AN ABSTRACT OF THE THESIS OF

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Title: EFFECT OF MOISTURE STRESS ON YIELD AND QUALITY OF WINTER WHEAT SEED

Abstract approved: [signature]

Don F. Grabe

Two experiments were conducted to determine the effects of moisture stress on physiological changes that occur during the vegetative and reproductive stages of the wheat (Triticum aestivum L.) plant, and to relate these effects to seed yield, quality and performance.

In a field experiment, different levels of moisture stress were obtained by establishing plots in two rainfall areas, and by planting on three different dates in the dryland area. Seed development and maturation occurred under extreme moisture stress in Moro (254 mm annual rainfall), while stress at Corvallis (1020 mm annual rainfall) was low. Plants from the early fall planting were subjected to the most stress because of the greater fall growth which removed much of the soil moisture.

Lowest seed yields occurred under the greatest moisture stress conditions, primarily because of a reduced number of seeds per spike.

Seed size was the quality component most affected by moisture stress. Smaller seed size was associated with lower soil water potential, higher leaf area index during vegetative growth, and higher specific leaf weight and water soluble carbohydrate content of the plants after anthesis. Water soluble carbohydrate content was particularly high in the rachises of the most severely stressed plants, indicating a reduced rate of translocation to the developing seeds. Embryo weight was also reduced in the more stressed plants in proportion to the reduction in seed weight.

The protein contents of seeds from all three moisture stress levels at Moro were similar. Seeds developed under the most severe water stress had the highest respiratory quotient and lowest glutamic acid decarboxylase activity. The growth rate of seedlings produced by these seeds was 29% lower than that from seeds from the less stressed plots.

A greenhouse experiment was conducted to study the effects of water stress under controlled conditions. Plants were grown under three moisture regimes (600, 300 and 150 ml water/pot/day) from the time awns were first visible on the main stem until maturity. Water-stressed plants had smaller leaf area and leaf dry weight, higher specific leaf weight, earlier leaf senescence, lower dry weight, and lower seed yield. On the other hand, water-stressed plants produced larger seeds, with heavier embryos, higher protein content, lower CO_2 evolution and lower respiratory quotient. These seeds in turn produced seedlings with greater vigor in terms of seedling growth rate.

Because of the compensation ability of the wheat plant, development of management practices to decrease certain yield components in favor of enhanced seed quality is worthy of further study.

Effect of Moisture Stress on Yield and Quality of Winter Wheat Seed

by

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Typed by Opal Grossnicklaus for Marcos Vinicius Assuncao

Dedicated

to my wife and my children

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

EFFECT OF MOISTURE STRESS ON YIELD AND QUALITY OF WINTER WHEAT SEED

INTRODUCTION

The Pacific Northwest is one of the important wheat production areas in the United States. Seasonal precipitation is highly variable between production areas and yield reductions due to the effects of drought are very common. The emphasis in wheat production research has been primarily on grain yield with few studies directed specifically toward seed production practices. Some information regarding the effects of planting date, stand establishment, plant population and fertilizer practices on seed yield and quality is available, but few facts are available regarding the effects of water stress on seed quality.

If maximum performance is to be expected from wheat seed, the effects of moisture stress and other detrimental environmental factors need to be identified and seed production practices geared toward minimizing their effects. It is clear that additional information is needed concerning the effects of water stress on plant growth and how these factors relate to seed yield, quality and performance.

The main purpose of the studies here reported was to determine the effects of water stress on yield and quality of winter wheat seed.

This thesis is divided into four sections: a literature review concerning general aspects of water stress on plant growth and yield; a manuscript involving the effects of moisture stress on plant growth and seed yield and quality under field conditions; a manuscript involving the effects of different water regimes on seed yield and quality in greenhouse studies; and an appendix of meteorological data, statistical analyses, and other information not reported in the two manuscripts.

LITERATURE REVIEW

Thorough reviews of plant responses to water deficiency have been reported by several investigators (38, 45, 73). More studies have been reported on the effects of water stress on wheat plants than for any other crop. This review is limited to those aspects of water stress that are related to the objectives of this study.

Effect of Water Stress on Yield

In a physiological study of wheat yield in India Asana *et al.* (8) observed that when stress occurred during the 4 weeks after spike emergence, yellowing of the stem and leaves was hastened, grain number was reduced, and the 1000-grain weight was increased. After the leaves and stem had yellowed, the rate of increase in grain weight was higher with a normal water supply. Later Asana and Saini (7) observed that intermittent drought after spike emergence affected yield by reducing the number and size of the grains. As a result of these studies Asana (2, 3) concluded that under conditions of adequate soil moisture spike number had the most effect on yield, whereas under conditions of stress, especially during the grain swelling period, grain number per spike, and sometimes the 1000-grain weight, had as much effect as spike number.

Robins and Domingo (70) studied the effects of moisture stress on yield and components of yield of spring wheat in the state of Washington. They reported that moisture stress before heading caused a marked secondary growth which increased the number of spikes but delayed the date of maturity. They observed the greatest reductions in yield when moisture stress was imposed during and following heading or during the maturation of the grain. Moisture stress during and following spike emergence generally resulted in fewer spikes, fewer spikelets per spike and fewer grains per spike.

Day and Intalap (26) conducted experiments at Tucson, Arizona, to study the effects of soil moisture stress at different stages of development (jointing, flowering, and dough) on the growth and yield of spring wheat. They said that stress at any stage of growth decreased grain yield. When wheat was stressed at jointing, reduced grain yield resulted from fewer spikes per unit area and fewer seeds per spike. However, they observed that when stress occurred at the flowering and dough stages, lower yields were caused by lighter seed weight.

Campbell (17), working with potted Chinook wheat in the greenhouse, observed that the highest yields were obtained when plants were grown under dry conditions until the booting stage and under wet conditions thereafter. Conversely, minimum grain yields were obtained when plants were grown under wet conditions until the booting stage and under dry conditions thereafter.

Brengle (16) reported that the most critical period for moisture in winter wheat in eastern Colorado was during tillering and early spring growth, because it was at those times that yield potential was formulated. Higher yields were dependent on adequate moisture during jointing and heading stages, but a favorable amount of water during this period did not overcome the detrimental effect of inadequate moisture during the preceding period. He concluded that it was impossible to predict yield of winter wheat on the basis of soil moisture at planting time because moisture during that period was not sufficient to carry the crop through maturity without additional water in the spring.

Effect of Water Stress on Nitrogen and Protein Content

The increase in nitrogen content of developing cereal inflorescences and grains is due to the movement of nitrogen-containing compounds into the spike (59). In wheat grain the percentage of protein increases during water stress, although total yield decreases; evidently, the total protein is inhibited but total carbohydrate production is inhibited even more (13).

Neales *et al*. (59) worked with potted wheat plants and observed that leaf removal at anthesis caused a significant reduction of nitrogen uptake by the culm and grain at maturity.

Ramon and Laird (67) working in "La Cal Grand," Central

Mexico, observed that the percentage of protein in wheat grain decreased as the available soil moisture was increased by irrigation. They said that this decrease of protein in wetter soils was due to a larger percentage of the nitrogen in the production of straw.

Terman *et al*. (81) observed an increased yield-protein relationship in wheat grain at each level of applied nitrogen in an irrigation-N rate experiment with hard red winter wheat at North Platte, Nebraska. They said that the main effect of applied N with adequate water was to increase yields, while the chief or entire effect with severe water stress was to increase protein content. However, they obtained an increase in both protein and yield in an intermediate stress situation. They concluded that the effect of N on yield and protein content depended greatly on water available for growth.

Effect of Leaf Area on Yield

Studies at Rothamsted, England, have shown the heavy dependence of grain production in cereals on the area and duration of the photosynthetic surfaces of the spikes, the flag leaf, and the uppermost node of the stem (82, 87, 88).

While working with semi-dwarf spring wheat genotypes at St. Paul, Minnesota, Johnson and Moss (41) observed an increase in the contribution of spikes, upper sheaths, and stem to total photosynthesis as the lower leaves became senescent. They said that in water stressed plants the site of photosynthesis was shifted away from the leaf lamina to the upper leaf sheaths, upper portions of the stem and the spike.

Berdahl et al. (10), also at St. Paul, Minnesota, observed that large-leaf lines of barley exceeded small-leaf lines in flag leaf area by 70% and in leaf area index by 25%. They observed that lines with small leaves produced more heads and higher grain yield than lines with large leaves when plants did not lodge; when lodging occurred, however, large-leaf lines had higher kernel weights and higher yield.

Puckridge (65), in Australia, reported that leaf area index reached a peak before anthesis and decreased progressively as water stress increased. He noted that shortening of the post-anthesis period and lower leaf area index at anthesis resulted in reduced post-anthesis photosynthesis and reduced grain yield. He emphasized the necessity of ensuring that anthesis occurs sufficiently early under Australian conditions to permit completion of grain filling before the onset of hot dry weather.

Wardlaw (84), another Australian scientist, worked with potted wheat plants and observed a progressive reduction in the rate of photosynthesis of wilting leaves, and even when light was limiting, the rate of photosynthesis of wilted leaves was lower than that of turgid leaves. However, Asana (3), also working with potted plants, reported greater yields in wheat varieties with rapid leaf senescence.

Spiertz *et al.* (79), working with spring wheat at Wageningen, The Netherlands, stated that the greater part of the assimilate available for grain filling was dependent on the size and duration of green organs in the period after flowering. They observed that green area duration from heading to ripening was more closely correlated with grain yield than was the green area duration in the period from flowering to ripening. On the other hand, Welbank *et al.* (89), in Australia, found that green area duration from flowering to ripening was more closely correlated with grain yield.

Fischer and Kohn (34, 35, 36), in New South Wales, Australia, observed that grain yield was closely correlated with leaf area duration after flowering, which in turn was related to leaf area index at flowering and to the rate of senescence of photosynthetic tissues. They said that the increase of senescence was associated with reduced post-flowering plant water stress, as indicated by the relative turgidity of the leaves.

According to the findings of the authors cited above and the observations of Luebs and Laag (52), the period in which cereal crops reach the largest leaf area seems to be of fundamental importance in the determination of yield. Luebs and Laag reported that barley plants with a large leaf area before stem elongation, as a result of an increase in the rate of nitrogen fertilizer, had a decrease in yield due to a severe water stress after heading. They worked at Moreno, California, and observed that leaf relative turgidity was 84, 65, and 52% two weeks before heading, when 0, 45, and 90 kg N/ha, respectively, were applied at emergence. Furthermore, they noted that the most stressed plants had the lowest leaf area index after heading due to a severe wilt and necrosis of leaf tissue. They concluded that any cultural practice that increases leaf area in regions of low rainfall is likely to increase evapotranspiration and consequently decrease water availability.

A measure of the unit dry weight per unit of leaf area, called specific leaf weight (SLW), has been used by many investigators to select plants for photosynthetic efficiency (9, 20, 21, 63). However, no reports were found in the literature referring to the application of this characteristic to studies of water stress in wheat.

Barnes et al. (9) enhanced the potential importance of SLW measurements in alfalfa when they found that increased SLW was associated with increased photosynthetic efficiency. Criswell and Shibles (21) worked with 20 genotypes of oats at Ames, Iowa, and observed a positive correlation of SLW with rates of photosynthesis. They said that for this reason SLW might be acceptable as a selection for leaf photosynthesis.

Another study involving the determination of SLW was reported by Chatterton et al. (20). These researchers worked with alfalfa and corn at Beltsville, Maryland, and found a positive correlation of

SLW with the fluctuation of total non-structural carbohydrates. They concluded that change in SLW could be used to measure photosynthate production-translocation balance and that such a change might reflect productivity potential.

Effect of Water Stress on Translocation

Changes in non-structural carbohydrate and protein content in wheat have been studied extensively and are the subject of numerous discussions by plant researchers. There is general agreement that water stress results in an increase in grain protein and in a decrease in total carbohydrate.

Content of water soluble carbohydrate and protein is dictated by photosynthesis and transport of photosynthetic products. Wardlaw (84), in Australia observed that the rate of translocation was reduced in wheat plants under desiccating conditions. He said that the decrease in the rate of translocation could result either from a decrease in the amount of photosynthate available for transport or from inhibition of the translocation process. Asana et al. (8) noted that the rapid termination of grain growth in the later stages of development of water stressed plants was associated with a rapid yellowing of the spike tissue, and suggested that the final decline in grain growth was the result of a reduced assimilate supply. Later, Asana and Basu (5) noted a late accumulation of sugar in the stem of stressed plants and concluded that stress had interfered with the transfer of assimilates into the grain.

In another paper, Wardlaw (85) reported an increase in senescence and reduction of photosynthesis due to water stress. He said that water deficit applied during the first 7 days following anthesis significantly reduced the final grain weight per spike. However, he observed a greater initial growth rate of individual grain in the most stressed plants due to a greater rate of cell division in the endosperm, but during the late stages of development this advantage was lost and grain growth prematurely ceased in stressed plants. He concluded that yield reduction was not due to limitation of substrate for grain growth, thus the supply of assimilates from the uppermost parts of the plants was always in excess of the grain requirements.

Jenner and Rathjen (39, 40) attempted to disprove the hypothesis that the production of assimilates by the plants was the limiting factor in the supply of sucrose in the wheat grain. They proposed that the flow of sucrose into the endosperm was limited by the capacity of the mechanism transporting sucrose on the final stages of its passage into the endosperm and that the rate of starch synthesis in the grain was dependent on the concentration of sucrose in the endosperm. Evans _et al_. (32) stated that the limitation of carbohydrate transport to the spike, within the spike, within the spikelets, and within the grain, merit further investigations, because there are a number of conditions in which the rate of assimilate production exceeds the rate of starch storage.

Dougherty et al. (30) at Canterbury, New Zealand, observed that poor grain set occurred in wheat that had lower levels of water soluble carbohydrate in the spike before emergence, and dry weights were lower in spikes that had less water soluble carbohydrate. They said that the rate of spike development was regulated by the level of assimilate, and that any factor which caused long-term reductions in assimilate supply should decrease spike growth rates. In another study, Dougherty and Langer (29) reported that nitrogen fertilizer and irrigation tended to delay spike development because these factors favored vegetative sinks and reduced the amounts of assimilates reaching the developing spikes. They concluded that any environmental and agronomic factors which altered the supply of substrate to the spike could affect its growth rate and yields.

Daynard et al. (27) at Ontario, Canada, studied the contribution of stalk water soluble carbohydrate to grain yield of corn. They observed a significant accumulation of carbohydrate in the stalk immediately after silking due to a limited grain sink capacity; later in the season, they observed a decrease of carbohydrates. They concluded that this decrease at the end of the season was due to a remobilization of soluble carbohydrates stored temporarily in the stalk.

Working with potted plants at Cambridge, England, Lupton (53) observed that very little of the carbon assimilated before anthesis was translocated to the wheat grain; however, the proportion translocated increased rapidly after anthesis until photosynthetic organs were no longer active. Wardlaw and Porter (86) also worked with potted wheat plants and observed that sugars previously accumulated in the stem contributed only 5-10% of the final spike dry weight. In another study with potted plants, Wardlaw (84) reported that grain growth was initially unaffected by several days of leaf wilting and this was accompanied by a change in distribution of assimilates from the lower parts of the plants to the grains. He said that water stress reduced the transfer of sugars from the assimilation tissue to the conducting tissue, and this in turn resulted in the accumulation of sugar by the leaf. However, he concluded that stress did not inhibit translocation within the conducting tissues.

Yu et al. (94) worked with potted wheat plants at Shanghai and observed a decrease of the carbohydrate supply to the spike by either defoliation or drought, or both. They observed that the most important organ for dry matter production during the ripening period was the leaf-blades, and water stress caused a considerable reduction in assimilation by leaf-blades, while that of other organs was little affected.

Seed Quality Components

The parental conditions affecting the potentiality of seeds have been discussed since 1918. Kidd and West (44) said that environmental factors acting upon seed development could affect the subsequent growth and yield of several crops. They called this concept "physiological pre-determination." For example, these authors stated that when the size of the seeds was altered by climatic or edaphic conditions acting through the parent plant any increase or decrease in yield from the seeds thus altered could only be a matter of physiological pre-determination.

Several investigators (48, 49, 50, 51, 68, 69, 74) have shown that seed protein content might affect seedling vigor. For example, Lowe and Ries (51) reported that small wheat seed (35 mg) with high protein content produced larger seedlings than large seeds (45 mg) of the same genetic constitution with low protein content. Lopez and Grabe (48) worked with wheat and barley seeds and found a positive relationship between seed protein and plant performance.

Ries and Everson (69) obtained wheat seed from different sources and determined the effects of protein content and seed size on subsequent seedling vigor. They observed that both environment and genotype affected the protein content of the seeds. They said that regardless of genotype or environment, seedling vigor was consistently related to seed protein. Seedling vigor was also related to seed size, but when differences in seed size were eliminated, seed protein content and seedling vigor relationships were significant.

Seed size has been shown to affect seedling vigor and grain yield (12, 28, 43, 75, 90). However, it is difficult to separate the influence of seed size from that of other seed quality attributes in their relation to seedling vigor. Large seeds produce larger seedlings and this advantage may persist to increase yield (90). Scott (75), as cited by Wood et al. (90) assessed the relative importance of embryo and endosperm size in winter wheat. Grains of uniform (80 mg) weight were either left intact or part of the endosperm was removed to give grain weighing 60, 40, or 20 mg; in all seeds the embryo size was similar (0.64 mg). Emergence of the 20 mg grain was delayed and fewer seedlings emerged. Still, seedling weight was closely related to the weight of reserves contained and not to the size of the embryo.

Bremner et al. (15) observed that wheat seed with small embryos had higher relative growth rates during the first 6 days of growth than seed with large embryos, regardless of the amount of reserves stored. After 6 days, embryos associated with large amounts of food reserves produced the largest seedlings.

Considering the attention given to the area of seed vigor, especially in the last 10-15 years, it is not surprising that several procedures for measuring seed vigor have been developed. Respiration rate has been shown to have a positive correlation with vigor during the early stages of germination and subsequent growth of the seedlings. However, this test has been used more extensively in studies involving seed storage and seed deterioration. Woodstock and Grabe (91) reported a positive correlation between rate of oxygen uptake during imbibition and later stages of germination and seedling growth in corn.

In many cases the activity of a particular enzyme can be related to seed viability and seedling vigor. For example, Grabe (36), investigating glutamic acid decarboxylase activity (GADA) as an index of seed deterioration and seedling vigor in corn and oats, found that of the various measurements considered, GADA was the most positive, followed in order by root length, cold test performance, and germination. Woodstock and Grabe (91) also found a positive correlation between GADA and seedling growth of corn.

MANUSCRIPT I

EFFECTS OF MOISTURE STRESS ON YIELD AND QUALITY OF WINTER WHEAT SEED

Abstract

The objectives of this study were to determine the physiological changes that occur during the vegetative and reproductive stages of the wheat (Triticum aestivum L.) plant under water stress, and to relate these changes to seed yield, quality and performance. Different levels of moisture stress were obtained by establishing plots in two rainfall areas, and by planting on three different dates in the dryland area.

Seed development and maturation occurred under extreme moisture stress in Moro (254 mm annual rainfall), while stress at Corvallis (1020 mm annual rainfall) was low. Plants from the early fall planting were subjected to the most stress because of the greater fall growth which removed much of the soil moisture.

Lowest seed yields occcurred under the greatest moisture stress conditions, primarily because of a reduced number of seeds per spike.

Seed size was the quality component most affected by moisture stress. Smaller seed size was associated with lower soil water potential, higher leaf area index during vegetative growth, and higher specific leaf weight and water soluble carbohydrate content of the plants after anthesis. Water soluble carbohydrate content was particularly high in the rachises of the most severely stressed plants, indicating a reduced rate of translocation to the developing

seeds. Embryo weight was also reduced in the more stressed plants in proportion to the reduction in seed weight.

The protein contents of seeds from all three moisture stress levels at Moro were similar. Seeds developed under the most severe water stress had the highest respiratory quotient and lowest glutamic acid decarboxylase activity. The growth rate of seedlings produced by these seeds was 29% lower than that from seeds from the less stressed plots.

Additional index words: Leaf area index, specific leaf weight, rachis water soluble carbohydrate, seed size, glutamic acid decarboxylase activity.

Introduction

Seed crops are produced under diverse environmental conditions of soil type and fertility, rainfall, temperature and length of growing season. Seeds of the same genotype produced in different areas may vary in performance potential because of the effects of these diverse environments. McFadden (15) found 16 percent differences in yield by planting barley seed lots produced in different locations in Canada. When seed lots of 'Hyslop' winter wheat from different areas in Oregon were placed in yield trials, yield ranged from 7853 to 6358 kg/ha (D. F. Grabe, personal communication). Mathenge (16) showed that the area of production had more effect on wheat seed size and seedling vigor than seeding rate or nitrogen fertilization rates.

In Oregon, soil moisture is a major environmental variable in the areas where wheat seed is produced, since annual rainfall in these areas often ranges from less than 254 mm to over 1020 mm. Numerous studies have demonstrated the deleterious effects of moisture stress on yield and components of yield of wheat. Depending on the stage of plant growth when moisture stress is imposed, such stress may lower yield and yield components (2, 10), reduce leaf area and leaf area duration (12, 19, 21, 22), reduce the relative turgidity of the leaves (12), and lower the rate of photosynthesis (5,11).

Water stress frequently increases the percentage of protein in the seed (5, 18, 20).

Translocation of carbohydrates to the developing seed is limited by water stress, with a resultant reduction in seed size (2, 3). Seed size, in turn, is known to affect seedling vigor and grain yield (7, 23). It is not known whether this yield reduction is due only to a smaller supply of food reserves, or whether other physiological processes in the seed may be impaired.

The objectives of this study were to determine the physiological changes that occur during the vegetative and reproductive stages of the wheat plant under water stress, and to relate these changes to seed yield, quality and performance. Different levels of moisture stress were obtained by establishing plots in two rainfall areas, and by planting on three different dates in the dryland area.

Materials and Methods

Field plots were established at the Sherman Unit of the Columbia Basin Agricultural Research Center on fallow Walla Walla silt loam soil, and at the Hyslop Crop-Science Field Laboratory on a Woodburn silt clay loam. Average annual rainfall is 254 mm at the Sherman Unit, near Moro, and 1020 mm at Hyslop Field Laboratory, near Corvallis.

'McDermid' semi-dwarf, soft, white winter wheat (Triticum aestivum L.) was planted in Moro on 1 and 30 September and 27 October 1977. Foundation seed was planted at the rate of 97 kg/ha with a deep-furrow drill. Plots were 6.1 m long with six rows spaced 0.35 m. Ammonium nitrate was broadcast at the rate of 40 kg/ha prior to seeding. Plots were planted in a randomized complete block design with three replications. In Corvallis three plots were seeded with Foundation seed of McDermid on October 20, 1977 at the rate of 101 kg/ha. Plots were 6.1 m long with six rows spaced 0.23 m. A Fall application of 336 kg/ha of 16-20-0 fertilizer was applied before seeding and 483 kg/ha of urea (46% N) was applied in the Spring.

Soil samples were taken at intervals throughout the growing season from 0-30 and 30-60 cm depths. The soil moisture content was determined gravimetrically (dry weight basis) and converted to soil water potential by use of a moisture tension curve.

Plants were harvested on 23 March, 7 and 21 April, 5 and 24 May, 8, 20 and 30 June, and 11 July in Moro; and 27 March, 8 and 24 April, 7 and 20 May, 4, 14 and 24 June, and 5 July in Corvallis. Plants from 30 cm of row were cut at soil level, separated into stem, green leaves (dry-senescent leaves were excluded), and spikes, placed in plastic bags, packed in ice, and transported to the laboratory for analysis. Six plants from each plot were uprooted for determination of plant growth stage according to Zadoks' (46) decimal code for growth stages of cereals.

Leaf area was determined by using a portable area meter (Model LI-3000 LAMBDA Instruments Corporation). Dry weight of component parts was determined after placing plants in a microwave oven for 40 seconds and in a forced draft oven at 70 C for 36 hours. Specific leaf weight was calculated by dividing total leaf dry weight by total leaf area. After drying, the spikes were further separated into awn + bracts, rachis, and seeds, redried, and weighed. Content of water soluble carbohydrates of plant parts was determined by the method of Yemm and Willis (26).

Yield components were determined on plants from 1 m of a central row of each plot prior to harvest. Components measured were spikes per m^2, seeds per spike, and 1000-seed weight.

Seeds from each planting date and location were evaluated for various quality components. Weight of 1000 seeds was determined from two sub-samples of 1000 seeds. For determination of embryo weight, three sub-samples of 100 seeds were soaked in water for 2 hours, the embryos removed and placed in a drying oven at 100 C for 1 hour and 70 C for 23 hours. The percentage of seeds larger than screen size 7 was determined by shaking 100 g samples over a 7/64 x 3/4 (2.78 mm x 19.05 mm) slotted hand screen.

Seed protein content was determined by the procedures of Nelson and Sommers (17) and Bremmer and Edwards (6).

To determine seedling dry weight, three replications of 25 seeds were planted in wet rolled towels and seedlings were allowed to grow for 15 days at 25 C. After 15 days, all normal seedlings were oven-dried for 1 hour at 100 C and for 23 hours at 70 C and weighed. Shoot dry weight was determined by planting three replications of 50 seeds in moistened perlite at a depth of 2 cm. After 15 days in the greenhouse at alternating temperatures of 15.5-21 C, shoots were removed with a razor blade, placed in an oven for 1 hour at 100 C and 23 hours at 70 C and weighed.

Seed respiration was determined manometrically as described by Woodstock and Justice (25). Rates of oxygen uptake and carbon dioxide evolution during a 2-hour period were measured in a Gilson differential respirometer at 20 C. Fifteen seeds were placed in 15-ml flasks with 2 ml water, with flasks shaken at 100 oscillations/minute.

Tests were replicated twice.

Glutamic acid decarboxylase activity was determined by the method described by Linko (14), using a Gilson differential respirometer at 30 C.

Simple correlation was used to estimate the relationships between variables involved in these studies. Least significant difference (LSD) at the 5% level was used for comparisons of means of yield, components of yield and seed quality.

Results and Discussion

Effects of Soil Moisture Stress on Plant Development

Soil moisture during fall and winter was sufficient for normal establishment and growth at both locations. At the beginning of spring growth, seedlings at Corvallis had 6 leaves, 8 tillers, and 2 nodes. In Moro, the early seeding had 5 leaves, 9 tillers, and 1 node, the middle seeding 5 leaves and 4 tillers, and the late seeding 4 leaves and 2 tillers. These growth stages corresponded to 16-28-32, 15-29-31, 15-24, and 14-22, respectively, in Zadoks' (27) decimal code. Differences in plant development were related to planting date and temperature, rather than moisture, since the average temperature from September to March was 9 C in Corvallis and 6 C in Moro. The average temperature from September to October in Moro was 12 C, which favored the emergence of the early and middle seeding; however, the average temperature from November to January in Moro was 2 C which delayed the emergence of the late seeding.

Changes in soil water potential at the 0-30 and 30-60 cm depths are shown in Figures 1a and 1b. Differential moisture stress developed prior to anthesis. The excessive fall growth of the early seeding reduced the soil water potential to -21 and -7.5 bars, at 0-30 and 30-60 cm depths, respectively, at anthesis, while there was little or

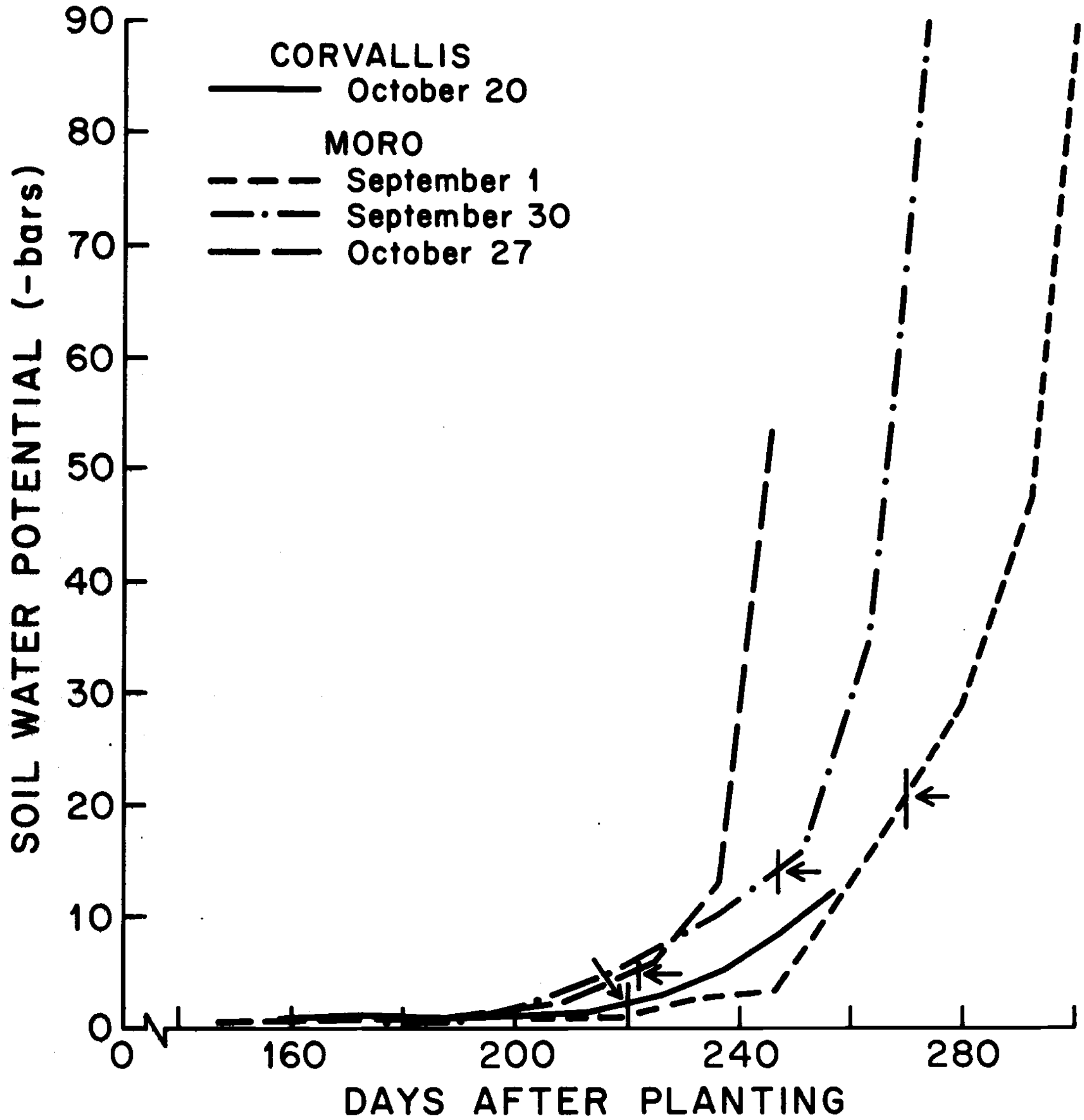

Figure 1a. Soil water potential in wheat plots at 0-30 cm depth as affected by locations and planting date. Arrows indicate beginning of anthesis.

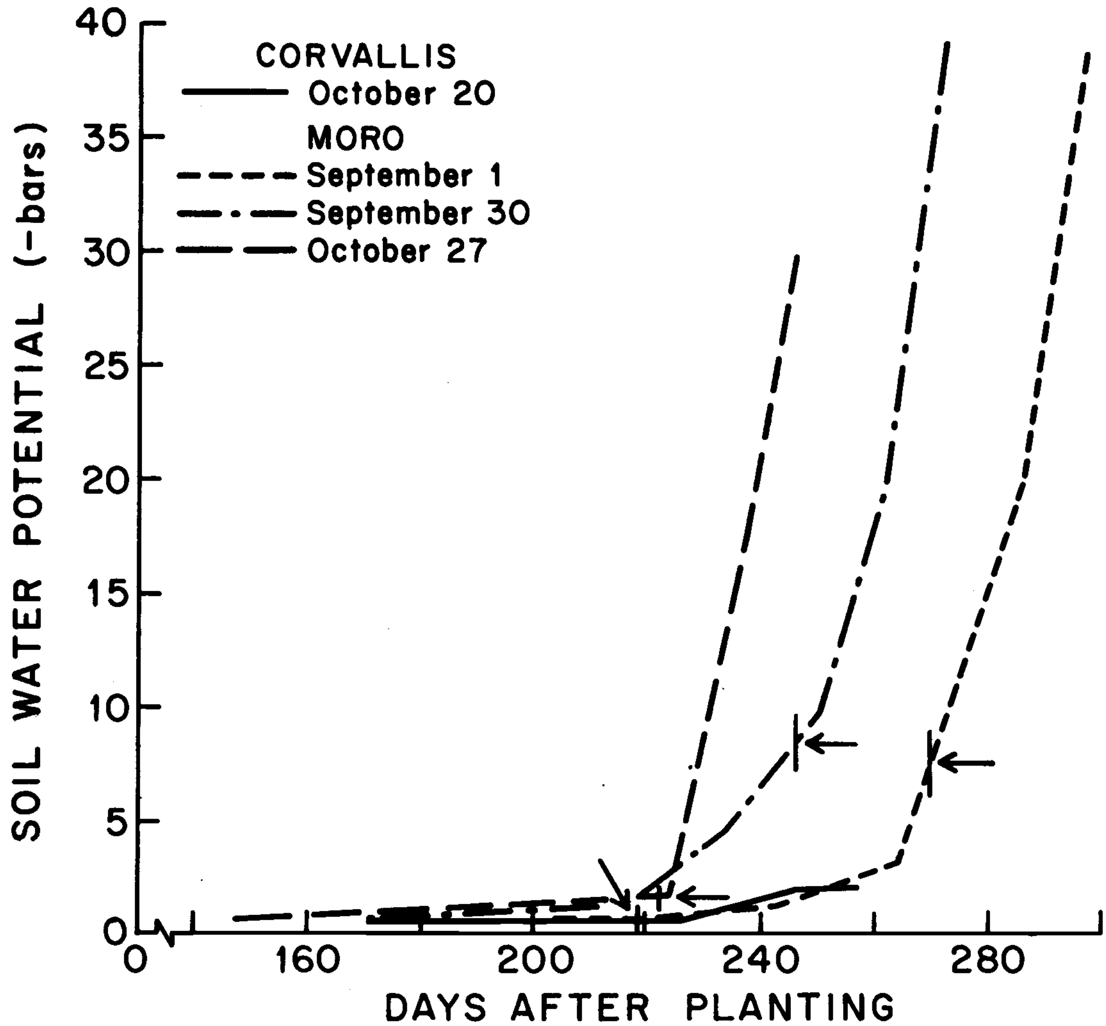

Figure 1b. Soil water potential in wheat plots at 30-60 cm depth as affected by locations and planting date. Arrows indicate beginning of anthesis.

no soil moisture stress at Corvallis. Seed development and maturation occurred under extreme moisture stress in Moro, while stress at Corvallis was low.

Plants at Moro were relatively free of disease, but plants at Corvallis were severely attacked by stripe rust. This made it difficult to differentiate between the effects of moisture stress and disease on seed characteristics in Corvallis.

Leaf Area, Dry Weight and Specific Leaf Weight. Plants in Corvallis were much larger, reaching a maximum LAI of 6.2, compared to 3.3 in Moro (Figure 2). In Moro, the LAI was highest in the early seeding because of the early fall growth. In all cases, LAI reached a maximum before anthesis and declined rapidly thereafter.

The maximum LAI extended for a period of 1 month in Corvallis. In Moro, LAI extended for 1 month in the middle seeding, but the period of maximum LAI was very brief in the early and late seedings. At anthesis, LAI was 3.2 in Corvallis and ranged from 1.1 to 1.4 in Moro.

Leaf dry weight (Figure 3) was closely correlated with LAI (r=.965**). Aase (1) suggested that leaf dry weight measurements can be substituted for leaf area in growth analyses studies because the method of measurement is much simpler and requires less specialized equipment. However, in our studies and in those of

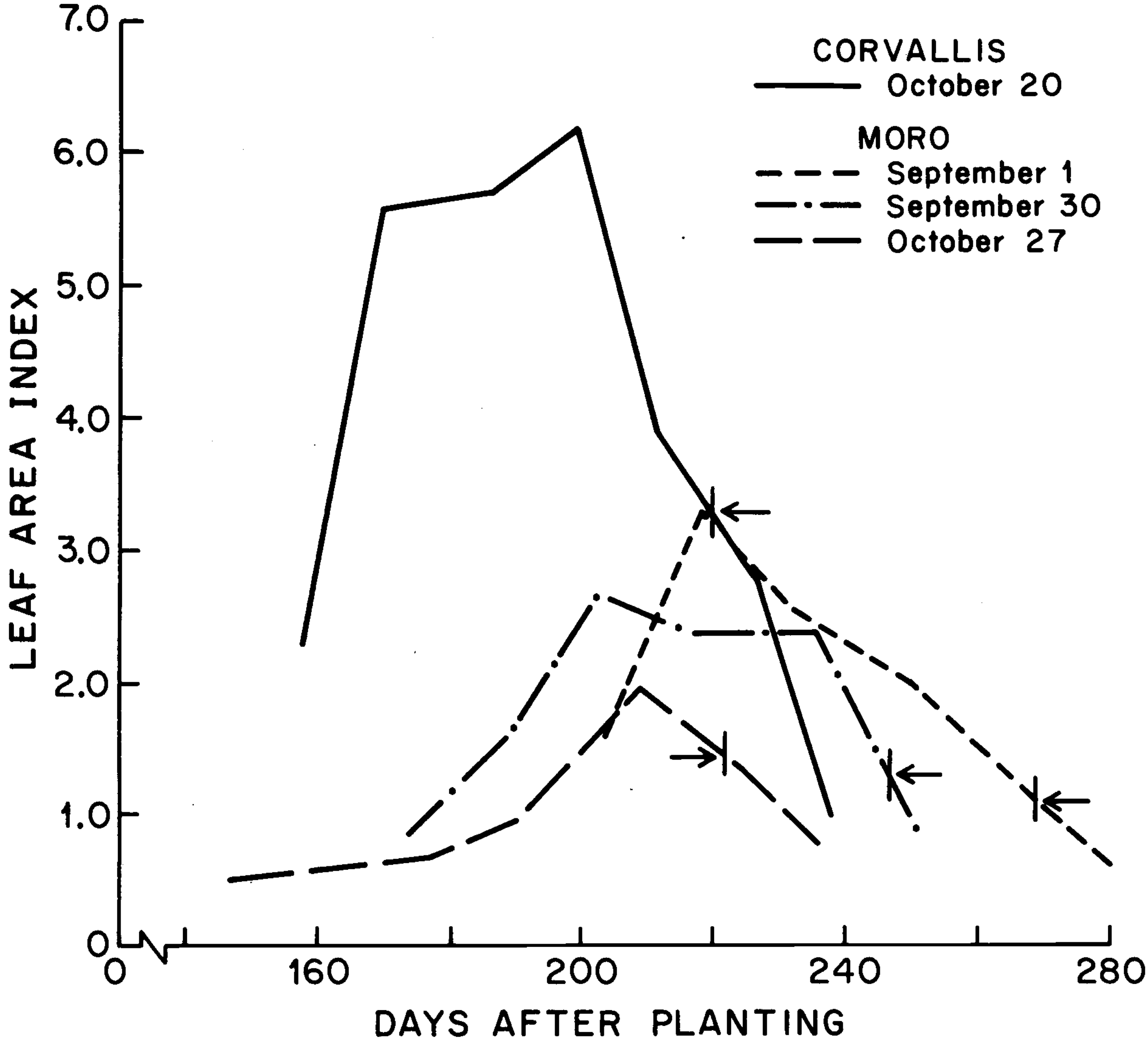

Figure 2. Leaf area index of McDermid wheat as affected by location and planting date. Arrows indicate beginning of anthesis.

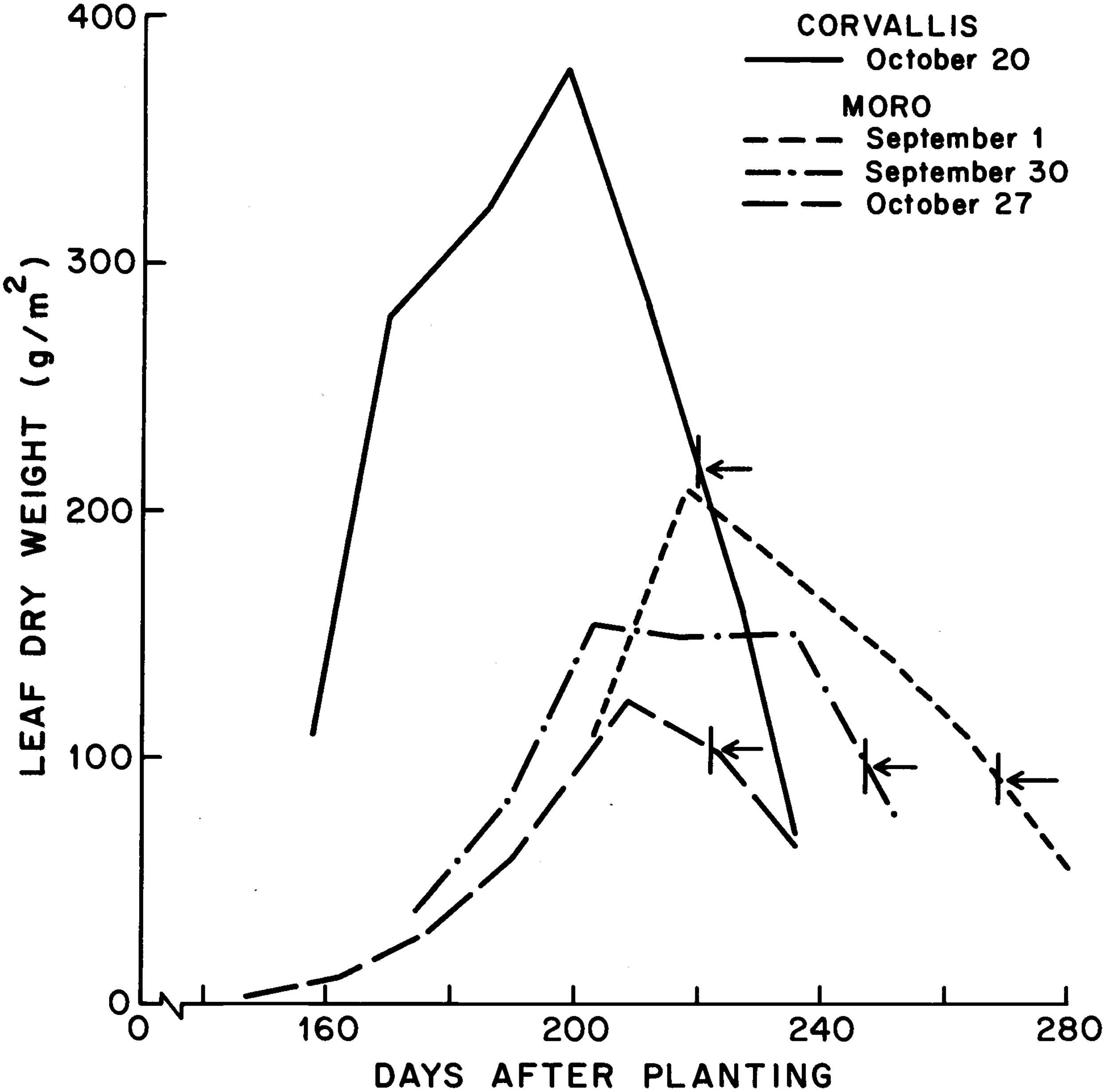

Figure 3. Leaf dry weight of McDermid wheat as affected by location and planting date. Arrows indicate beginning of anthesis.

other investigators (4, 8, 9), it was necessary to measure both leaf area and dry weight to determine specific leaf weight (SLW).

SLW remained relatively constant during the vegetative stage of the crop, followed by a rapid increase prior to and following anthesis (Figure 4). The higher SLW in the most stressed plants was closely correlated (r=.715*) with the higher amounts of water soluble carbohydrates in the leaves (Figure 5).

Water Soluble Carbohydrates (WSC). Water soluble carbohydrate content in several plant parts is shown in Figures 5 to 10. In general, the highest accumulation of WSC occurred in plants under the most severe water stress. In nearly all cases, WSC content decreased during heading and seed development as they were utilized in seed formation. The retention of WSC in the rachis of the early seeding (Figure 7), was associated with a lower rate of translocation and subsequent reduction in seed size.

Yield and Components of Yield. Seed yields and components of yield are shown in Figure 12. Highest yields were obtained in Corvallis, despite the high incidence of disease and high temperatures during early seed development. In Moro, lowest yields were obtained from the early seeding which matured under the highest moisture stress. This yield reduction was primarily due to a lower number of seeds per spike since there were as many spikes/m^2 as in the middle seeding. Smaller seed size from the early planting was a

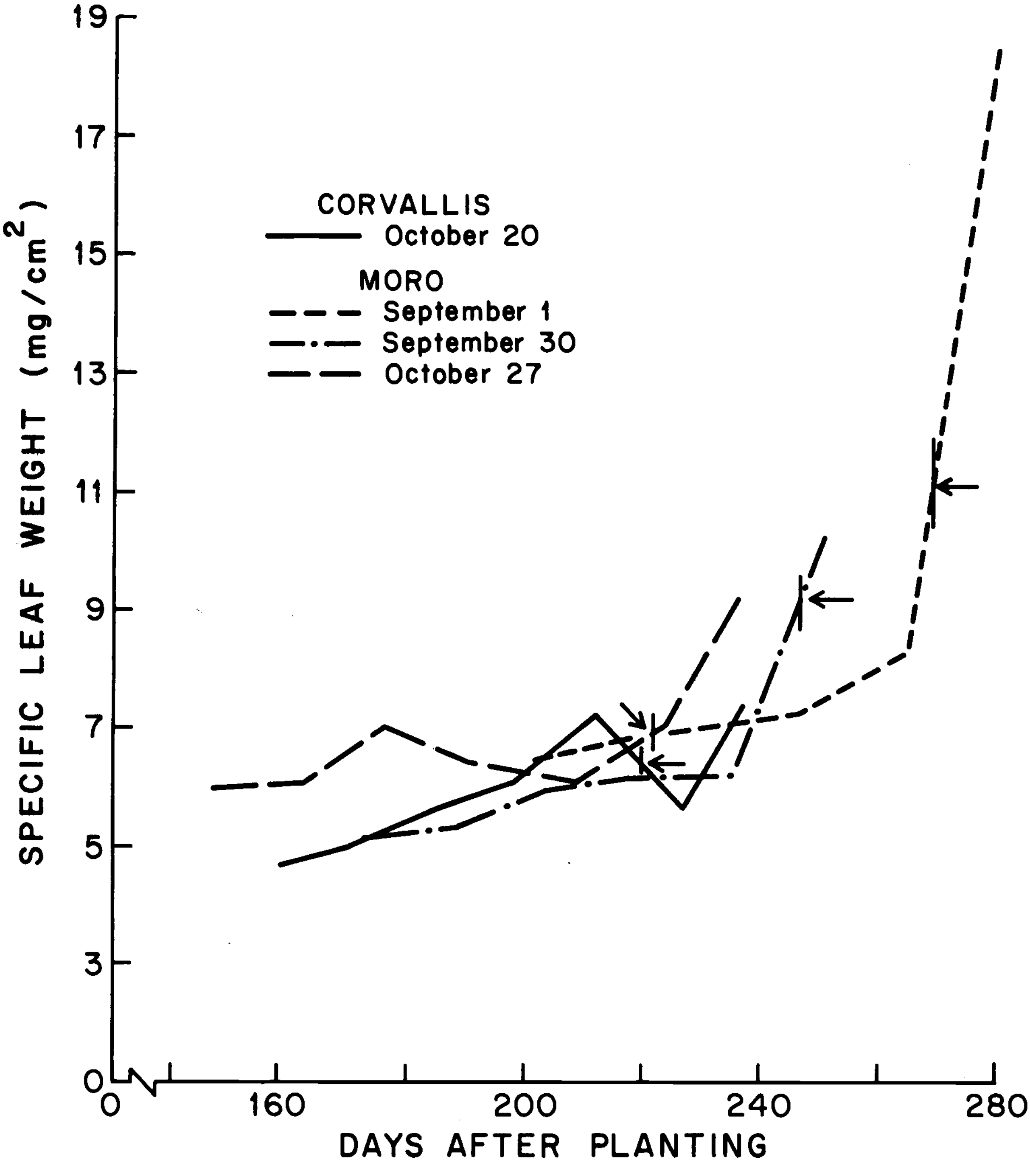

Figure 4. Specific leaf weight of McDermid wheat as affected by location and planting date. Arrows indicate beginning of anthesis.

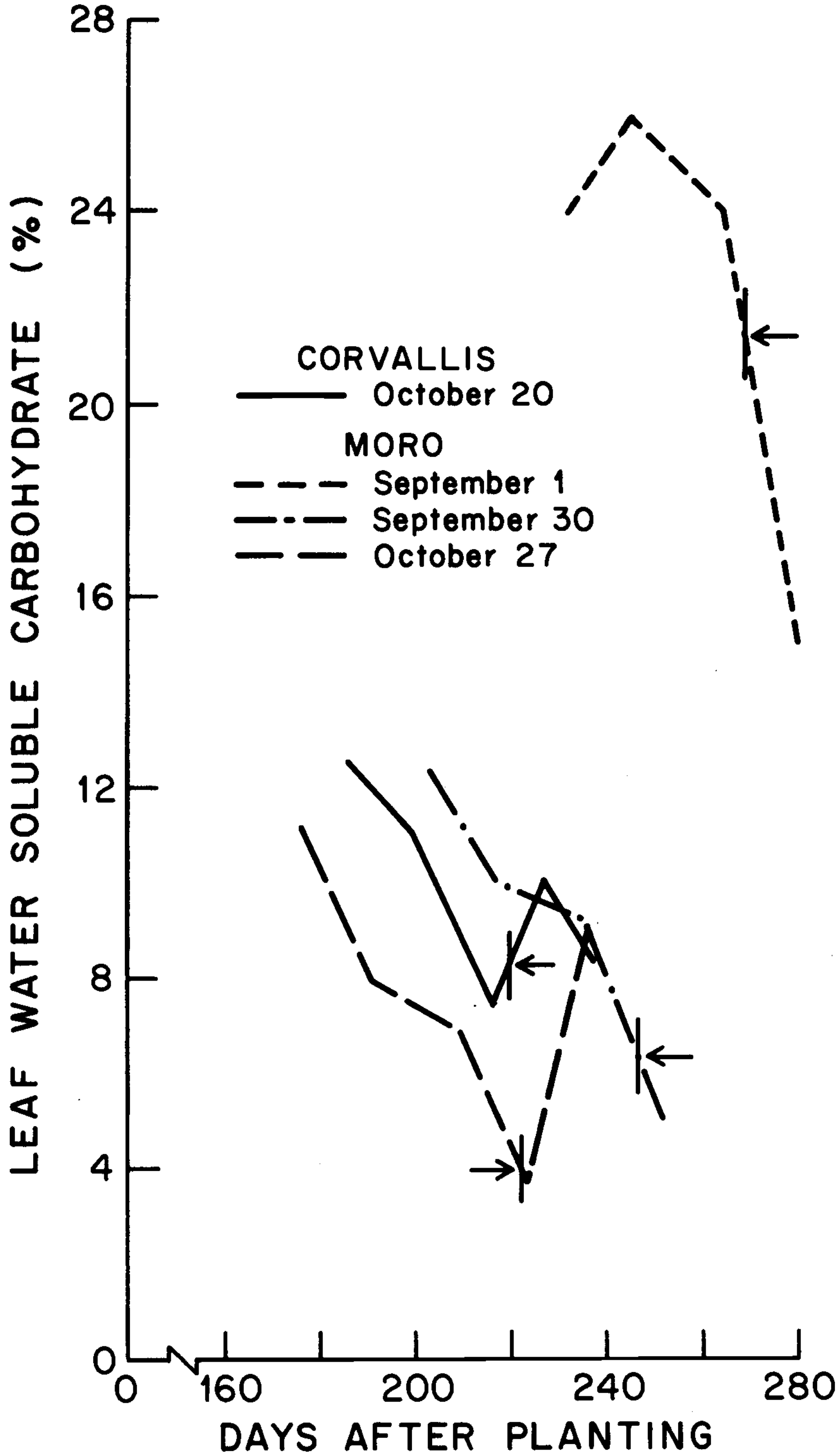

Figure 5. Water soluble carbohydrates of McDermid wheat leaves as affected by location and planting date. Arrows indicate beginning of anthesis.

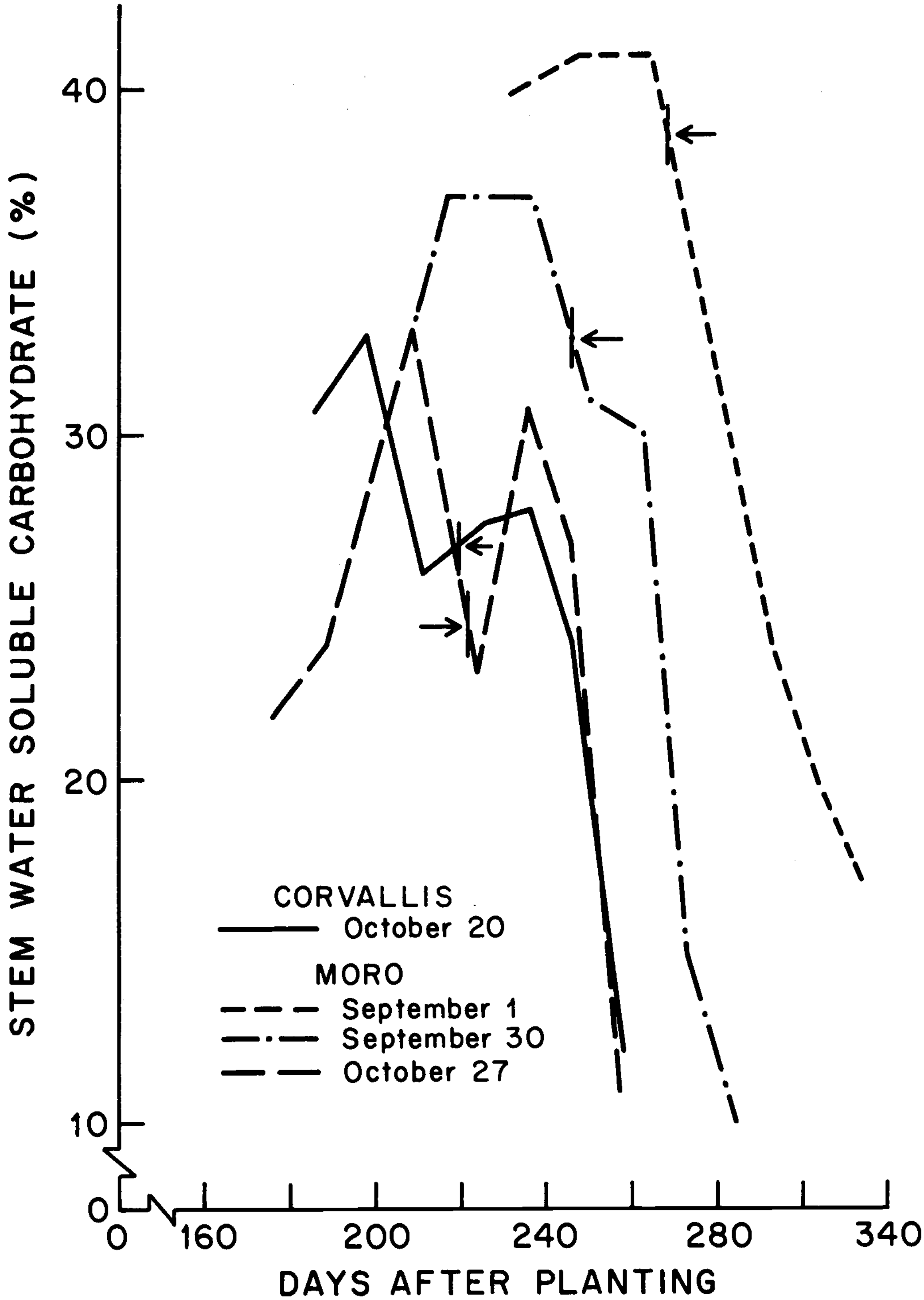

Figure 6. Water soluble carbohydrates of McDermid wheat stems as affected by location and planting date. Arrows indicate beginning of anthesis.

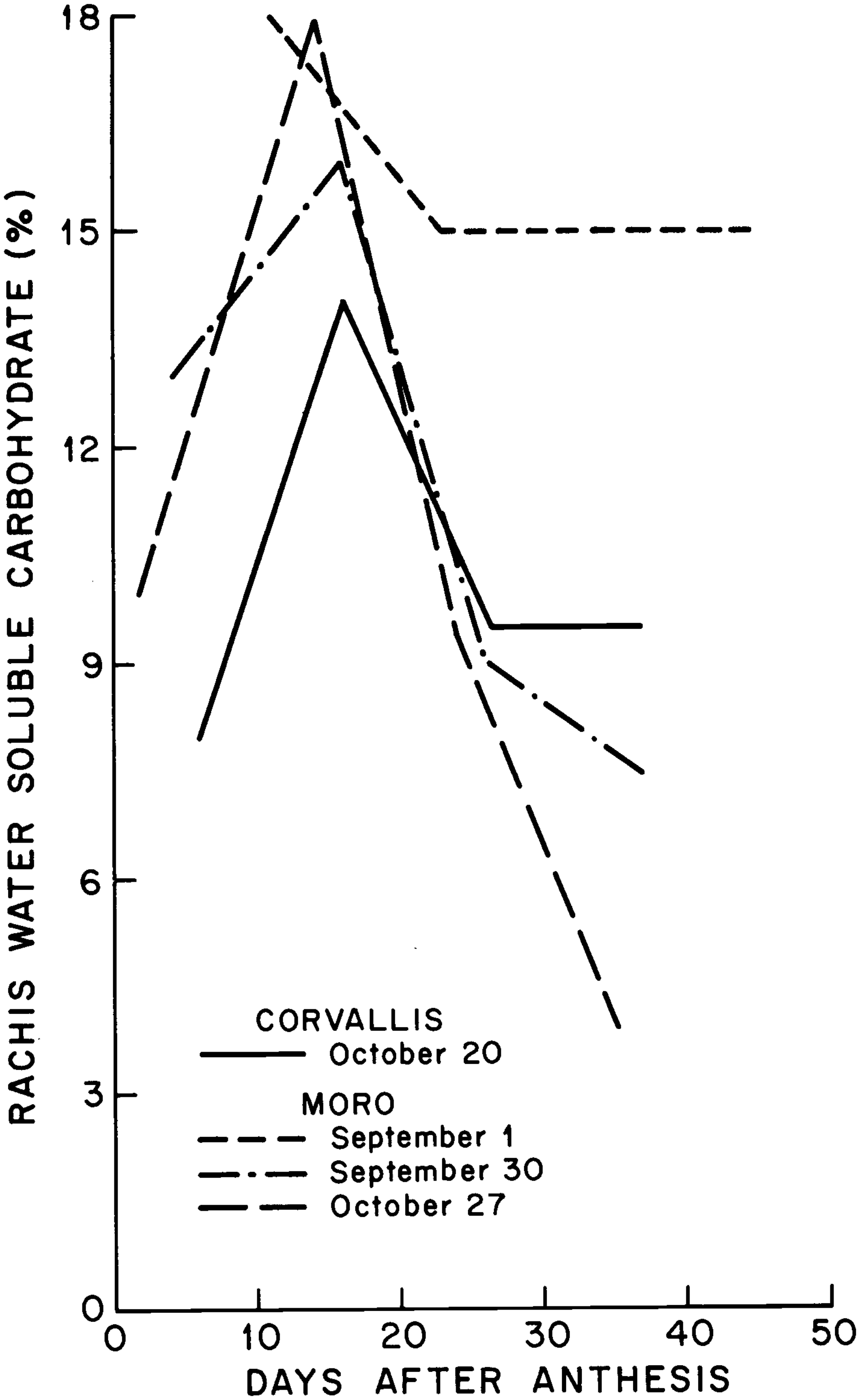

Figure 7. Water soluble carbohydrates of McDermid wheat rachises as affected by location and planting date.

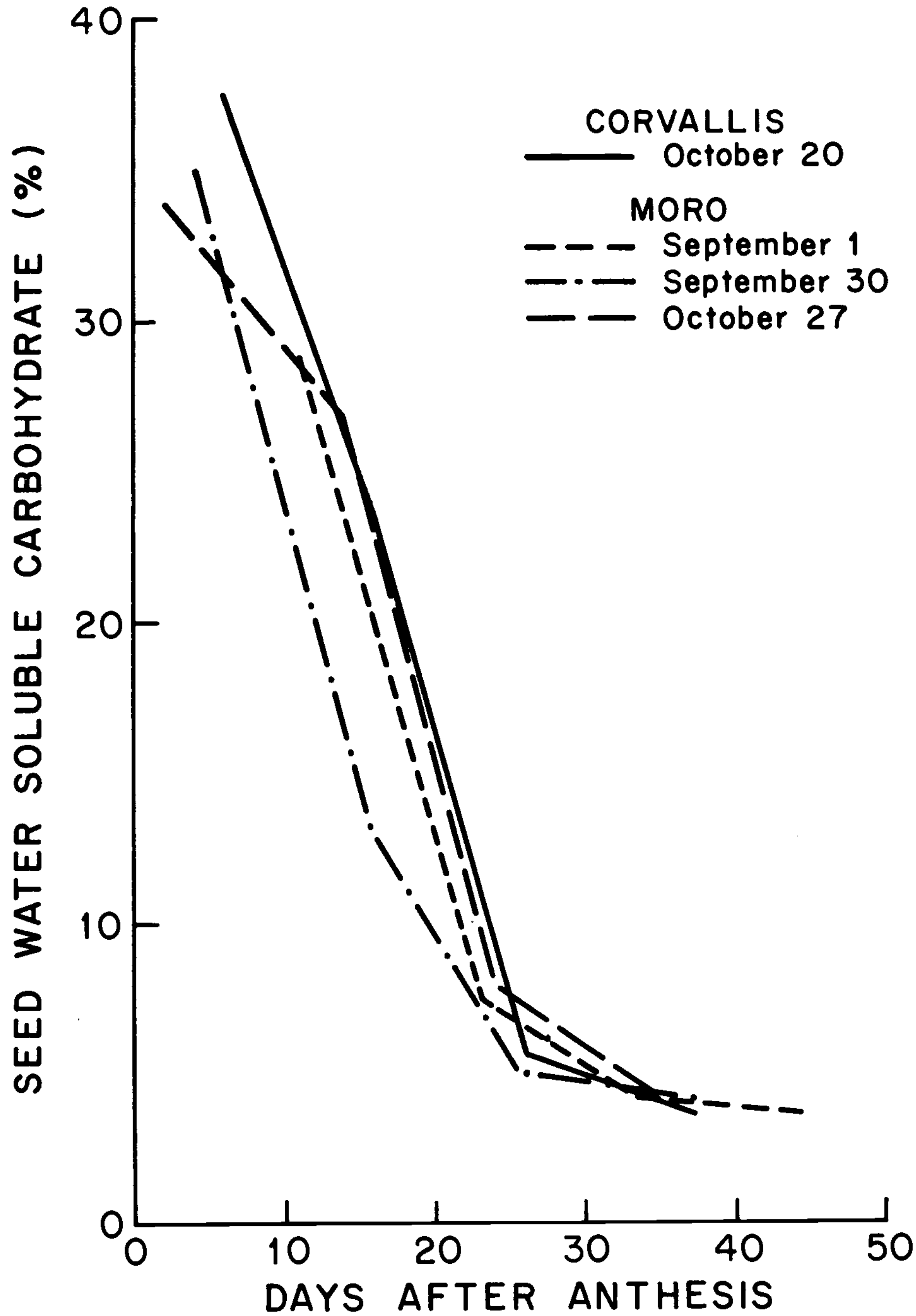

Figure 8. Water soluble carbohydrates of McDermid wheat seeds as affected by location and planting date.

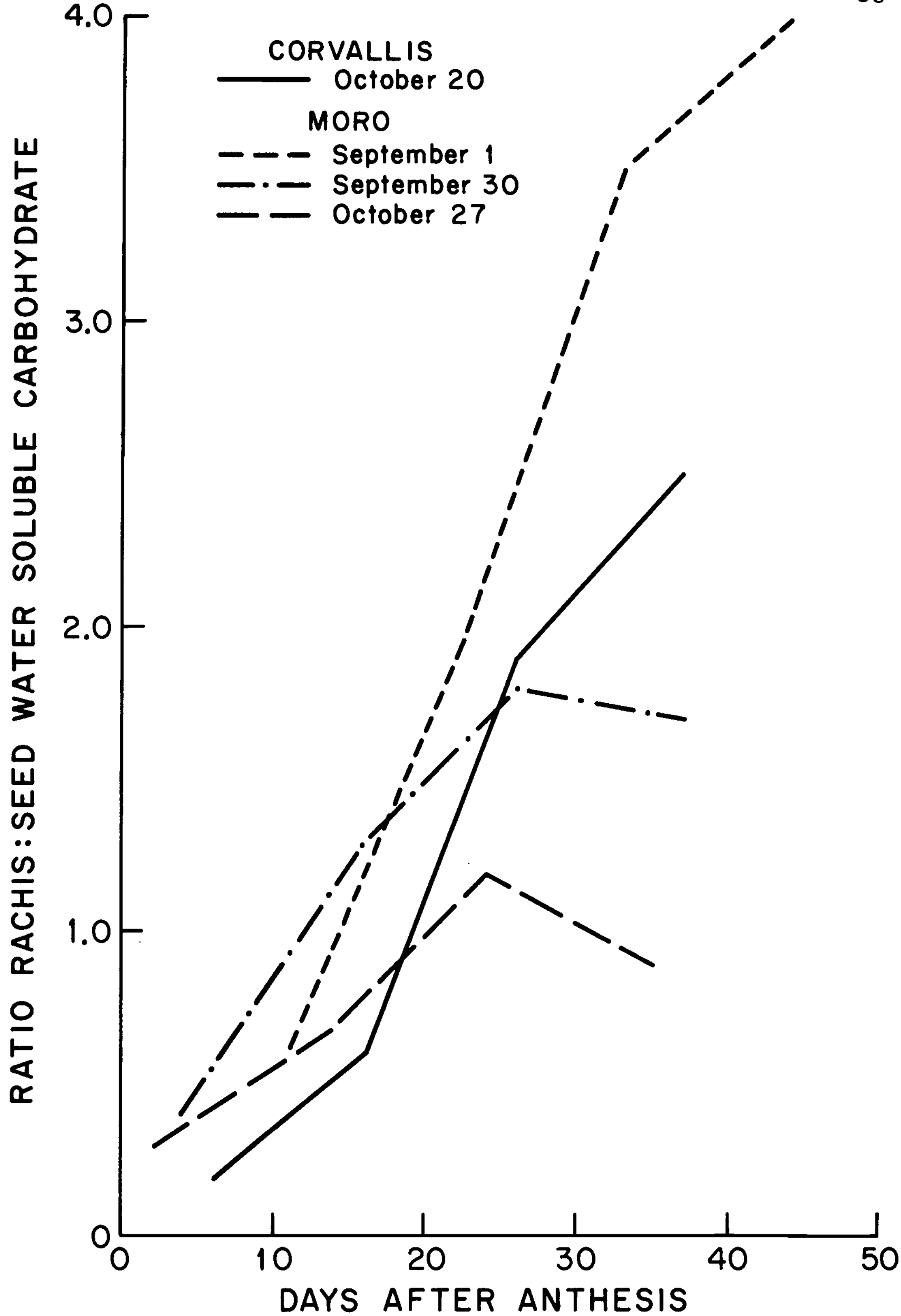

Figure 9. Ratios of rachis:seed water soluble carbohydrate of McDermid wheat as affected by location and planting date.

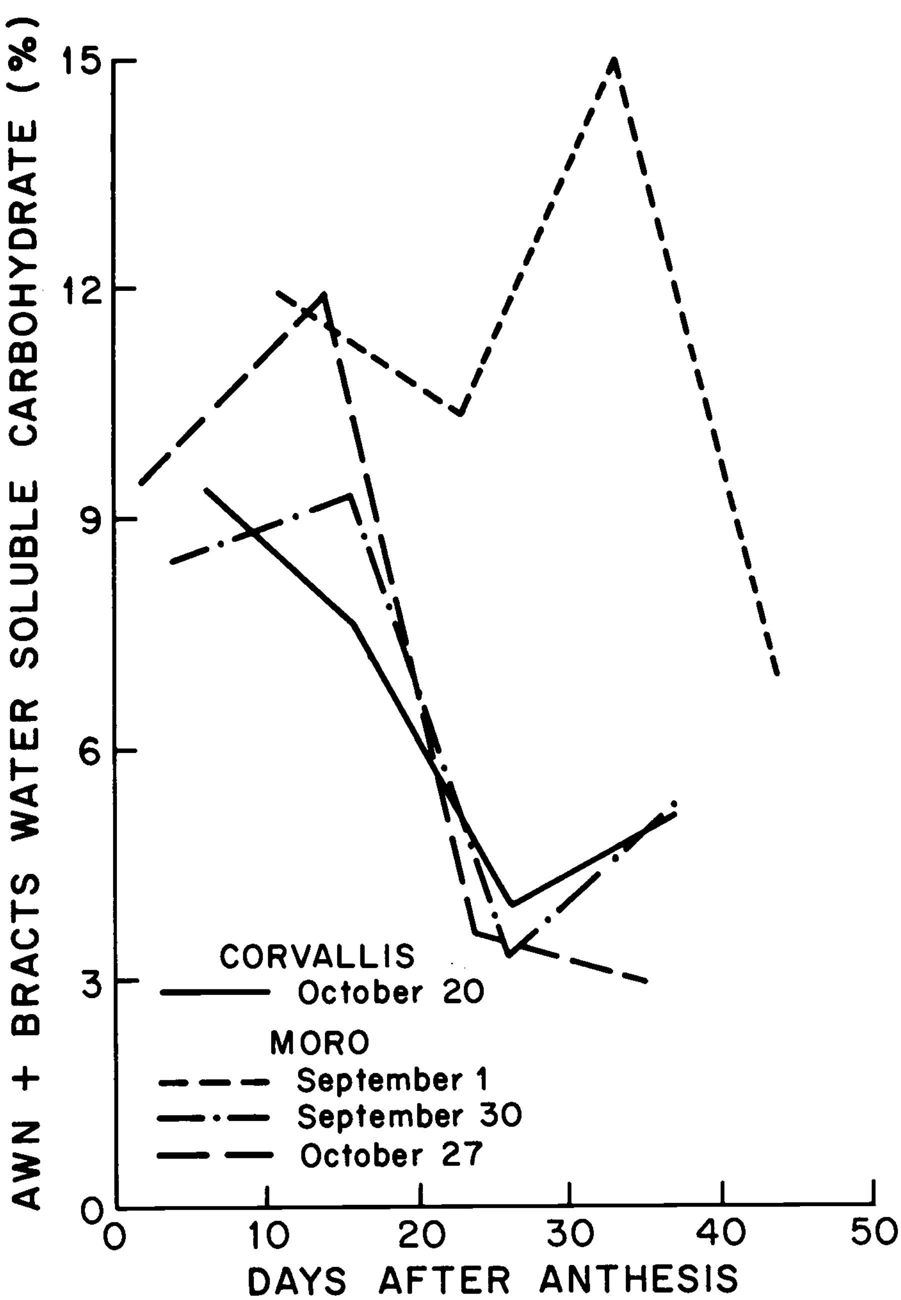

Figure 10. Water soluble carbohydrates of McDermid wheat awns+bracts as affected by location and planting date.

secondary factor causing lower yields. Seed development from anthesis onward was generally slower in the early seeding (Figure 11).

Although the late seeding had fewer spikes/m^2, there were more seeds/spike which led to yields nearly equal to the middle seeding. This would probably not have occurred with normal rainfall during the reproductive period.

Effects of Soil Moisture Stress on Seed Quality Components

Seed development during the 1978 season was atypical at both locations. In Corvallis, a combination of high temperatures, stripe rust and other diseases reduced yield and seed size and caused a high percentage of shrivelled seed. Farmers' yields in the general area were reduced 50-60%. Whereas in normal years McDermid seed in the Corvallis area averages approximately 40 g/1000 seeds, seeds harvested from the research plots averaged only 33.65 g/1000. In Moro, on the other hand, seeds were heavier than normal, ranging from 33.53 to 39.72/1000, compared to approximately 30 to 33 g/1000 in normal years. The increased weight is attributed to the 36 mm of rainfall received in April compared to the normal 19 mm. In spite of these departures from the norm, water stress had obvious effects on seed quality components. Results are most meaningful in Moro where effects of moisture stress were not masked by the effects of stripe rust and other environmental variables.

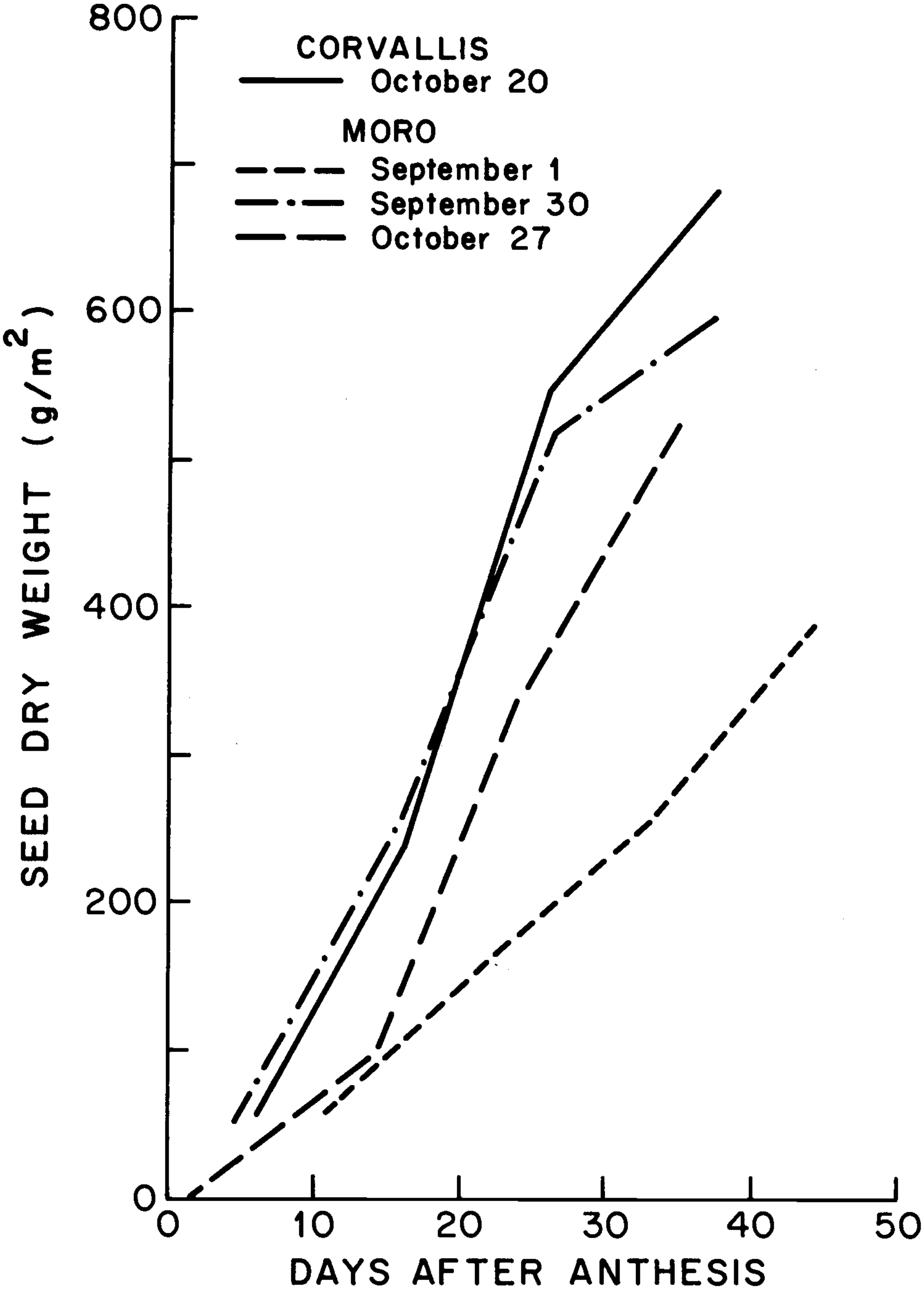

Figure 11. Yields of McDermid wheat seed as affected by location and planting date.

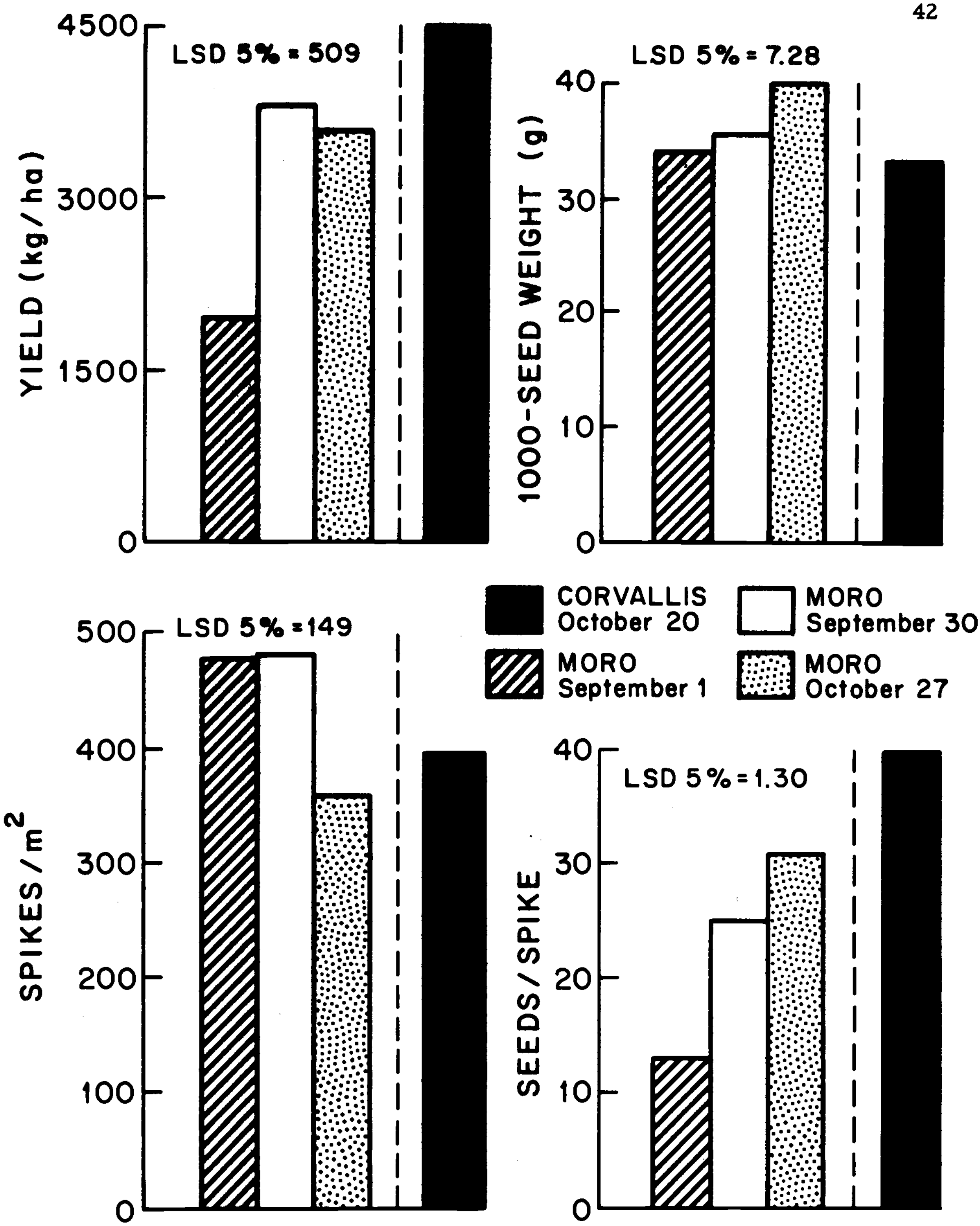

Figure 12. Yield and components of yield of McDermid wheat as affected by location and planting date. L. S. D. at the 5% level for Moro.

Seed Size and Weight. Seed size (weight) was the quality component most affected by moisture stress. Seeds from the late seeding in Moro were over 6 g/1000 seeds heavier than those from the early seeding (Table 1). Soil water stress in the early planting was much greater during the seed development period, particularly during the first several days after anthesis (Figure 1a and 1b). Increases in seed weight were closely correlated with increases in soil moisture (r=.825**).

The size of the more stressed seeds, as measured by the percentage of seeds held on a 7/64 x 3/4 in. (2.78 x 19.05 mm) slotted screen, was also reduced (Table 1). Embryo weight was also reduced in the more stressed plants in proportion to the reduction in seed weight (Table 1).

Seed weight was negatively correlated (r=-.826**) with the larger LAI (Figure 2) of the early seeding during the vegetative period. The excessive growth of the early seeding evidently depleted the soil moisture supply so less was available for seed development. The LAI of the late seeding, although lower during the vegetative development, was higher at anthesis and early seed development, leading to a positive correlation (r=.817**) with seed weight.

The content of WSC of leaves and stem was considerably higher in the early seeding (Figures 5 and 6), an indication of a lower rate of translocation of carbohydrate to the developing spikes under high

Table 1. Seed weight, embryo weight and percentage of seeds larger than screen size 7 of McDermid wheat as affected by location and planting date.

Location	Planting date	1000-seed weight	100-embryo weight	Larger than screen size 7+
		g	mg	%
Corvallis	October 20	33.65	78.47	14.99
Moro	September 1	33.53	72.33	24.75
	September 30	35.36	74.50	36.03
	October 27	39.72	86.67	44.27
L.S.D. 5%		5.08	6.38	4.96

+Percentage of seed lot held over a 7/64 x 3/4 (2.78 x 19.05 mm) screen.

moisture stress. This in turn led to a higher SLW in the early seeding (Figure 4). In the period following anthesis, content of WSC was always higher in the rachis, awns and bracts of the early seeding, indicating less translocation of WSC to the seeds. The amount of carbohydrates in the rachis was especially high in the early seeding, as indicated by the high rachis:seed water soluble carbohydrate ratio (Figure 9).

Protein Content. The protein content of seeds from all three planting dates was similar (Table 2). Other studies (5, 18, 20) have shown that seed protein content increases under water stress conditions. This was not demonstrated in the present study since all seeds in Moro matured under some degree of moisture stress.

Physiological Characteristics. Seeds from the early seeding had a higher RQ and lower glutamic acid decarboxylase activity (Table 2). In studies with deteriorated seeds, these characteristics are correlated with lower seedling growth rate (13, 24). A similar relationship existed in this study, with the seeds from the early seeding producing seedlings with 29% less dry weight than those from the late planting (Table 3).

Table 2. Protein content, CO_2 evolution (CO_2), respiratory quotient (RQ) and glutamic acid decarboxylase activity (GADA) of McDermid wheat seed as affected by location and planting date.

Location	Planting date	Protein	CO_2	RQ	GADA
		%	µl/seed		µmole/g seed/hr
Corvallis	October 20	10.35	1.33	0.50	26.1
Moro	September 1	8.53	2.07	0.73	13.6
	September 30	8.74	1.87	0.58	18.1
	October 27	8.70	1.90	0.66	19.5
L.S.D. 5%		0.97	0.29	0.06	2.1

Table 3. Seedling and shoot dry weight of McDermid wheat as affected by location and planting date.

Location	Planting date	Seedling dry weight	Shoot dry weight
		mg/seedling	
Corvallis	October 20	17.24	12.42
Moro	September 1	12.83	8.45
	September 30	14.23	8.27
	October 27	18.10	9.68
L.S.D. 5%		1.82	0.71

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MANUSCRIPT II

EFFECT OF MOISTURE STRESS ON YIELD AND QUALITY OF WINTER WHEAT SEED UNDER GREENHOUSE CONDITIONS

Abstract

The objective of this study was to determine the effects of water stress on yield and quality of winter wheat seed. Plants were grown in the greenhouse under three moisture regimes (600, 300 and 150 ml water/pot/day) from the time awns were first visible on the main stem until maturity. Soil water potential and several growth parameters were analyzed. Water-stressed plants had smaller leaf area and leaf dry weight, higher specific leaf weight, earlier leaf senescence, lower dry weight, and lower seed yield. On the other hand, water-stressed plants produced larger seeds, with heavier embryos, higher protein content, lower CO_2 evolution and lower respiratory quotient. These seeds in turn produced seedlings with greater vigor in terms of seedling growth rate.

Because of the compensation ability of the wheat plant, development of management practices to decrease certain yield components in favor of enhanced seed quality is worthy of further study.

Additional index words: Leaf area, specific leaf weight, seed size, seed protein, seed respiration, seedling vigor.

Introduction

Yield and quality of winter wheat seed may decrease under low soil moisture conditions (13, 15). In wheat grain, the percentage of protein increases during water stress although total yield decreases; evidently total protein production is inhibited but total carbohydrate production is inhibited even more (4).

Yield and protein content of wheat depend greatly on the availability of water for growth. Terman et al. (20) found an increase in both yield and protein in an intermediate stress situation. Asana et al. (1) observed that when stress occurred during the 4 weeks after spike emergence, grain number was reduced but the 1000-grain weight was increased.

Seed size and protein content are known to affect seedling vigor and grain yield (3, 6, 10, 11, 12). Large seed and high protein seed tend to be superior to small and low protein seed for planting purposes (10, 13, 21).

There have been few studies regarding the quality and performance of wheat seed produced under water stress. Such information should be valuable to plant breeders in developing varieties with improved seed quality traits, and in developing improved seed production methods.

The objective of this study was to determine the effects of water stress on yield and quality of winter wheat seed under controlled conditions. It is difficult, under field conditions, to isolate the effects of water stress from those of disease, air temperature, and other environmental factors. Therefore a greenhouse experiment was deemed desirable to standardize variables except moisture stress. Three moisture regimes were imposed from the time awns were first visible on the main stem until maturity. Seed yield, quality and performance were evaluated in relation to physiological aspects of plant growth under water stress.

Materials and Methods

Seedlings of 'McDermid' semi-dwarf, soft, white winter wheat (Triticum aestivum L.) were vernalized and transferred to a greenhouse. Seedlings were planted, one per pot, in 15-cm diameter plastic containers filled with a sterilized soil-peat moss mixture containing 4 parts soil to 1 part peat moss by volume. One hundred twenty g of 13-13-13 fertilizer and 340 g of lime were added to each 0.21 m^3 of soil mixture. When the first node was observed, 2 g of Osmocote fertilizer (19-6-12) was applied to each container. The containers received 600 ml of water every day until the first awns were visible on the main tiller. After this stage plants were submitted to three moisture regimes by adding 600, 300 or 150 ml water each day to each pot. Plants were grown with a temperature of 15.5 C and a daylength of 12 hours until heading. After heading the same temperature was maintained but the daylength was extended to 14 hours until plant maturity. The moisture treatments were arranged in a randomized complete block design with five replications. There were five containers per moisture regime.

Soil samples were taken 10, 21, 26 and 33 days after the beginning of anthesis of the main tiller. Samples were taken from the entire depth of the pot with a 1.5-cm aluminum pipe. The moisture content was determined gravimetrically (dry weight basis) and converted to soil water potential by use of a moisture tension curve.

Plants were harvested by cutting them at soil level. They were separated into stem, green leaves, dry leaves, and spikes, placed in plastic bags, packed in ice, and transported to the laboratory for analyses.

The total number of leaves per plant was counted and the percentage of green leaves was determined. Leaf area was obtained by using a portable area meter (Model LI-3000 LAMBDA Instruments Corporation). Dry weight of component parts was determined after placing plants in a microwave oven for 40 seconds and in a forced draft oven at 70 C for 36 hours. Specific leaf weight was calculated by dividing green leaf weight by green leaf area. After drying, the seeds were removed from the spikes, redried and weighed.

Yield and components of yield were determined. Components measured were spikes per plant, seeds per spike, and 1000-seed weight.

Seeds were evaluated for various quality components. Weight of 1000 seeds was determined by dividing the weight of the seeds from each plant by the number of seeds and converting to 1000-seed weight. For determination of embryo weight, four subsamples of 100 seeds were soaked in water for 2 hours, the embryos removed and placed in an oven at 100 C for 1 hour and 70 C for 23 hours. The percentage of seeds larger than screen size 7 was determined by shaking the seeds produced by each plant over a 7/64 x 34" (2.78 x

13.05 mm) slotted hand screen.

Seed protein content was determined by the procedures of Nelson and Sommers (14) and Bremmer and Edwards (5).

To determine the effects of seed quality on seedling root length, four replications of 15 seeds were planted in wet rolled towels and roots were measured after 2, 3, 4, and 5 days at 25 C. Seedling dry weight was determined by planting three replications of 15 seeds in wet rolled towels. After 15 days at 25 C, all normal seedlings were oven-dried for 1 hour at 100 C and 23 hours at 70 C and weighed.

Seed respiration was determined manometrically as described by Woodstock and Justice (23). Rates of oxygen uptake and carbon dioxide evolution during a 2-hour period were measured in a Gilson differential respirometer at 20 C. Fifteen seeds were placed in 15-ml flasks with 2 ml water, and flasks were shaken at 100 oscillations/minute. Tests were replicated twice.

Results and Discussion

The magnitude of water stress was indicated by soil water potential (Figure 1). During the first 21 days after anthesis, plants in all three moisture regimes took up water rapidly, gradually lowering the soil water potential. Later, as leaf senescence increased, decreasing the leaf area available for transpiration, there was a corresponding increase in soil water potential as evapotranspiration decreased. Plants grown with lower soil water potential had a lower leaf area and leaf dry weight, rapid leaf senescence, higher specific leaf weight, and lower plant dry weight (Figures 2 to 6).

The higher specific leaf weight of the most stressed plants is an indication of an accumulation of water soluble carbohydrates in these leaves (2, 7). This, together with a lower leaf area, contributed to lower seed yields per plant (8, 9, 18, 19).

The effects of the three moisture regimes on yield and components of yield are shown in Table 1. The most stressed plants had the lowest yield due to less spikes per plant and less seeds per spike. No difference was observed in 1000-seed weight. The non-stressed plants had the highest yield, more spikes per plant and more seeds per spike. However, no difference was observed in the number of seeds per spike in plants watered with 600 ml and 300 ml water/day. Seed development from anthesis onward was generally

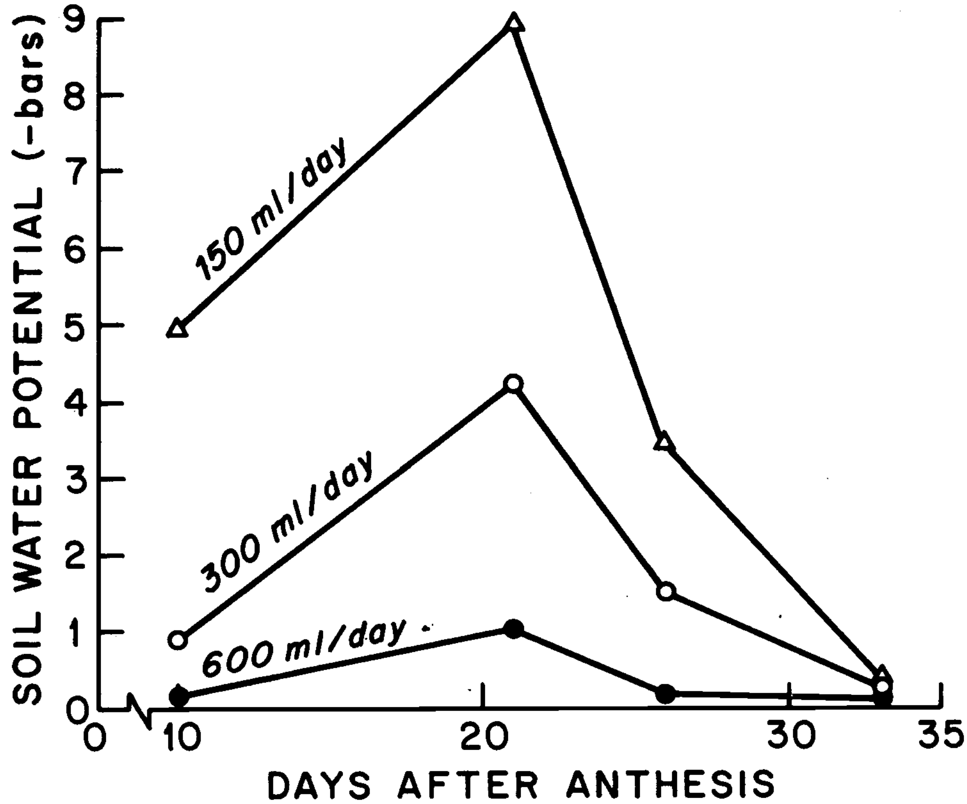

Figure 1. Soil water potential in McDermid wheat pots as affected by three moisture regimes.

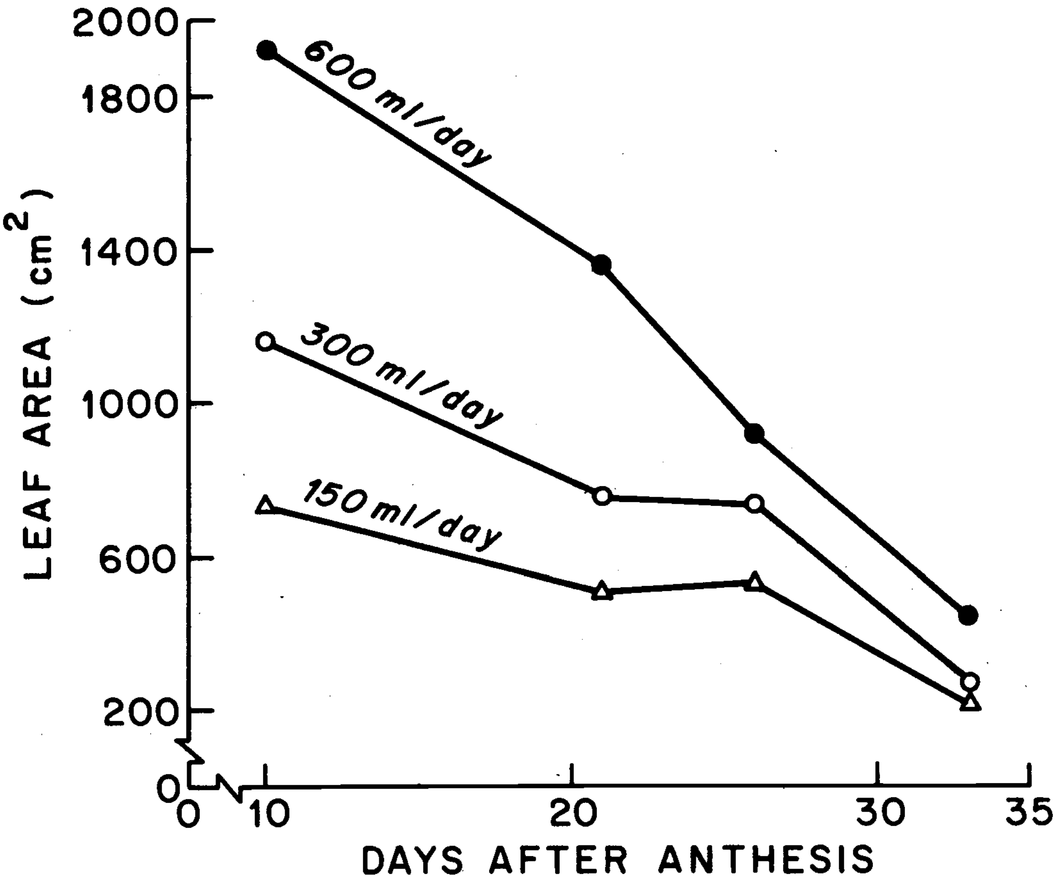

Figure 2. Leaf area of McDermid wheat plants as affected by three moisture regimes.

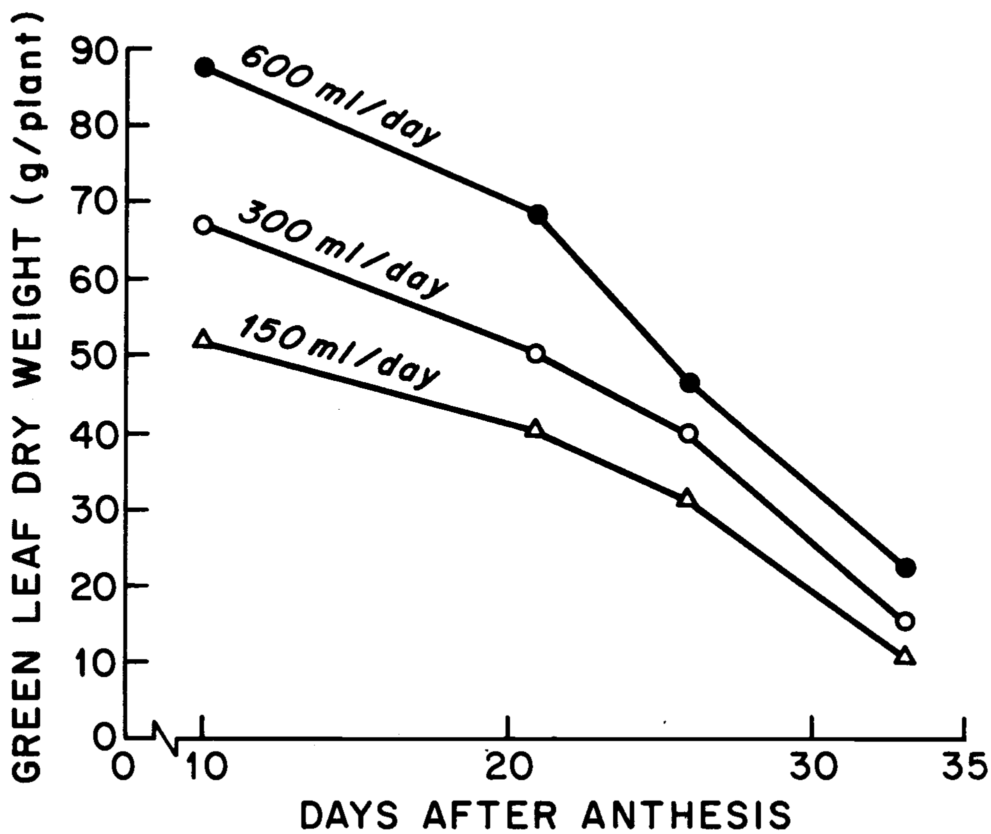

Figure 3. Green leaf dry weight of McDermid wheat plants as affected by three moisture regimes.

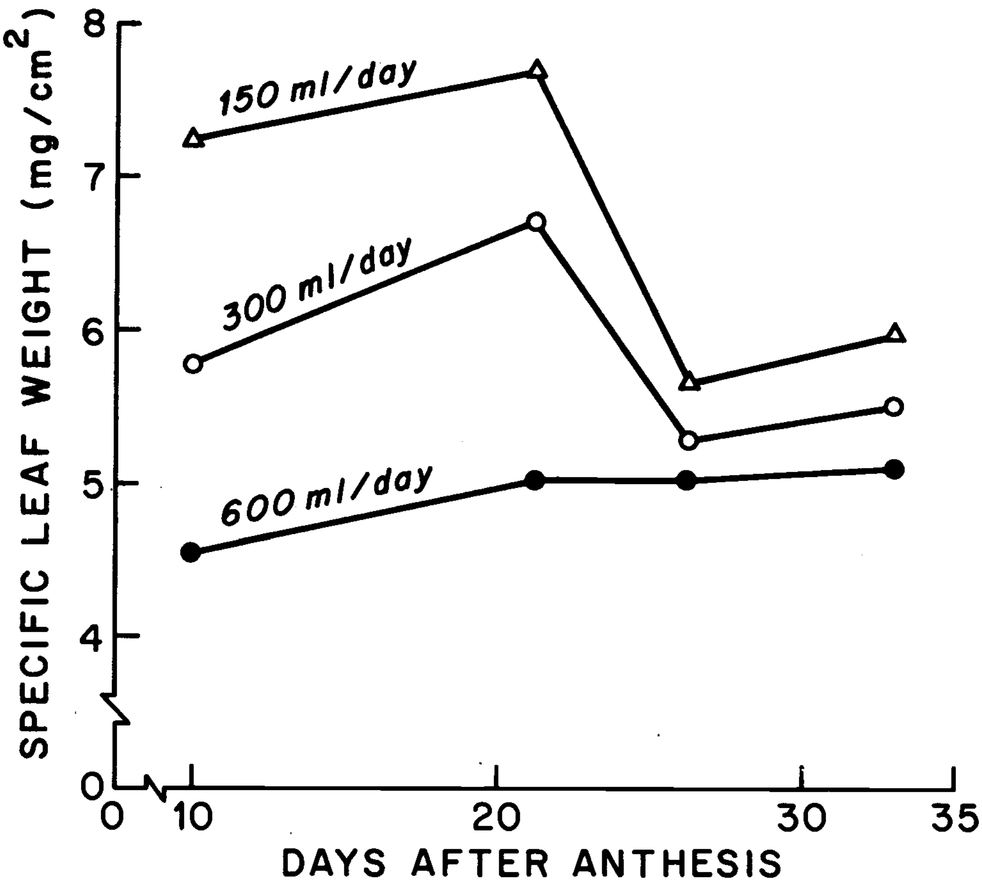

Figure 4. Specific leaf weight of McDermid wheat plants as affected by three moisture regimes.

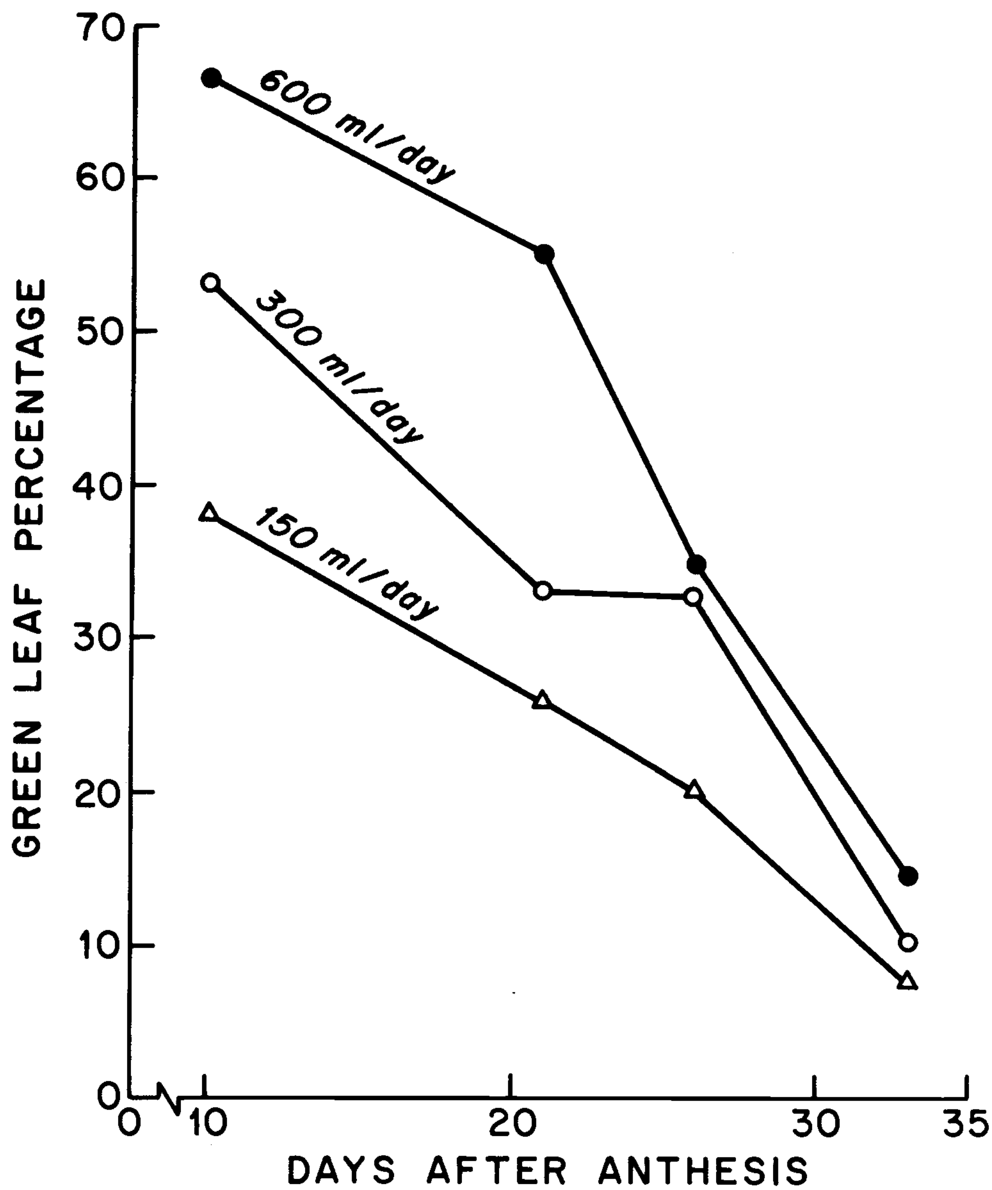

Figure 5. Green leaf percentage of McDermid wheat plants as affected by three moisture regimes.

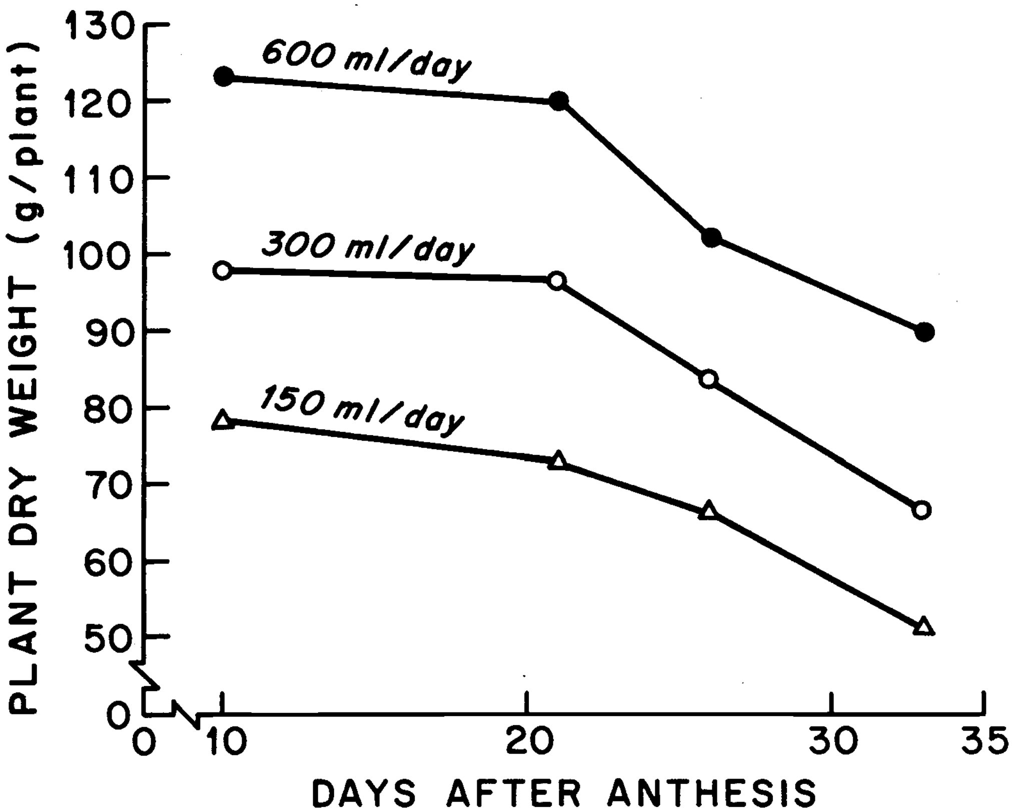

Figure 6. Dry weight of McDermid wheat plants as affected by three moisture regimes.

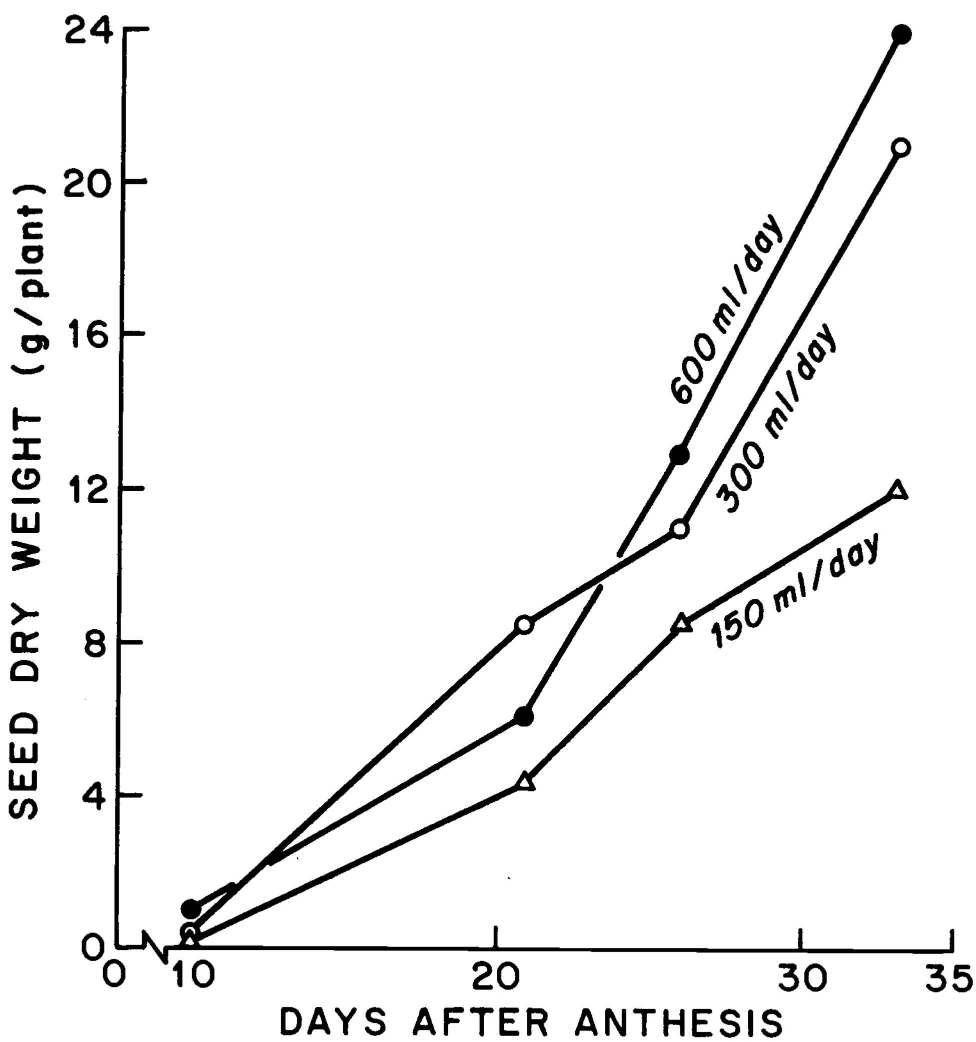

Figure 7. Yields of McDermid wheat seed as affected by three moisture regimes.

Table 1. Yield and components of yield of McDermid wheat grown under three water regimes.

Water regime	Seed yield	Spikes per plant	Seeds per spike	1000-seed weight
ml/day	g/plant			g
600	40.57	15.80	58.82	44.35
300	30.67	13.40	57.10	39.38
150	19.71	9.20	44.76	47.24
L.S.D. 5%	1.91	2.75	5.39	9.24

Table 2. Percentage of seeds larger than screen size 7 and embryo weight of McDermid wheat grown under three water regimes.

Water regime	Larger than screen size 7[+]	100-embryo weight
ml/day	%	mg
600	59.19	96.12
300	43.73	87.27
150	79.57	103.47
L.S.D. 5%	13.97	10.59

[+]Percentage of seed held over a 7/64 x 3/4" (2.78 mm x 19.05 mm) screen.

slower in the most stressed plants (Figure 7).

Water stress reduced the number of seeds produced per plant from 944 to 405. Although the stressed plants had less total leaf area to support seed development, there were fewer seeds to compete for the available photosynthate. The net effect was that the seeds on the stressed plants were considerably larger and had larger embryos (Table 2).

The chemical and physiological attributes of the seeds from water stressed plants were also enhanced (Table 3). Seeds from plants watered with 150 ml and 300 ml/day had 5.3 and 3.7% more protein than those watered with 600 ml/day. Seeds from the most stressed plants had lower CO_2 evolution and a lower respiratory quotient. These characteristics are considered indicators of good seed quality (16, 17, 22).

The increased size and protein content of seeds from the stressed plants led to greater seedling vigor of these seeds as measured by longer root length and greater seedling dry weight (Table 4).

Although it is difficult to extrapolate the results of greenhouse trials to field conditions, certain information obtained may have application to commercial seed production. It has been shown previously (13) that lower seed yields are not necessarily related to poorer seed quality. The wheat plant is frequently able to compensate for fewer

Table 3. Protein content, CO_2 evolution (CO_2), and respiratory quotient (RQ) of McDermid wheat seed as affected by three water regimes.

Water regime	Protein content	CO_2	RQ
ml/day	%	µl/seed	
600	13.54	1.43	1.12
300	17.20	1.10	1.10
150	18.82	1.00	0.64
L.S.D. 5%	0.68	0.20	0.17

Table 4. Root length and seedling dry weight of McDermid wheat seed as affected by three water regimes.

Water regime	Root length, days after imbibition				Seedling dry weight
	2	3	4	5	
ml/day		mm			mg/seedling
600	16.4	50.2	89.5	121.2	25.65
300	21.5	58.6	101.2	131.4	24.55
150	24.1	58.9	101.4	132.4	28.22
L.S.D. 5%	4.5	4.9	3.9	6.7	1.21

tillers or fewer seeds per spike by producing larger seeds of good performance potential. Because of the compensation ability of the wheat plant, development of management practices to decrease certain yield components in favor of enhanced seed quality is worthy of further study.

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APPENDICES

Appendix Table 1. Average monthly rainfall and temperature data for Hyslop Farm for 1977/1978 crop year and long term averages.

	Rainfall		Temperature	
	77/78 crop year (mm)	30-year average (mm)	77/78 crop year (°C)	30-year average (°C)
Sept.	90.9	33.3	15.0	16.7
Oct.	65.5	96.1	11.9	11.7
Nov.	205.0	153.4	6.4	7.2
Dec.	280.2	173.5	6.4	5.0
Jan.	186.4	179.3	5.5	3.9
Feb.	108.7	117.6	7.4	6.1
Mar.	54.6	106.7	9.4	7.8
Apr.	125.2	63.5	9.4	10.0
May	91.7	44.9	11.9	13.3
June	23.9	29.2	17.2	16.1
July	7.4	8.4	16.8	18.9
Total	1239.5	1005.9	Average 10.7	10.6

Appendix Table 2. Average monthly rainfall and temperature data for Moro for 1977/1978 crop year and long term averages.

	Rainfall		Temperature	
	77/78 crop year (mm)	10-year average (mm)	77/78 crop year (°C)	10-year average
Sept.	20.3	10.4	13.9	15.0
Oct.	5.6	19.8	9.7	9.4
Nov.	50.8	46.2	3.8	4.4
Dec.	81.8	49.3	1.9	0.5
Jan.	71.1	36.6	0.9	0.0
Feb.	33.3	23.1	3.6	3.3
Mar.	18.8	20.6	7.5	5.0
Apr.	36.1	19.1	8.3	7.8
May	10.9	16.8	9.4	11.7
June	11.2	14.5	16.3	16.7
July	11.9	3.3	16.5	20.0
Total	353.8	259.7	Average 8.3	8.5

Appendix Table 3. Growth stage of McDermid wheat, according to Zadoks' decimal code, Corvallis, Oregon.

Sampling date	Zadoks' decimal code	Description of plants
March 27	15, 28, 31	Five leaves unfolded on main shoot, 8 tillers; 1 node.
April 8	16, 28, 32	Six leaves unfolded on main shoot; 8 tillers; 2 nodes.
April 24	15, 28, 33	Five leaves unfolded on main shoot; 8 tillers; 3 nodes.
May 7	15, 28, 33	Five leaves unfolded on main shoot; 8 tillers; 3 nodes.
May 20	35, 58	Five nodes; emergence of inflorescence completed.

Appendix Table 4. Growth stages of McDermid wheat, according to Zadoks' decimal code, as influenced by planting date, Moro, Oregon.

Planting date	Sampling date	Zadoks' decimal code	Description of plants
	March 23	18, 29, 30	Eight leaves unfolded on main shoot; 9 tillers; pseudostem erection.
	April 7	15, 29, 31	Five leaves unfolded on main shoot; 9 tillers; 1 node.
September 1	April 21	15, 29, 32	Five leaves unfolded on main shoot; 9 tillers; 2 nodes.
	May 5	15, 29, 33	Five leaves unfolded on main shoot; 9 tillers; 3 nodes.
	May 24	34, 58	4 nodes; emergence of inflorescence completed
	March 23	14, 23	Four leaves unfolded on main shoot; 3 tillers.
	April 7	15, 24	Five leaves unfolded on main shoot; 4 tillers.
September 30	April 21	15, 28, 31	Five leaves unfolded on main shoot; 8 tillers; 1 node.
	May 5	15, 29, 32	Five leaves unfolded on main shoot; 9 tillers; 2 nodes.
	May 24	34, 49	Four nodes; first awns visible.
	March 23	13, 20	Three leaves unfolded on main shoot; no tillers.
	April 7	14, 22	Four leaves unfolded on main shoot; 2 tillers.
October 27	April 21	14, 23	Four leaves unfolded on main shoot; 3 tillers.
	May 5	14, 24, 30	Four leaves unfolded on main shoot; 4 tillers; pseudostem erection.
	May 24	15, 29, 32	Five leaves unfolded on main shoot; 9 tillers; 2 nodes.

Appendix Table 5. Days for total leaf senescence of McDermid wheat as affected by location and planting date.

Location	Planting date	Time to senescence	
		after planting	after anthesis
		days	days
Corvallis	October 20	245-248	25-28
Moro	September 1	282-285	13-16
	September 30	262-265	15-18
	October 27	242-245	20-23

Appendix Table 6. Analyses of variance of yield and components of yield of McDermid wheat, Moro, Oregon.

Source of variation	Degrees of freedom	Mean squares	F-value
			Yield
Planting date	2	3021430.0	59.83**
Replications	2	22950.8	
Error	4	50497.6	
Total	8		
			Spikes/m^2
Planting date	2	13391.8	3.10^{ns}
Replications	2	8851.9	
Error	4	4315.5	
Total	8		
			Seeds/spike
Planting date	2	265.15	150.08**
Replications	2	2.60	
Error	4	22.52	
Total	8		
			1000-seed weight
Planting date	2	30.37	4.02^{ns}
Replications	2	5.70	
Error	4	7.56	
Total	8		

**Significant at the 1% level.

^{ns}Not significant.

Appendix Table 7. Analyses of variance of 100-embryo weight and percentage of seeds larger than screen size 7 of McDermid wheat, Moro and Corvallis.

Source of variation	Degrees of freedom	Mean of squares	F-value
			100-embryo weight
Lots	3	119.69	10.43**
Error	8	11.48	
Total	11		
			Larger than screen 7
Lots	3	492.89	70.97**
Error	8	6.94	
Total	11		

**Significant at the 1% level.

Appendix Table 8. Analyses of variance of protein content of McDermid wheat seed, Moro and Corvallis.

Source of variation	Degrees of freedom	Mean of squares	F-value
Lots	3	2.18	8.05**
Error	8	0.27	
Total	11		

**Significant at the 1% level.

Appendix Table 9. Analyses of variance of seedling and shoot dry weight of McDermid wheat, Moro and Corvallis.

Source of variation	Degrees of freedom	Mean squares	F-value
			Seedling dry weight
Lots	3	20.30	21.59**
Error	8	0.94	
Total	11		
			Shoot dry weight
Lots	3	11.01	78.64**
Error	8	0.14	
Total	11		

**Significant at the 1% level.

Appendix Table 10. Analyses of variance of CO_2 evolution and respiratory quotient of McDermid wheat seed, Moro and Corvallis.

Source of variation	Degrees of freedom	Mean squares	F-value
			CO_2 evolution
Lots	3	0.305	13.26**
Error	8	0.023	
Total	11		
			RQ
Lots	3	0.03046	31.40**
Error	8	0.00097	
Total	11		

**Significant at the 1% level.

Appendix Table 11. Analyses of variance of glutamic acid decarboxylase activity of McDermid wheat seed, Moro and Corvallis.

Source of variation	Degrees of freedom	Mean squares	F-value
Lots	3	80.36	64.29**
Error	8	1.25	
Total	11		

**Significant at the 1% level.

Appendix Table 12. Simple correlation coefficients between soil water potential, leaf area index, specific leaf weight and yield and components of yield of McDermid wheat, Moro, Oregon, 1978.

Measurements	Sampling date	Yield	Spikes per m^2	Seeds per spike	1000-seed weight
Soil water potential	May 5	n. s.	.666*	n. s.	n. s.
	May 24	-.742*	n. s.	-.947**	-.795*
	June 8	-.692*	n. s.	-.901**	-.794*
	June 20	-.825**	n. s.	-.907**	n. s.
	June 30	n. s.	n. s.	n. s.	n. s.
Leaf area index	March 23	-.826**	n. s.	-.976**	-.713*
	April 7	-.821**	n. s.	-.980**	-.731*
	April 21	n. s.	n. s.	n. s.	-.681*
	May 5	n. s.	n. s.	n. s.	n. s.
	May 24	.817**	n. s.	n. s.	n. s.
	June 8	.708*	n. s.	.918**	.679*
Specific leaf weight	March 23	-.810**	-.694*	n. s.	n. s.
	April 7	n. s.	n. s.	n. s.	n. s.
	April 21	n. s.	n. s.	n. s.	n. s.
	May 5	-.693*	-.689*	n. s.	n. s.
	May 24	-.769*	n. s.	-.795*	n. s.
	June 8	n. s.	-.821**	n. s.	n. s.

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 13. Simple correlation coefficients between soil water potential, leaf area index, specific leaf weight and 100-embryo weight and percentage of seeds over screen 7 of McDermid wheat, Moro, Oregon, 1978.

Measurements	Sampling date	100-embryo weight	% Seeds over screen 7
Soil water potential	May 5	-.679*	n. s.
	May 24	-.732*	-.911**
	June 8	n. s.	-.818**
	June 20	n. s.	-.933**
	June 30	n. s.	n. s.
Leaf area index	March 23	-.783*	-.934**
	April 7	-.804**	-.975**
	April 21	-.906**	-.746*
	May 5	-.878**	n. s.
	May 24	n. s.	n. s.
	June 8	.828**	.922**
Specific leaf weight	March 23	n. s.	n. s.
	April 7	n. s.	n. s.
	April 21	n. s.	n. s.
	May 5	n. s.	n. s.
	May 24	n. s.	-.728*
	June 8	-.712*	-.797*

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 14. Simple correlation coefficients between soil water potential, leaf area index, specific leaf weight, and seedling and shoot dry weight of McDermid wheat, Moro, Oregon, 1978.

Measurements	Sampling date	Seedling dry weight	Shoot dry weight
Soil water potential	May 5	n. s.	-.697*
	May 24	-.931**	n. s.
	June 8	-.927**	n. s.
	June 20	-.806**	n. s.
	June 30	n. s.	n. s.
Leaf area index	March 23	-.900**	-.693*
	April 7	-.891**	-.735*
	April 21	-.827**	-.934**
	May 5	n. s.	-.900**
	May 24	n. s.	n. s.
	June 8	.881**	.804**
Specific leaf weight	March 23	n. s.	n. s.
	April 7	n. s.	n. s.
	April 21	n. s.	n. s.
	May 5	n. s.	n. s.
	May 24	n. s.	n. s.
	June 8	n. s.	n. s.

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 15. Simple correlation coefficients between soil water potential, leaf area index, specific leaf weight, and glutamic acid decarboxylase activity (GADA), CO_2 evolution, and respiratory quotient of McDermid wheat, Moro, Oregon, 1978.

Measurements	Sampling date	GADA	CO_2 evolution	Respiratory quotient
Soil water potential	May 5	n. s.	n. s.	n. s.
	May 24	-.876**	n. s.	n. s.
	June 8	-.922**	n. s.	n. s.
	June 20	-.866**	n. s.	n. s.
	June 30	n. s.	n. s.	n. s.
Leaf area index	March 23	-.928**	n. s.	n. s.
	April 7	-.924**	n. s.	n. s.
	April 21	n. s.	n. s.	n. s.
	May 5	n. s.	n. s.	n. s.
	May 24	n. s.	n. s.	-.732*
	June 8	.871**	n. s.	n. s.
Specific leaf weight	March 23	n. s.	n. s.	.909**
	April 7	n. s.	n. s.	n. s.
	April 21	n. s.	n. s.	n. s.
	May 5	-.791*	n. s.	n. s.
	June 8	-.669*	.714*	n. s.

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 16. Simple correlation coefficients between water soluble carbohydrates of plant parts and yield and components of yield of McDermid wheat, Moro, Oregon, 1978.

Water soluble carbohydrates of:	Sampling date	Yield	Spikes per m^2	Seeds per spike	1000-seed weight
Leaf	April 21	-.952**	n. s.	-.886**	n. s.
	May 5	-.959**	n. s.	-.949**	n. s.
	May 24	-.921**	n. s.	-.965**	n. s.
	June 8	-.921**	n. s.	-.928**	n. s.
Stem	April 21	-.951**	n. s.	-.963**	n. s.
	May 5	n. s.	n. s.	n. s.	-.743*
	May 24	-.723*	n. s.	-.862**	n. s.
	June 8	n. s.	n. s.	-.761*	n. s.
	June 20	n. s.	n. s.	n. s.	.704*
	June 30	n. s.	-.750*	n. s.	n. s.
	July 11	-.926**	n. s.	-.814**	n. s.
Seed	June 8	.910**	n. s.	.764*	n. s.
	June 20	n. s.	n. s.	n. s.	.743*
	June 30	n. s.	n. s.	.672*	.731*
	July 11	.752*	n. s.	n. s.	n. s.
Rachis	June 8	-.808**	n. s.	-.961**	-.804**
	June 20	n. s.	n. s.	n. s.	n. s.
	June 30	-.933**	n. s.	-.882**	n. s.
	July 11	-.827**	n. s.	-.888**	n. s.
Awn+bracts	June 8	-.855**	n. s.	-.725*	n. s.
	June 20	n. s.	n. s.	n. s.	n. s.
	June 30	-.946**	n. s.	-.925**	n. s.
	July 11	-.718*	n. s.	-.932**	n. s.

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 17. Simple correlation coefficients between water soluble carbohydrates of plant parts and 100-embryo weight and percentage of seeds over screen 7 of McDermid wheat, Moro, Oregon, 1978.

Water soluble carbohydrates of:	Sampling date	100-embryo weight	% seeds over screen 7
Leaf	April 21	n. s.	-.855**
	May 5	n. s.	-.917**
	May 24	n. s.	-.932**
	June 8	n. s.	-.901**
Stem	April 21	-.793*	-.960**
	May 5	-.874**	-.889**
	May 24	-.777*	-.842**
	June 8	-.831**	-.787*
	June 20	n. s.	.801**
	June 30	.780*	n. s.
	July 11	n. s.	-.744*
Seed	June 8	n. s.	.734*
	June 20	.874**	.881**
	June 30	.932**	.832**
	July 11	n. s.	n. s.
Rachis	June 8	-.721*	-.907**
	June 20	.666*	n. s.
	June 30	n. s.	-.827**
	July 11	-.744*	-.920**
Awn+Bracts	June 8	n. s.	n. s.
	June 20	n. s.	n. s.
	June 30	n. s.	n. s.
	July 11	n. s.	n. s.

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 18. Simple correlation coefficients between water soluble carbohydrates of plant parts and seedling and shoot dry weight of McDermid wheat, Moro, Oregon, 1978.

Water soluble carbohydrates of:	Sampling date	Seedling dry weight	Shoot dry weight
Leaf	April 21	-.699*	n. s.
	May 5	-.711*	n. s.
	May 24	-.760*	n. s.
	June 8	n. s.	n. s.
Stem	April 21	-.859**	n. s.
	May 5	-.922**	-.900**
	May 24	-.824**	-.902**
	June 8	-.831**	-.917**
	June 20	.740*	n. s.
	June 30	n. s.	.860**
	July 11	n. s.	n. s.
Seed	June 8	n. s.	n. s.
	June 20	.898**	.899**
	June 30	.891**	.887**
	July 11	-.849**	n. s.
Rachis	June 8	-.802**	-.716*
	June 20	n. s.	n. s.
	June 30	n. s.	n. s.
	July 11	-.736*	n. s.
Awn+bracts	June 8	n. s.	n. s.
	June 20	n. s.	n. s.
	June 30	n. s.	n. s.
	July 11	n. s.	n. s.

*, **Significant at the 5 and 1% level, respectively.

Appendix Table 19. Simple correlation coefficients between water soluble carbohydrates of plant parts and glutamic acid decarboxylase activity (GADA), CO_2 evolution (CO_2), and respiratory quotient (RQ) of McDermid wheat, Moro, Oregon, 1978.

Water soluble carbohydrates of:	Sampling date	GADA	CO_2	RQ
Leaf	April 21	-.904**	n. s.	.697*
	May 5	-.918**	n. s.	.710*
	May 24	-.956**	n. s.	n. s.
	June 8	-.868**	n. s.	.743*
Stem	April 21	-.892**	n. s.	n. s.
	May 5	-.815**	n. s.	n. s.
	May 24	-.834**	n. s.	n. s.
	June 8	-.577*	n. s.	n. s.
	June 20	.952**	n. s.	n. s.
	June 30	n. s.	n. s.	n. s.
	July 11	-.864**	n. s.	.801**
Seed	June 8	.764*	n. s.	-.802**
	June 20	.800**	n. s.	n. s.
	June 30	.728*	n. s.	n. s.
	July 11	n. s.	n. s.	-.716*
Rachis	June 8	-.902**	n. s.	n. s.
	June 20	n. s.	n. s.	n. s.
	June 30	-.866**	n. s.	.798**
	July 11	-.806**	n. s.	n. s.
Awn+bracts	June 8	-.725*	n. s.	.792*
	June 20	n. s.	n. s.	n. s.
	June 30	-.920**	n. s.	.715*
	July 11	-.865**	n. s.	n. s.

*, **Significant at the 5 and 1% levels, respectively.

Appendix Table 20. Analysis of variance of soil water potential in pots of McDermid wheat grown under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
Replications	4	0.424	
Water regime (WR)	2	89.822	273.14**
Sampling date (SD)	3	51.636	157.02**
WRxSD	6	13.617	41.41**
Error	44	0.329	
Total	59		

** Significant at the 1% level.

Appendix Table 21. Analyses of variance of leaf area of McDermid wheat grown under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
Replications	4	39698.4	
Water regime (WR)	2	2212730.0	349.13**
Sampling date (SD)	3	2327420.0	367.22**
WR x SD	6	262366.0	41.39**
Error	44	6337.9	
Total	59		

**Significant at the 1% level.

Appendix Table 22. Analyses of variance of number of leaves and percentage of green leaves of McDermid wheat grown under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
			Number of leaves
Replications	4	481.97	
Water regime (WR)	2	419.02	1.69[ns]
Sampling date (SD)	3	16.58	
WR x SD	6	310.13	
Error	44	248.53	
Total	59		
			Percentage of green leaves
Replications	4	124.13	
Water regime (WR)	2	1940.69	80.58**
Sampling date (SD)	3	4163.48	172.87**
WR x SD	6	221.71	9.20**
Error	44	24.08	
Total	59		

**Significant at the 1% level.

[ns]Not significant.

Appendix Table 23. Analyses of variance of green leaf dry weight and specific leaf weight of McDermid wheat grown under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
			Green leaf dry weight
Replications	4	0.58	
Water regime (WR)	2	25.27	103.71**
Sampling date (SD)	3	74.34	305.04**
WR x SD	6	1.82	7.46**
Error	44	0.24	
Total	59		
			Specific leaf weight
Replications	4	0.25	
Water regime (WR)	2	14.10	49.00**
Sampling date (SD)	3	3.61	12.56**
WR x SD	6	1.76	6.11**
Error	44	0.29	
Total	59		

**Significant at the 1% level.

Appendix Table 24. Analyses of variance of yield and components of yield of McDermit wheat grown under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
			Yield
Replications	4	20.03	1.16
Water regime	2	70.09	40.72**
Error	8	1.72	
Total	14		
			Spikes/plant
Replications	4	5.10	1.44
Water regime	2	55.80	15.72**
Error	8	3.55	
Total	14		
			Seeds/spike
Replications	4	73.40	5.36
Water regime	2	336.31	24.57**
Error	8	13.68	
Total	14		
			1000-seed weight
Replications	4	4.72	0.26
Water regime	2	79.13	4.32^{ns}
Error	8	18.30	
Total	14		

**Significant at the 1% level.

^{ns}Not significant.

Appendix Table 25. Analyses of variance of percentage of seeds larger than screen size 7, and 100-embryo weight of McDermid wheat seed produced under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
			Larger than screen 7
Water regime	2	129.24	16.94**
Error	9	7.63	
Total	11		
			100-embryo weight
Water regime	2	263.19	6.00*
Error	9	43.83	
Total	11		

*, **Significant at the 5% and 1% levels, respectively.

Appendix Table 26. Analyses of variance of protein content of McDermid wheat seed produced under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
Water regime	2	14.6558	315.74**
Error	3	0.0464	
Total	5		

**Significant at the 1% level.

Appendix Table 27. Analyses of variance of root length of McDermid wheat seedlings from seeds produced under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
			2 days after imbibition
Water regime	2	38.06	4.77*
Error	9	7.98	
Total	11		
			3 days after imbibition
Water regime	2	38.03	10.59**
Error	9	9.26	
Total	11		
			4 days after imbibition
Water regime	2	184.46	30.19**
Error	9	6.11	
Total	11		
			6 days after imbibition
Water regime	2	152.49	8.69**
Error	9	17.54	
Total	11		

*, **Significant at the 5% and 1% levels, respectively.

Appendix Table 28. Analyses of variance of seedling dry weight of McDermid wheat from seeds produced under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
Water regime	2	10.652	29.10**
Error	6	0.366	
Total	8		

**Significant at the 1% level.

Appendix Table 29. Analyses of variance of CO_2 evolution (CO_2) respiratory quotient (RQ) of McDermid wheat seed produced under three water regimes.

Source of variation	Degrees of freedom	Mean squares	F-value
			CO_2
Water regime	2	0.15860	40.98**
Error	3	0.00387	
Total	5		
			RQ
Water regime	2	0.14747	49.32**
Error	3	0.00299	
Total	5		

**Significant at the 1% level.

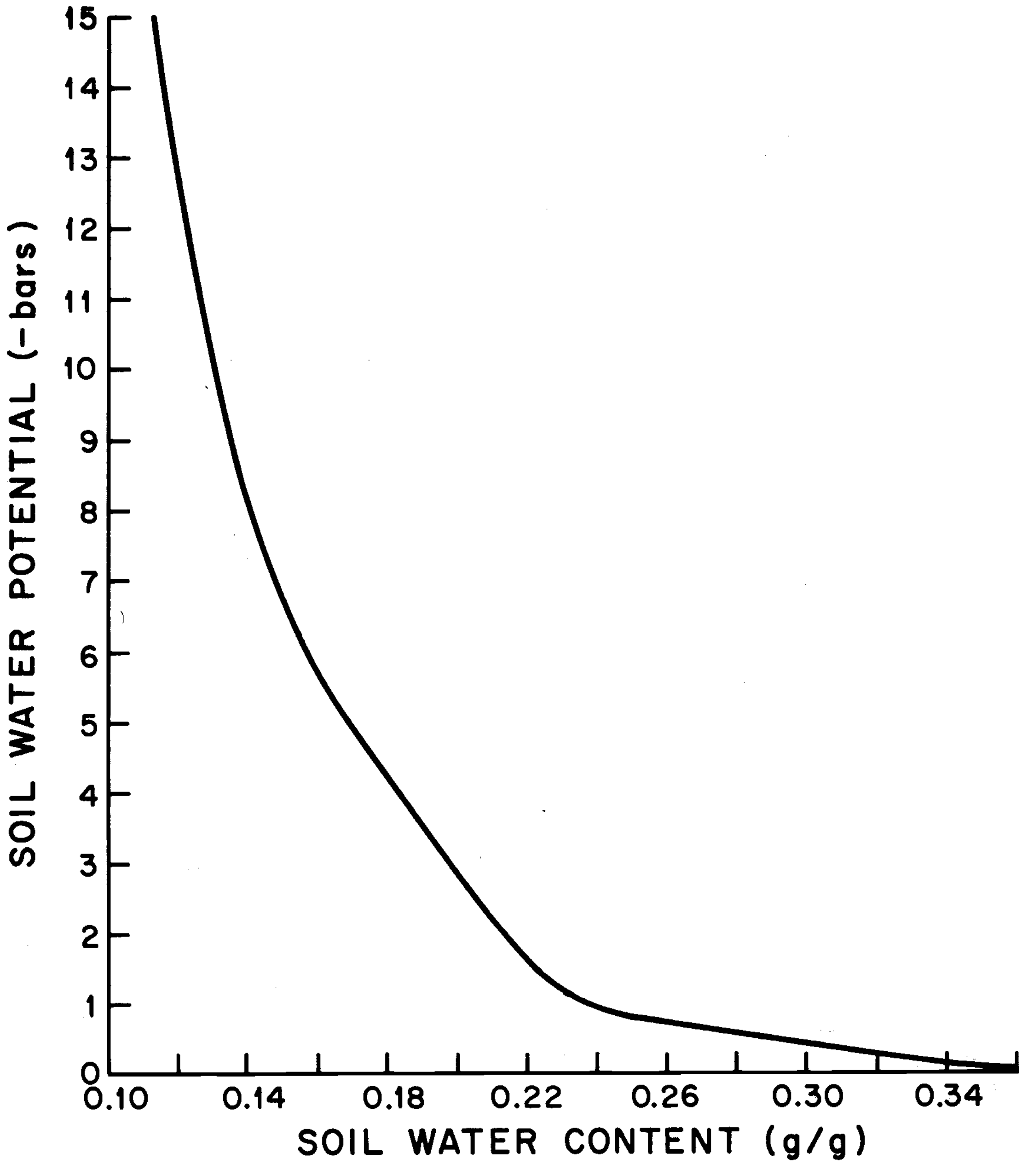

Figure 1. Soil moisture tension curve for a Woodburn silt clay loam soil. Hyslop Farm, Corvallis, Oregon.

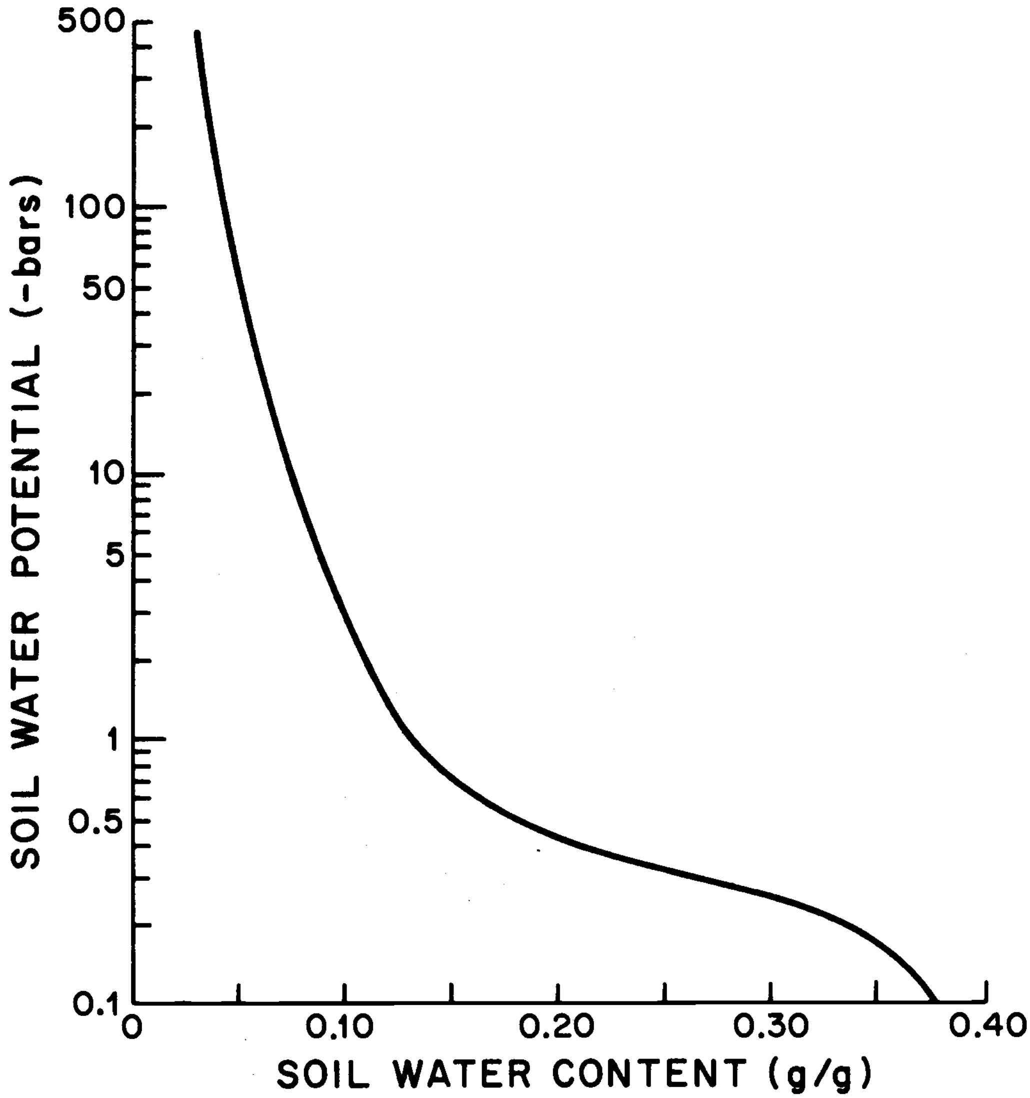

Figure 2. Soil moisture tension curve for a Walla Walla silt loam soil. Moro, Oregon.

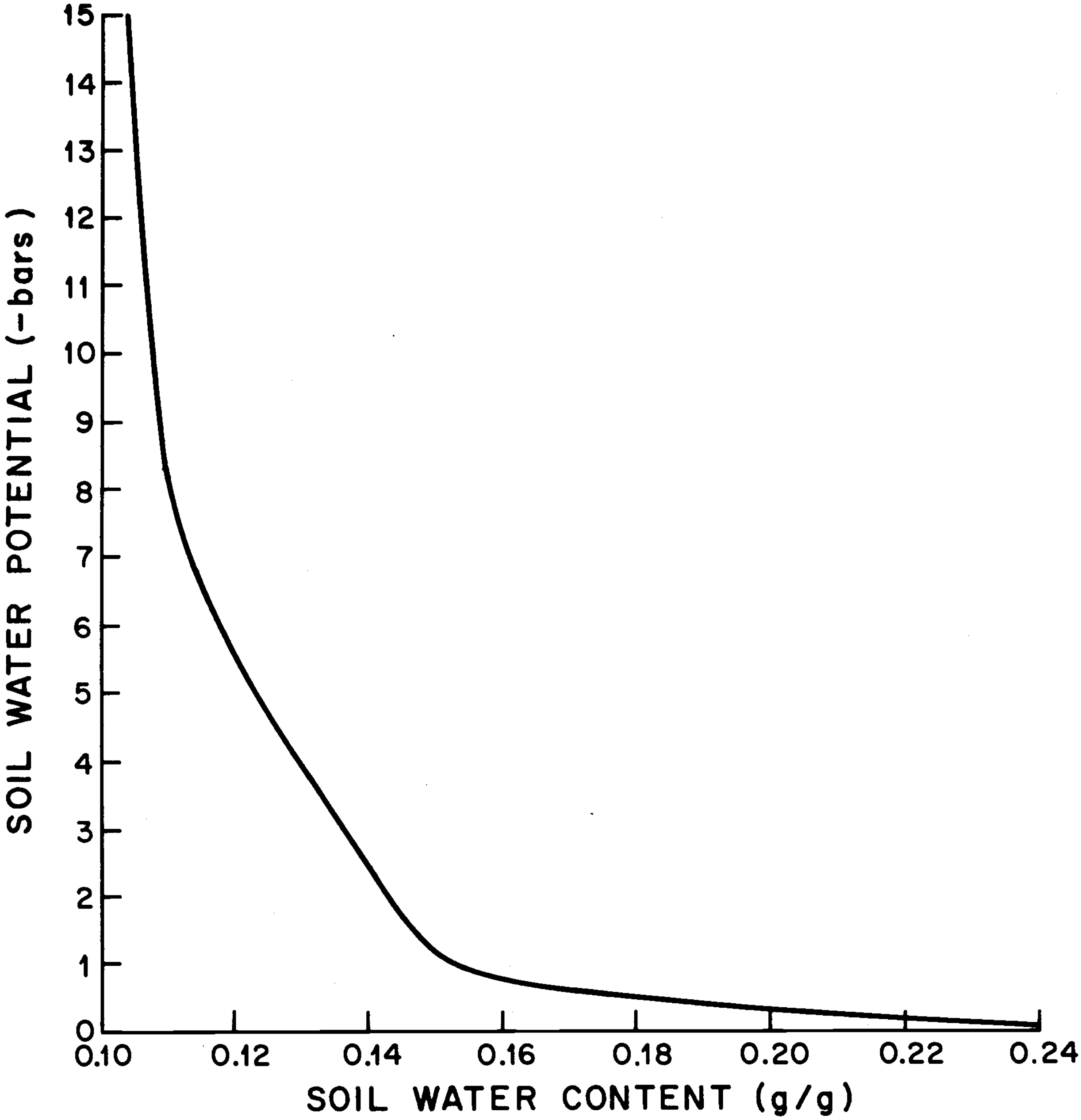

Figure 3. Soil moisture tension curve for a soil-peat moss mixture containing 4 parts soil to 1 part peat moss by volume.