesis awaits further experimentation.

In general, the activity of diclofop methyl on wild oats appeared to be quite sensitive to moisture stress. Even the short period of reduced soil moisture levels which occurred during the soil drying phase prior to spraying was sufficient to cause a significant reduction in the control of wild oats. Extending the stress period after spraying resulted in further decreased in control. While the small differences that occurred in diclofop methyl retention, penetration, translocation, and metabolism of diclofop methyl in stressed compared to unstressed wild oats may not individually account for the observed reductions in control, in the field these events would be occurring consecutively and/or simultaneously and may together be sufficient to result in reduced wild oat control. Moreover, a longer period of moisture stress or

an equivalent period of more severe stress before or after spraying than the moderate stress used in these studies, might significantly alter the previously mentioned parameters.

The mode of action of diclofop methyl has not yet been determined. Morrison et al. (1981) suggested that diclofop methyl may interfere with the normal progression of the cell cycle and thereby arrest cell division. Shimabakuro et al. (1979) suggested that diclofop methyl functions as a strong auxin antagonist thus interfering with cell elongation and presumably cell division since auxin is involved in both processes. In a study on the growth of wild oats, Sharma et al. (1977) concluded from height and leaf number measurements that a period of rapid cell division and elongation occurs early in the growth of wild oats. Both cell elongation and cell division have been shown to be very sensitive to water stress (Acevedo et al., 1971; McCree and Davis, 1974; Terry et al., 1971). The early inhibition of leaf area, tiller number, and height of wild oats subjected to water stress would also have been due to inhibition of both cell division and cell elongation. If the activity of diclofop methyl depends on interference with cell division or cell elongation, this may explain the reduced activity of the herbicide on stressed wild oats in which cell division and elongation were already inhibited.

An alternative mechanism to account for the phytoxic action of diclofop methyl was suggested by Hoppe (1981). Hoppe found decreased incorporation of ^{14}C-acetate into the lipids of corn root tips

treated with diclofop methyl and postulated that the herbicide may have interfered with fatty acid synthesis. In cotton plants subjected to water stress, the incorporation of ^{14}C-acetate and ^{14}C-malonate into internal leaf lipids was increased by about 57% (Weete et al., 1978). A similar stimulation of fatty acid synthesis occuring in water-stressed wild oats might overcome the inhibitory effect of diclofop methyl on fatty acid synthesis and thereby reduce the control achieved.

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APPENDIX

Appendix Table 1. Effect of various SMC regimes on the water potential of the most recently fully expanded leaf of wild oats.[a]

Week	Treatment:	Leaf water potential[b]			
		High	High-low	Low	Low-high
		bars			
1		- 2.9	- 7.5	>- 1.0	- 9.4
2[c]		- 2.4	>- 1.0	-17.5	-14.4
3		- 2.5	- 0.6	>- 1.0	- 1.6
4		- 4.0	-12.7	- 2.6	- 5.3
5[d]		---	---	---	---
6		-15.7	-15.6	- 6.9	- 5.3
7		-25.1	-10.2	-14.8	- 2.8
8		-23.0	-21.5	-10.4	- 5.8

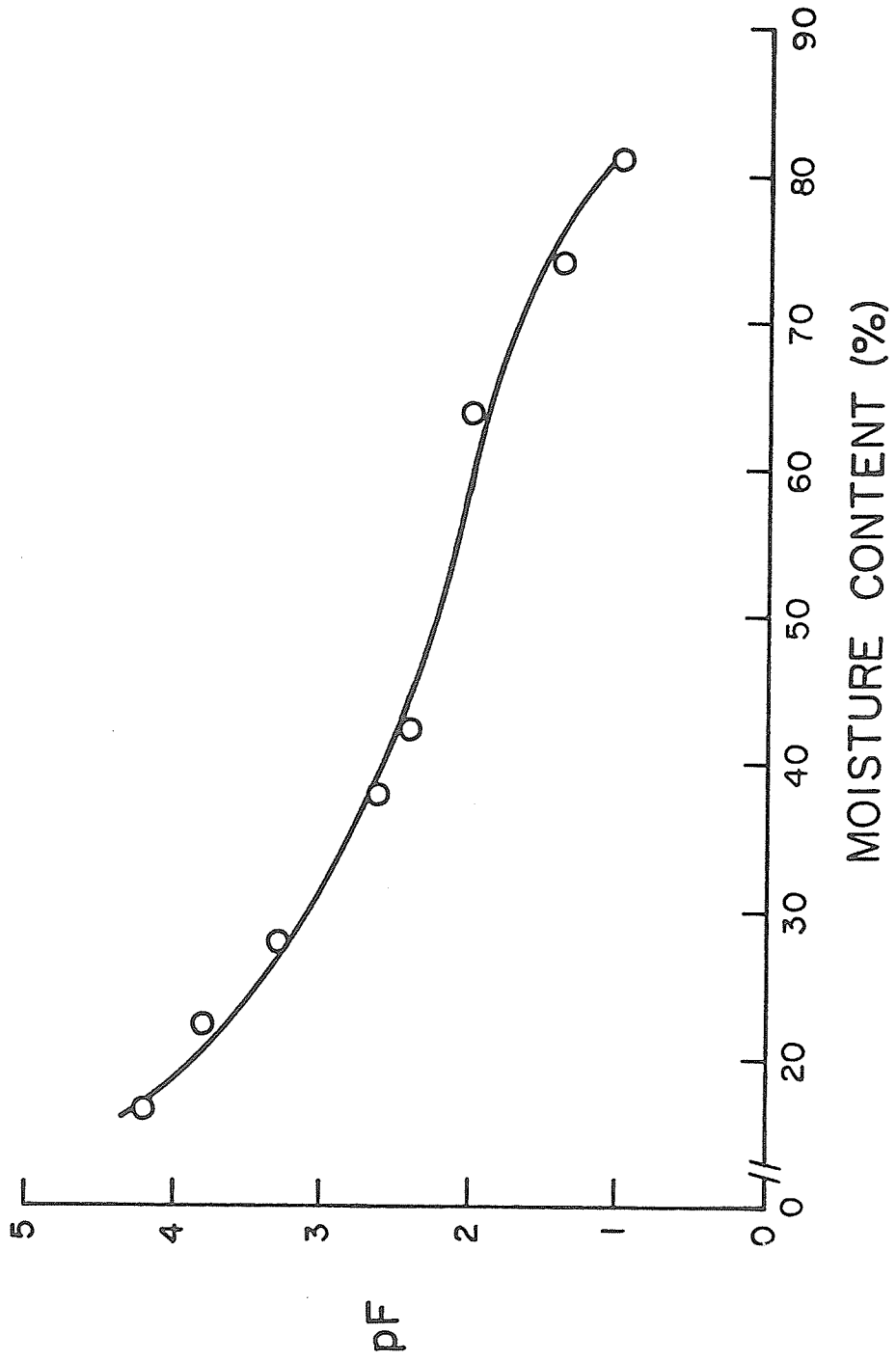
[a]Sampling started at the two-leaf stage.

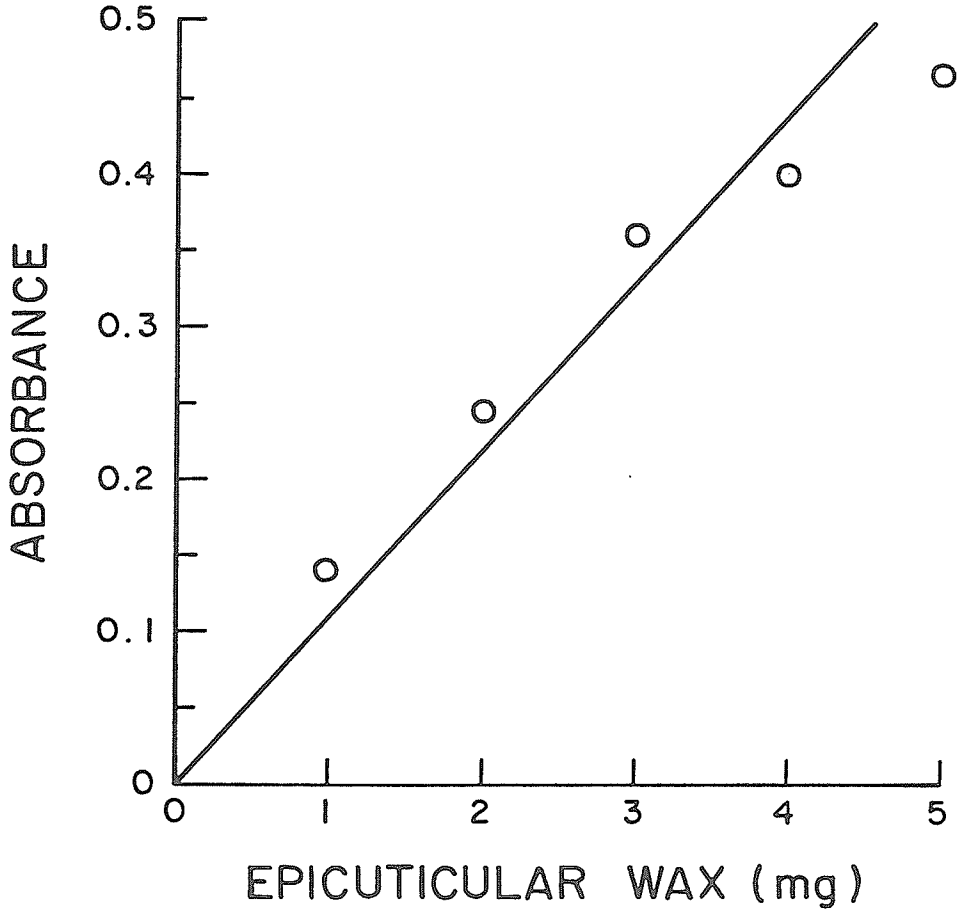
[b]Non-replicated samples.

[c]Low-high treatment rewatered to 20% SMC; water withheld from the high-low treatment until the SMC declined to 10%.

[d]Problems with instrumentation prevented sampling.

Appendix Figure 1. Moisture release curve for Altona clay loam soil constructed from pressure plate apparatus data and gravimetric soil water content. The equation of the line ($r = 0.99$) was determined by polynomial regression to be:
$Y = 7.0583-(0.2197)x + (0.0036)x^2-(2.2335 \times 10^{-5})x^3$.

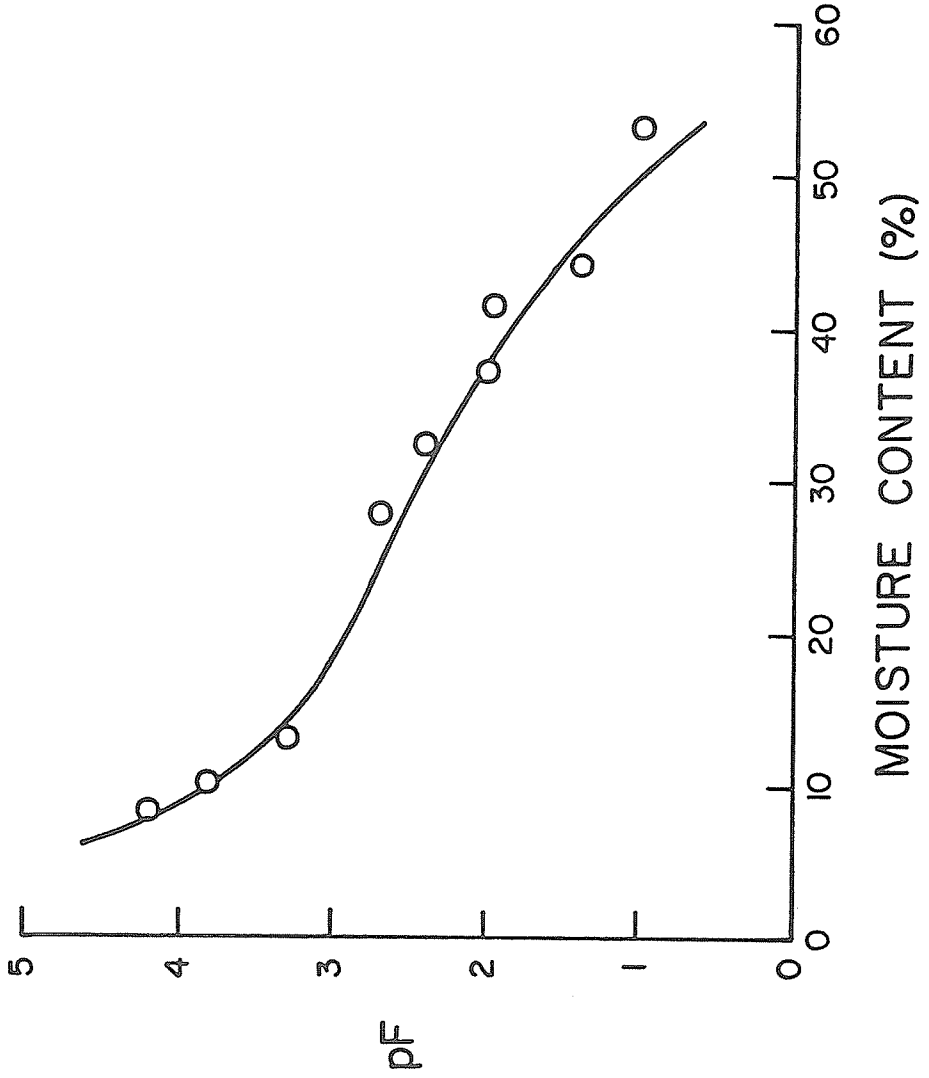

pF
5
4
3
2
1
0
0
20
30
40
50
60
70
80
90
MOISTURE CONTENT (%)

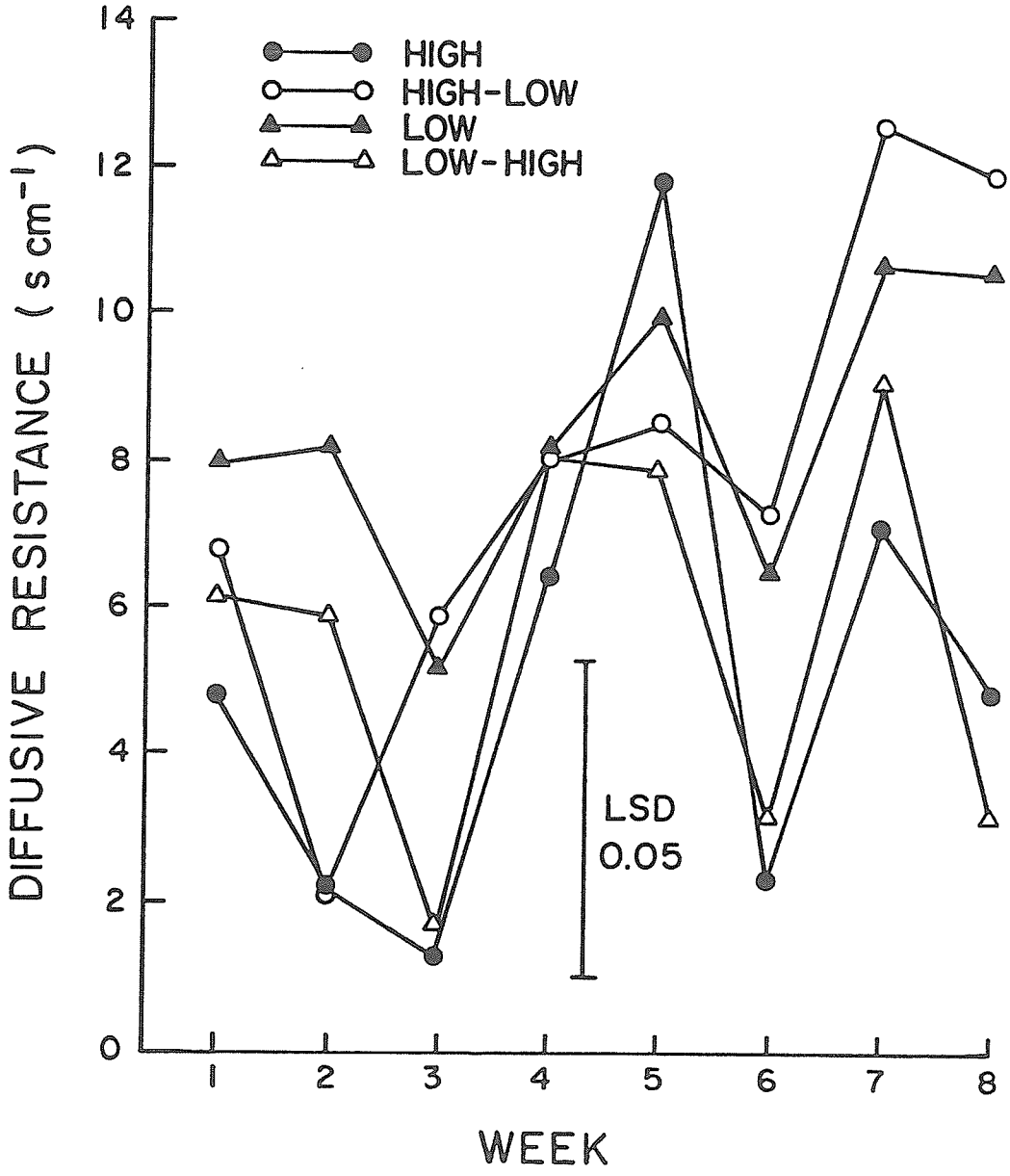


Appendix Figure 2. Calibration curve relating the quantity of epicuticular wax present to absorbance at 590 mm. Wax used in the preparation of the curve was collected from leaves of wild oats.

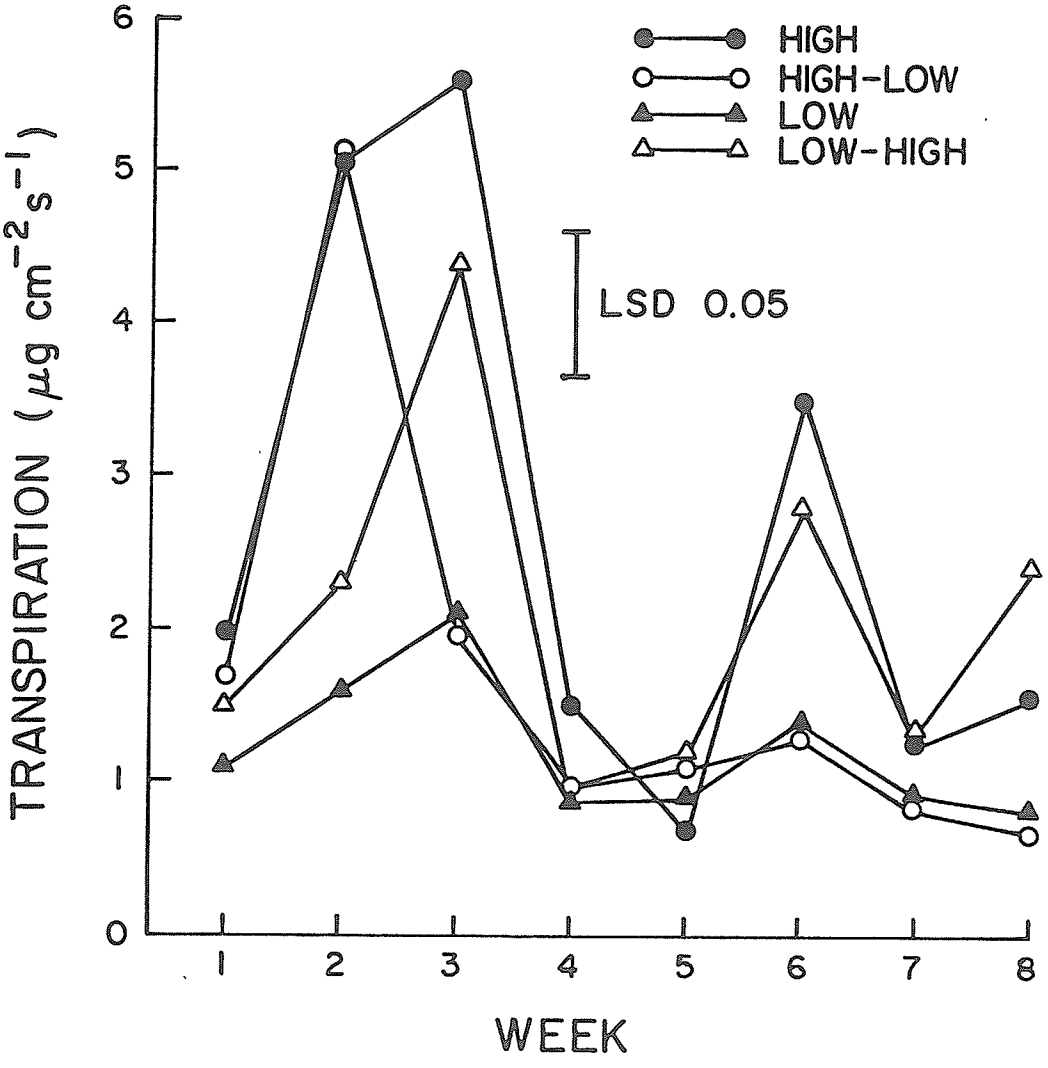
Appendix Figure 3. Moisture release curve for Almasippi very fine sandy loam constructed from the average of 3 years of pressure plate apparatus data and gravimetric soil water contents. The equation of the line ($r = 0.98$) was determined by polynomial regression to be:

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


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

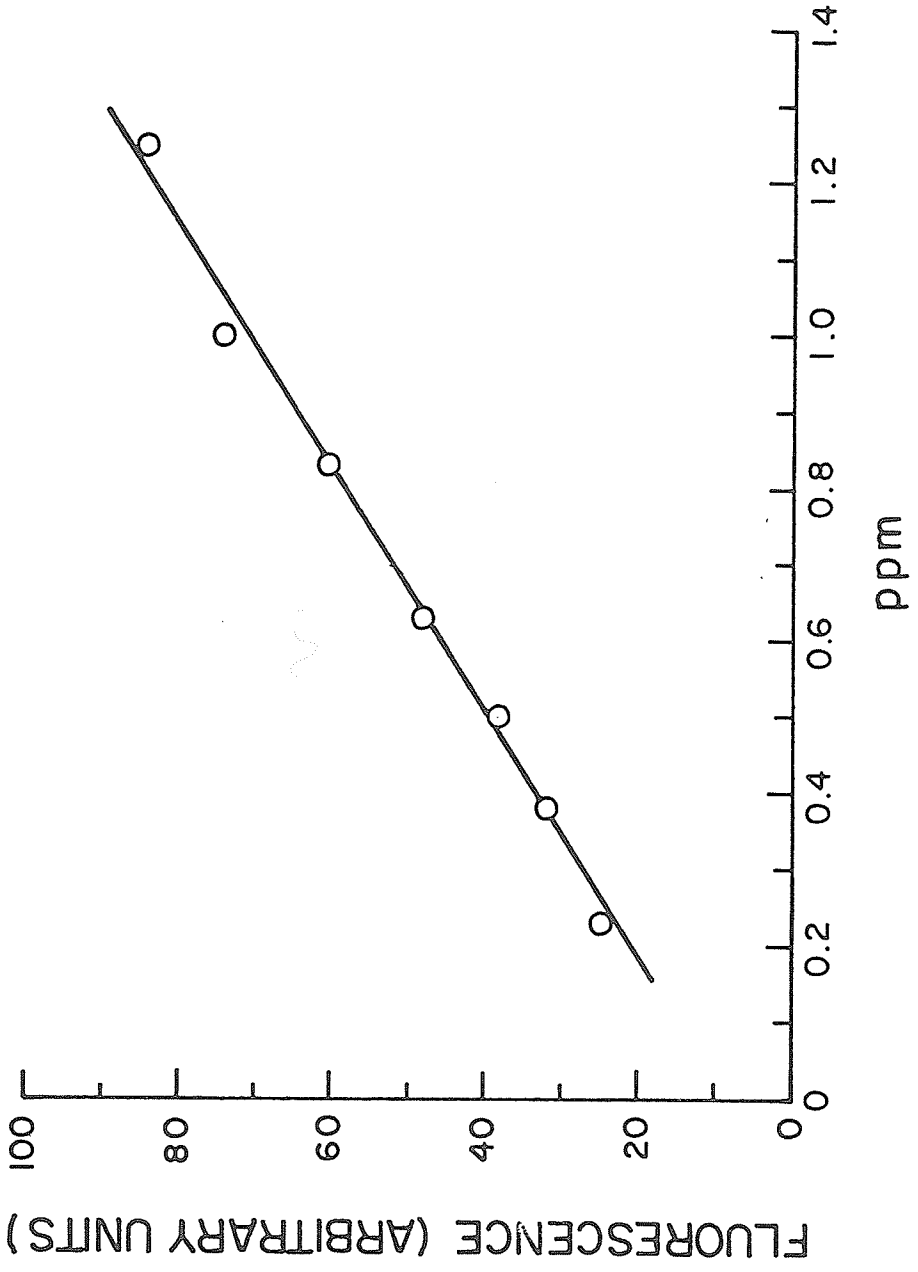


Appendix Figure 4. Effect of various SMC regimes on the stomatal diffusion resistance of wild oats from the two-leaf stage to maturity. At the four-leaf stage (week 2), the SMC in the low-high treatment was increased from 10 to 20% for the duration of the experiment and water was withheld from the high-low treatment until the SMC decreased to 10%.



Appendix Figure 5. Effect of various SMC regimes on the transpiration rate of wild oats from the two-leaf stage to maturity. At the four-leaf stage (week 2), the SMC in the low-high treatment was increased from 10 to 20% for the duration of the experiment and water was withheld from the high-low treatment until the SMC decreased to 10%.

Appendix Figure 6. Calibration curve relating the amount of dye present in a solution of diclofop methyl (0.5 kg/ha a.i.) to fluorescence.


FLUORESCENCE (ARBITRARY UNITS)
0
20
40
60
80
100
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
ppm