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Title: ADAPTABILITY OF WINTER WHEAT CULTIVARS TO DRYLAND CONDITIONS AND THEIR RESPONSE TO WATER STRESS

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Winter wheat cultivars (Triticum aestivum) were evaluated for their response to water stress and adaptability to a wide range of moisture limited environments. Grain yield was analyzed for ten cultivars at six locations across four years. Regression of the cultivar mean on the year-location mean was used as a measure of the environmental response of a particular cultivar. Plant water status (leaf osmotic potential and water potential) during the grain filling period, along with grain yield and yield components were determined at three locations for fifteen cultivars under space-planted conditions in 1972 and for ten cultivars under solid-seeding in 1973. Five cultivars were evaluated for plant water status and rates of growth during reproductive development and for final grain yield and yield components at a severely stressed location in 1973.

Drought resistance, described as yielding ability under severe soil moisture stress, was found to be the result of avoidance, tolerance and escape characteristics. Plant water status influenced the components of yield when their development occurred during a period of high external stress. However, the relative importance of plant water status to final yield varied depending on the magnitude of the direct effect of spike number on yield. Drought avoidance was the ability to maintain a high plant water status when under high external stress conditions. In the cultivar Yamhill, the stable growth rate during inflorescence development and the extended period of grain filling may have resulted from the ability of this cultivar to avoid drought. These characteristics, also, may explain the large spikelet number and the high kernel weight of Yamhill. Even though Hyslop and Wanser had a moderate and high internal water stress, respectively, they were relatively tolerant of stress in terms of high growth rates during the grain filling period. The high yielding ability of Wanser and McDermid under high stress conditions was primarily related to a large number of spikes. This trait was considered an escape characteristic because tillering was established before the onset of severe stress. The club wheats neither avoided or tolerated internal water stress under solid-seeded conditions nor did they have sufficient tillering capacity to compensate for the effect of stress on the later-developed components.of yield. Nugaines, Hyslop and Rew maintained a moderate internal stress during later development but differed in their yield component responses. The yield of Nugaines depended primarily on a high tillering capacity, whereas the yield of Hyslop and Rew depended on a balance of contributions from all the components of yield.

Widely adapted cultivars, such as Hyslop and McDermid, not only yielded well under severe stress conditions but had the genetic potential to respond adequately to more favorable moisture conditions. Cultivars specifically, adapted to lower yielding environments, such as Yamhill and Wanser, were able to avoid, tolerate or escape drought but were limited in one or more of their yield component responses to better conditions. Conversely, cultivars specifically adapted to high yielding environments, such as Nugaines and Paha, lacked the ability to consistently yield well under high stress environments but had a high response to more favorable moisture conditions.

Cultivars best adapted to dryland cultivation should have the highest yield under stress conditions as expressed through the components of yield by one or a combination of avoidance, tolerance or escape characteristics. These cultivars should also have the maximum expression in, and balance among, the components of yield for maximum response to more favorable moisture conditions. This goal may be obtained by selection in favorable as well as stressed environments and by testing throughout the range of the environments where the cultivar is expected to be grown. Because high yield under stress was found in this study to be manifested through different characteristics of the plant the breeder should be aware of traits which may contribute to drought resistance, but he should not be restricted to a particular ideotype when breeding for yield under conditions of high moisture stress.

Adaptability of Winter Wheat Cultivars to Dryland Conditions and Their Response to Water Stress

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ADAPTABILITY OF WINTER WHEAT CULTIVARS TO DRYLAND CONDITIONS AND THEIR RESPONSE TO WATER STRESS

I. INTRODUCTION

The major wheat-producing areas of the world are located in semi-arid regions. Available moisture is a major yield-limiting factor in these areas. Large seasonal variations in the amount and distribution of rainfall are characteristic of many of these regions, and drought is frequently a problem. In the dryland wheat-growing areas of the Pacific Northwest, the crop is dependent primarily on stored soil moisture from rainfall during the fallow period and the fall and winter months of the crop year. Little additional moisture is available after the vegetative stage of growth in the early spring. Grain yields are relatively high in the Pacific Northwest in comparison with other dryland wheat growing regions of the world. The variability of rainfall over the region and from season to season causes wide variation in grain yields. In the shallow soil areas, grain yields are frequently restricted because of the early depletion of moisture reserves.

Much of the effort to improve dryland wheat yields has been directed toward cultural practices which increase the amount of soil moisture available to the crop. More recently, breeding efforts have caused dramatic increases in wheat yields in the irrigated and high rainfall areas of the Pacific Northwest. However, under the more severely stressed conditions grain yields of the new cultivars have yielded generally the same and, in some instances, lower than the previously developed cultivars. Because of the variability in moisture conditions, the need to develop drought resistant cultivars which also yield well over a wide range of moisture conditions is apparent. However, there is little understanding of the relationship between wide adaptability and drought resistance. Drought resistance is described in terms of yielding capacity under severe soil moisture stress, whereas adaptability is evaluated in terms of ability to yield well throughout the range of environmental conditions in which the crop is grown.

Much research has been conducted on the effect of water stress on growth and development and the metabolic processes in plants. Much of the knowledge derived from these studies is unclear and contradictory. A major reason for this inadequate understanding is the failure of many workers to assess adequately the degree of stress imposed in their experiments. Contributions to the concept of plant water status along with recent development in techniques and equipment to rapidly and accurately measure this trait has enabled workers to overcome this problem. Measurement of plant water status is now recognized as an essential component of all research concerned with water relations in plants.

Although considerable research had been conducted on the physiology of drought resistance in cereals, little use of this has been made in the breeding for drought resistance. A partial explanation for this is the failure of investigators to recognize the complex nature of drought resistance. Much of the research represented attempts to find some simple index of measuring drought resistance by means of a number of easily identifiable physiological or morphological traits. Another problem has been the failure to evaluate adequately the degree of drought resistance in the genotypes used in the experiments.

An understanding of how drought resistance and dryland adaptability is expressed in the plant would be useful to the breeder by enabling him to identify genotypes for use in crossing with other parents. A knowledge of developmental and morphological traits which contribute to drought resistance, as well as adaptability, would enable the establishment of an efficient selection procedure for use in segregating generations. A knowledge of field drought resistance would also provide a basis for studying the physiological nature of drought resistance in the genotypes being considered.

The purpose of this study was to characterize the phenotypic expression of drought resistance and assess the adapatability of winter wheat cultivars to dryland conditions. This was accomplished by the assessment of (1) the yield response of cultivars to a wide range of moisture-limiting environments and (2) the response of cultivars to water stress in terms of plant water status, growth and development, the components of yield, and final grain yield.

II. LITERATURE REVIEW

Types of Drought Resistance

Drought resistance consists of many complex mechanisms and interactions. Failure to recognize this has led to the lack of success for some of the earliest workers in establishing a sound physiological basis for drought resistance in plants (Aadmodt and Johnson, 1936). Maximov (1929) was one of the early workers to recognize the complexity of the situation. He developed a water balance concept which takes into consideration the absorption of water by plant roots and the transpiration or loss of water from the plant shoot. This enabled him to develop a concept of xeromorphic structure and to acertain the morphological, anatomical, and physiological traits which help to determine the degree of drought resistance. Because drought resistance is relative, certain mesophytes appear to have xerophytic traits and can be considered drought resistant in relation to other mesophytic species and even to genotypes within the same species.

The complexity of the problem necessitates one to first measure drought response in terms of avoidance and tolerance mechanisms. Levitt (1972) classifies drought avoiders into: (1) the water savers, which avoid drought by water conservation, and (2) the water spenders, which avoid drought by absorbing water rapidly enough to keep up with extremely rapid water loss. Both types of adaptation enable the plant to keep a high water status in relation to stresses imposed by the environment. Ephemerals or drought escapers, have mechanisms, such as earliness of maturity, which enable them to escape water stress in part or entirely.

Drought avoidance mechanisms are largely anatomical in nature, although this type of resistance develops due to stress effects on physiological processes (Levitt, 1972). The water savers restrict transpiration long before wilting occurs. This can be related to action of stomata and to cuticle formation on the shoot structure. Water spenders, by use of their extensive root system, absorb sufficient soil moisture to allow higher transpiration rates without causing stress in the plant. As a result they are more able to keep their stomata open through the day which permits more photosynthetic production due to increased CO_2 exchange.

Drought or desiccation tolerance is considered to be the ability of the protoplasm to survive serious reduction in water content (Parker, 1972). This protoplasmic resistance has been the focal point for much of the drought resistance research in the past 40 years. In determining dessication tolerance, the amount of dessication and the effect on the plant must be measured. Tolerance to dessication has some relation to heat and cold tolerance, although this cannot be precisely equated.

One type of drought tolerance is described as dehydration tolerance in which the metabolic functions are relatively unaffected under conditions of internal stress. Drought tolerance can also take the form of avoidance of turgor loss under stress by the accumulation of sufficient cell solutes. With plant turgor maintained in spite of water stress, cell division and enlargement can continue. This mechanism has been proposed to be the cause of drought resistance in certain wheat cultivars which were adapted to dry conditions (Aadmodt and Johnson, 1936; Walter, 1955).

Where late rains may occur during the growing season, drought tolerance, as it affects survival through a drought period, may mean the difference in whether some crop is produced or a total crop failure occurs (Sullivan, 1971). But drought avoidance may be more important in dry climates where the crop relies almost entirely on the stored soil moisture available at the beginning of the growing season.

Concept and Measurement of Plant Water Status

Because water is the medium in which all metabolic processes are carried out, a change in plant water status would be expected to affect these processes and ultimately total crop production. Much of the inconclusive and contradictory research on the relationships of plant growth, crop yields, and soil moisture has occurred because attention has been centered on only one part of the soil-plant water system (Kramer, 1963). Too much emphasis has been placed on soil moisture stress and too little on plant water status through which soil moisture has only an indirect effect on plant processes. Plant water status takes into consideration soil moisture stress as well as the plant's response to atmospheric conditions. Plant water status would probably be more related to crop yields (Kramer, 1963). Before we can understand the progress that has been or will be made by plant breeding, it is absolutely necessary that plant water stress be measured directly in all future drought research (Sullivan, 1971). Only when plant response to drought stress in numerous situations and environments is understood, will greater progress be expected.

Plant water status is a highly dynamic character influenced by soil, plant, and atmospheric conditions which make it difficult to control experimentally. Two basic measurements, water content and chemical activity, have been used to determine plant water status.

The oldest method used, water content as a percentage of dry or fresh weight, is meaningless by itself because it does not indicate the degree of stress and it may change due to changes in dry weight. However, it has some use in comparisons between plants, cultivars, and times of day when compared on leaves or tissues of the same age (Barrs, 1968).

Relative water content or relative turgidity assesses the degree of plant stress because it relates water content in the tissue to what it would be at full turgidity. It has been widely used as a measurement of plant water stress. However, like water content, errors arise due to changes in dry weight, and therefore it changes in relative meaning with plant age, tissue, season, species, and other factors.

The chemical activity of water expressed as water potential (ψ) and osmotic potential ($\psi\pi$) are direct measures of the plant and cell water status. Water potential as expressed in bars or atmospheres of pressure is either zero at full turgidity or negative under conditions of stress. This is a measure of the total water activity of the plant tissue. Osmotic potential or "hydrature" is a measure of the vapor pressure of the cytoplasm or vacuole as compared to that of free water at a given temperature (Walter 1955). This is controlled by the solute concentration in the cell sap. The relationship of water potential and osmotic potential are given in the following equation:

$$\psi = \psi\pi + \psi p$$

where ψp, the pressure potential, is a measure of the cell turgidity. Another component, matric potential (ψm) is a measure of the degree of water-binding to the surfaces of cell colloids. This value is negligible, except in very dry tissue or in cells with small vacuoles and is usually disregarded. At full turgidity, $\psi\pi = \psi p$, and $\psi = 0$. When the transpiration rate of the shoot exceeds the rate of water absorption by the roots, a net loss of water in the plant occurs, causing a tension ($\psi p < 0$) in the xylem. As ψ decreases with increasing tension, $\psi\pi$ also decreases due to a higher concentration of cell solutes.

Realization that water flow is primarily along water potential gradients, gave lie to an earlier held belief that a plant can have a low $\psi\pi$ without suffering from water stress (Barrs, 1968). Osmotic potential decreases more slowly than ψ with dehydration, and in this sense, it is a less sensitive measure of plant water stress. Low ψ and ψp appear to have a direct effect on cell growth, whereas a low $\psi\pi$ may have a direct effect on injury to the protoplasm (Parker, 1972). Thus, assessment of plant water status takes on a different meaning in studying drought tolerance. Theoretically, a situation might exist where a plant has a low $\psi\pi$ which may be detrimental to the protoplasm but show a high ψ. Conversely, in the case of a negative ψp, a situation might exist where an effect on cell growth by a low ψ but may not be detrimental to protoplasmic constituents because of a high $\psi\pi$. This illustrates the need to assess all three components, ψ, $\psi\pi$, and ψp, when studying the effect of stress on plants and the type of drought resistance.

Because both ψ and $\psi\pi$ measure the energy status of the plant's water, they should be closely related to drought avoidance (Levitt, 1972). However, they cannot by themselves be a measure of drought resistance but must be related to the plant's response in terms of the final product.

Techniques used in measuring plant ψ and $\psi\pi$ have been reviewed extensively by Barrs (1968) and Sullivan (1971). Recent wide use has been made of the thermocouple pyschrometer because of its relative accuracy and utility. This instrument utilizes the principle of wet bulb depression or the cooling of one junction of a thermocouple when water evaporates from its surface. The magnitude of the inducted current is related to the humidity within the closed chamber in which the plant tissue is placed. The relative humidity is related to the water potential of the plant tissue or to the $\psi\pi$ of the expressed cell sap. Earlier sample chamber psychrometers had limited field use because of the elaborate instrumentation and the strict temperature control needed to obtain accurate readings. Recently, however, a miniature sample chamber psychrometer in which precise external temperature control is not needed has been shown to be useful in field work (Wiebe, et al., 1970).

The pressure bomb apparatus is used in measurement of xylem water potential. The technique involved directly measures the pressure needed to exude xylem sap from the cut-end portion of a leaf, stem, or root sample. The inverse of this value is regarded as the xylem ψ before the sample was excised from the plant. In many cases, this method has shown good agreement to the psychrometer method, although it cannot be used with all types of samples. This method offers advantages of accuracy, speed, and portability, which are needed in field research (Sojka, et al., 1973; Sullivan, 1971).

The Effect of Water Stress on Physiological Processes

The effect of water stress on physiological processes has been extensively reviewed by recent workers (Slayter, 1969, 1970; Crafts, 1968; Levitt, 1972). Because water stress affects almost all life processes, the integrated effects make study on a specific process very complex. Many effects of water stress on key processes, such as nutrient uptake, carbohydrate and protein metabolism, and translocation of ions and metabolites, are intimately linked with its effects on development (Slayter, 1970).

Transpiration provides an essential function of temperature control and is a necessary corollary of CO_2 absorption and O_2 escape (Crafts, 1968). Without a water potential gradient in the soil-plant-atmosphere system, no transpiration would occur. Except in the case of root pressure, this gradient becomes increasingly negative from the soil, up through the plant, and into the atmosphere. Therefore, all transpiring plants are under a degree of water stress. Diurnal fluctuations in transpiration rate occur when the evaporative demand of the atmosphere changes and the plant responds to these changes.

Stomates are important in regulating transpiration and therefore, to a degree, water stress in the plant. They act as a physical barrier to movement of water vapor out of the leaf. Stomatal number and degree of opening determine the amount of resistance to water movement due to stomatal control. Actual closing can occur during the day under high evaporative demand. The daily duration and degree of opening are important in maintaining the optimal balance between transpiration and CO_2 exchange.

Initiation and differentiation of vegetative and reproductive primordia, and cell enlargement are very sensitive to water stress (Slayter, 1970). Primordia initiation may be stopped upon temporary stress, but the effect is not permanent. Cell division is slowed by stress, but upon relief of stress cell division tends to "catch up" and in some cases, surpass levels of the well-watered controls.

Cell enlargement is sensitive to even slight levels of stress and is one of the first observable signs of water stress. "Catching up" to previous levels of enlargement is largely precluded by the laying down of rigid cell walls. This is the major cause of stunting which is a common symptom of stress. Cell enlargement is related to the turgor (ψp) of the cell, but enlargement may cease well before incipient plasmolysis ($\psi p = 0$) occurs.

The effect of water deficits on cell enlargement is also related to the ultimate source and sink capacity. Total leaf area may be restricted by even the diurnal variation in water stress in plants under irrigation, thus limiting the photosynthetic capacity or source size. The total sink capacity such as grain size and number can be influenced directly or indirectly by water stress. Fisher (1970) found that the major effect of stress on wheat just before ear emergence was directly on grain number per ear rather than through its effect on photosynthetic capacity.

Hastened senescence is the primary effect of water stress on mature plant tissues. Fischer (1970) found that final grain size (kernel weight) in wheat was indirectly affected by the effect of water stress on the photosynthetic area over time (photosynthetic area duration). Stress causes hastened migration of phosphorus and nitrogen from older to younger tissues. Also, the stomata tend to remain closed and become nonfunctional.

The effect of water stress on plant hormones may affect leaf senescence and protein synthesis, as well as stomatal opening and closing (Slayter, 1969; Livine and Vaadia, 1972). Cytokinin production in the shoots and roots is very sensitive to water stress. Smaller amounts of cytokinins translocated to the leaves could cause a higher rate of senescence. The chemical CCC (2-Chloroethyltrimethyl-ammoniumchloride) applied to wheat plants has been shown to increase drought resistance by its positive affect on root growth (Humphries, et al., 1967; Slayter, 1970). This may be due to increased cytokinin production as well as increased water absorption. Higher abscisic acid levels as well as lower cytokinin levels in water stressed plants appear to have an effect on stomatal closing (Livine and Vaadia, 1972).

Water deficit effects on nitrogen metabolism and protein synthesis are related to continued development. Nitrogen reductase activity is higher sensitive to moisture stress and protease activity is increased at higher stress levels. Stutte and Todd (1967) showed that water stress caused a decrease in the large molecular weight protein fraction (> 100,000) and an increase in small molecular weight protein fraction in wheat leaves. Varieties characterized as drought resistant showed less decrease in the large molecular weight protein fraction suggesting that more proteins kept their active quaternary structure and fewer were being broken down into their inactive subunits.

Free amino acids, especially proline, accumulate upon water stress. Free proline may act as a storage compound for carbon and nitrogen when starch and protein synthesis are reduced under stress conditions. Measurement of free proline in stressed barley plants has been proposed as a measure of drought tolerance, where the supposedly drought tolerant varieties have a higher proline accumulation (Singh, _et al._, 1972).

Protein synthesis is also affected by nucleic acid levels. Although DNA content is not affected until severe stress, RNA levels are sensitive to lower stress levels (Slayter, 1970). Stutte and Todd (1968) found that water stress lowered the RNA level and caused an increase in the RNA (G+C)/(A+U) ratio. In the drought resistant wheat, Cheyenne, the RNA ratio was less affected than the non-resistant Ponca variety. Upon water stress, polysome formation also tends to decrease, which could be due to a direct effect or through the effect on m-RNA synthesis (West, 1966).

Water deficits have an indirect effect on photosynthesis. Levels of available CO_2 are reduced because of stomatal closure. Direct effects on the photosynthetic apparatus appear only at relatively high stress levels. Brix (1962), in studying loblolly pine and tomato plants, reported similar decreases in photosynthetic and transpiration rates with transpiration rate quite dependent on the degree of stomatal opening.

Water stress may also affect photosynthesis through its affect on sink size. Under stress, more assimilates were found in wheat leaves, and there was a slower more prolonged movement of nutrients out of them (Slayter, 1970). Barlow (1974) found that a decrease in photosynthesis of a young corn plant with a stress of more than -12 to -13 bars was attributable to nonstomatal as well as stomatal differences. The effect of differential elongation of the young leaf (sink) at mild stress and the accumulation of photosynthates in the expanded leaf (source) indicated an indirect effect of mild stress on photosynthesis through its affect on limiting sink size.

Respiration seems less affected by water stress than photoshythesis. Significant respiration has been detected at quite high stress levels (Brix, 1962). Photorespiration appears to increase with moderate stress. This could be due to an indirect increase in internal temperature caused by stomatal closure (Slayter, 1969).

Sugar utilization and starch hydrolysis appear to decrease and increase, respectively, when water stress occurs. The increase in sugar content has been proposed to be a survival mechanism in the plant by maintaining turgidity by decreasing the solute potential ($\psi\pi$).

Generally, translocation is reduced with increased stress. However, the translocation pathway appears to be capable of functioning efficiently under water stress, and the effects on translocation arise indirectly by the effect of stress on source and sink capacity (Wardlaw, 1967, 1969).

The Effect of Water Stress During Development on Grain Yield and Its Components

The detrimental affect of a given water stress on grain yield varies depending on its duration and the stage of development in which water stress occurs. In grain growing areas, where the crop relies almost completely on stored soil moisture, the degree of stress progressively increases throughout the growing season. Thus, stress effects on succeeding stages of development are compounded to produce the final overall yield reduction. Yield in cereals is made up of components whose development are separated, to some degree, during the ontogeny of the plant. Therefore, the study of stress effects on different stages of development and the yield components determined during these developmental stages would give an insight into total yield reduction caused by water stress. Varietal differences in yield appear, in part, to be due to the differential ability to avoid stress during critical stages of development.

From germination through the vegetative phase, the effect of water stress on yield would be through reduction of the number of tillers per unit area. However, temporary stress during the tillering stage appears to have little affect on yield due to the possible compensatory effects of the later developed components of yield (Wells and Dubetz, 1966). Asana (1961) found that the number of ear-bearing tillers contributed most to grain yield under irrigated conditions, whereas under drought, other components sometimes contributed as much or more to final yield.

Tiller production reaches a maximum around the time of head initiation and from there the number of tillers per unit area are reduced even under well-watered conditions (Gingham, 1970). Late tillering can compensate for tiller loss from early severe drought if it is followed by adequate moisture (Chinoy, 1961). However, excessive and late tillering is considered wasteful of soil moisture because many tillers die or produce few seeds.

Grain yield in cereals is most severely affected by temporary water stress during inflorescence development before anthesis (Day and Intlap, 1970; Fischer, 1970, 1973; Slayter, 1969, 1970; Wells and Dubetz, 1966). The potential grain number per head is determined during this period. Slight stress reduces the rate of spikelet primordia initiation more so than primordia development, but initiation appears to catch up with nonstressed controls if stress is not prolonged. Number of spikelets appears to be determined by the balance between initiation rate and spikelet development (Nichols and May, 1963). Slower initiation and spikelet development could partially explain the effect of prolonged drought in cereals. Floret development in wheat, a character determining the potential number of grains per spikelet, is primarily affected by water stress on the supply of assimilates (source size) and nitrogen uptake (Fischer, 1970; Slayter, 1969). Capacity to produce a high number of florets per spikelet may provide a compensatory mechanism for the effect of early temporary stress on tillering and number of spikelets.

Water stress at anthesis can markedly reduce fertilization and grain set in most cereals, especially in corn. Because water stress occurs in many regions along with hot dry atmospheric drought, this could partly be due to pollen dehydration or more probably to the lack of pollen tube extension because of dehydrated stigmas (Slayter, 1969).

Final kernel weight is affected by pre-flowering and, more importantly, post-flowering water stress (Asana, 1961; Fischer, 1970). Fischer (1970) noted that a major determinant of kernel weight is the source-sink ratio, which is determined by the following formula.

$$\text{Source-sink ratio} = \frac{\text{photosynthetic area duration}}{\text{grains per head}}$$

Pre-flowering stress increases the source-sink ratio by limiting the number of grains per spikelet. Post-flowering stress decreases the source-sink ratio by shortening the functional period of the photosynthetic tissue. Therefore, the grain filling period may have a compensatory effect on earlier determined components which were affected by temporary stress. However, this compensatory effect may be limited by what seems to be the ultimate genetic potential for grain size (Fischer, 1970). This would suggest that a cultivar with large kernel size potential would be more adapted because of its high compensatory ability on other yield component affected by moderate or temporary stress. The effect of water stress during the grain filling period cannot be compensated for because kernel weight is the final component of yield.

Plant Characteristics Which Contribute to Yield and Adaptability in Stress Environments

In breeding for varieties adapted to dry areas, the breeder should have a knowledge of the genotypic differences in physiological and morphological traits which may contribute to total drought resistance. This is needed so that he can select parents with these traits for recombination. He can also use this knowledge to supplement his normal criteria for selection in the segregating generations.

Stand Establishment

Stand establishment can be a problem in many semiarid regions. This first stage of growth, if limiting, can reduce the ultimate yield potential in a cereal crop. Germination and stand survival under water stress, coleoptile and primary root lengths, and seedling vigor have all been related to the genotypic ability to establish a good stand and to yield well under water stress conditions. Differences in these components within genotypes and among genotypes, have been widely shown (Wright, 1971).

Cultivars known to be adapted to dryland conditions have shown the ability to germinate and to develop coleoptiles rapidly in osmotic solutions which induce stress (Hurd, 1971; Oleinikova and Kozhushko, 1970; Roy and Murty, 1970). Roy and Murty (1970) have successfully used a technique of visual scoring for vigor of germinated seeds in an osmotic solution as compared to that in pure water. They proposed that screening for early seedling vigor in the field, as well as the lab, is advantageous in selecting segregates which are adapted to dryland conditions.

Stand establishment is particularly a problem in some dry areas of the Pacific Northwest (Donaldson and Nagamitsu, 1973). Early deep seeding in dry soil can cause problems with emergence. Many semidwarf wheats lack the seedling vigor and coleoptile length needed for these conditions. Club wheats, such as Moro and Omar, are recognized for their strong, fast emergence. Few common wheats grown in this area have been identified to be as good as the club wheats.

Ching and Kronstad (1972) recognized genotypic differences in synthesis and utilization of ATP in embryos and seedlings of two wheat varieties. Yamhill wheat, which is recognized as having vigorous emergence, had a higher energy level and energy charge than the cultivar Hyslop.

Earliness

Although earliness of maturity is not a true drought resistance mechanism, it can play a deciding role in enabling the plant to partially escape drought. Studies have shown that within a wide range of germplasm, most of the "drought resistance" could be attributed to earliness (Chinoy, 1961; Derera, *et al.*, 1969). However, this is complicated by the fact that in many dry climates, moisture conditions are highly variable from season to season. For instance, in one year an early maturing variety may be favored, whereas in another season a late variety may yield better due to more favorable moisture conditions.

Within a maturity group, a cultivar's ability to extend its photosynthetic life during grain filling can be a decided advantage with respect to final kernel weight and yield (Asana, 1961). This may be more related to drought avoidance than tolerance and may be important in regions where the crop is dependent on stored soil moisture throughout the growing season. The combination of rapid early development from emergence to heading and a longer grain filling period could be a decided advantage over a cultivar which wastes moisture by having a slow early development and a shorter grain filling period (Hurd, 1971).

Tillering

High tillering capacity can compensate for stand loss and can be responsible for a good ground cover which may assist holding the top soil. However, extra tillers which do not produce seed are wasteful of moisture which may be needed later in more critical stages of development. Hurd (1971) stated that tillering ability which gives plasticity to a plant, allowing it to adapt from season to season, may be a luxury which cannot be afforded in dry areas. Wheat breeders have proposed selecting for synchronous tillering in which all heads contribute more or less equally to grain yield in order to obtain maximum moisture utilization (Bingham, 1970; Hurd, 1971; Roy and Murty, 1970).

Awns

Generally, cereal genotypes with awns have been found to yield better and have a higher kernel weight under dry conditions than awnless cultivars. But under more favorable moisture conditions, awns have shown no real advantage.

The awn is considered to be a xeromorphic structure because of its much reduced leaf character and large concentration of chlorenchyma cells (Grundbacker, 1963). Although awns contribute to a higher transpiration rate, they have the ability to produce more assimilates per unit of water transpired. They also have a favorable position above the leaf canopy for light interception and CO_2 exchange. Awns are also younger and more physiologically active than leaves at a time which coincides with intense carbohydrate accumulation in the grain. This possibly gives them the capability to remain active after leaf senescence. Evans, *et al.* (1972) found that awned ears contributed more assimilates to grain filling under dry conditions than under irrigated conditions. The awned ears also consistently contributed more to grain filling than awnless ears.

Stomates

Wide differences in stomatal density and size have been found among wheat genotypes. Guard cell length and stomate number are not necessarily related. In general, high stomate number and small size have been related to drought resistant species and cultivars, but this is not an absolute situation (Khurshid and Yusuf, 1967; Martin, 1930; Pavlov, 1930). Teare, et al. (1971) found that the club wheats had fewer stomates per unit area than the common wheats. In these studies, however, leaf area in relation to stomate numbers was not considered. This may be more related to total plant transpiration and therefore, to the degree of stress. For instance, a plant may have a low number of stomata per unit area but would transpire as much or more than a plant with high stomatal frequency and lower total leaf area. Within a genotype, a plant stressed during leaf elongation would have a higher stomatal frequency and smaller size along with a reduced leaf area.

The daily activity of stomates probably plays a major role in enabling a plant to avoid stress while making maximum use of CO_2 in the atmosphere. A cultivar could certainly avoid stress simply by keeping its stomates closed. However, this would have a detrimental effect on yield because it would restrict CO_2 uptake. Genotypic differences in daily periods of stomatal opening have been observed (Kaul and Crowle, 1971; Khurshid and Yusuf, 1967; Sojka, 1973). In one study (Khurshid and Yusuf, 1967), stomates of drought hardy cultivars were found to remain open two to three hours longer during the day than those of less hardy cultivars.

Roots

Roots play an important role in enabling the plant to avoid stress. A rapidly penetrating and extensive root system is essential for cultivars grown in semiarid areas. Genotypic differences in wheat have been noted in root extensiveness and depth (Derera, et al., 1969; Hurd, 1964, 1968, 1971; Katyal and Subbian, 1971). Hurd (1971) found that Pelisser, the most drought resistant durum wheat in Canada, had a relatively small proportion of its roots in the top four inches of soil. By the time the soil had dried down to several inches, Pelisser had established an extensive root system lower down in the soil. Thatcher, another drought resistant cultivar, was shown to penetrate more rapidly in near dry soil than in moist soils and more rapidly than other cultivars in all soil moistures. Thatcher also responded to stress by increasing its root branching in moist soil below the dry layer. Cultivars also respond differently in different soil types. Loam soil was found to accentuate varietal differences more than the clay soil at both high and low moisture levels.

Controversy has arisen as to whether the new semidwarf varieties extend their roots to the same depths as the tall varieties. If this is so, it would limit their adaptation to dry areas. Under limited moisture conditions in the greenhouse, differences between tall and short varieties have been shown (Welsh, 1973; Hurd, 1971). However, studies have shown that semidwarfs deplete soil moisture to the same depths as tall varieties in dryland field conditions (Holbrook and Welsh, 1973; Taylor and Hashimi, 1972). Semidwarfs were also higher yielding and had higher water use efficiency.

Number and branching of primary roots of young wheat seedlings have been related to genotypic ability to yield well under water stress conditions (Aamodt and Johnston, 1936; Kandurov and Nefedov, 1965).

Plant Water Status

The rate of water loss from cut shoots has been used in assessing drought resistance. A positive correlation between drought resistance and water retention from cut wheat plants has been demonstrated (Bayles, et al., 1939; Sandhu and Laude, 1958).

Martin (1930) compared corn and sorghum with respect to physiological aspects of drought resistance. Sorghum had less internal water stress ($\psi\pi$) in the leaves than corn. This was attributed to leaf stomata and cuticle layers. Sorghum had less water loss from detached shoots than corn indicating that the leaf cuticle prevented water escape.

Osmotic potential ($\psi\pi$) was used quite extensively in earlier work as a measure of drought resistance in certain wheat varieties (Aamodt and Johnson, 1936; Bartel, 1947; Newton and Martin, 1930; Pavlov, 1930). Cultivars which were believed to be drought resistance had a lower $\psi\pi$. This could not be explained in terms of drought avoidance because a lower $\psi\pi$ generally indicates a higher internal stress. The varieties may have maintained turgor by a tolerance mechanism which caused the low $\psi\pi$. However, drought resistance, with respect to the cultivar yield response and adaptability to dry conditions, was not well defined in these studies.

Kaul (1967, 1969) and Kaul and Crowle (1971) studied the relations between water status and productivity of spring wheat varieties in dryland areas in Saskatchewan, Canada. Consistent genotypic differences in ψ, $\psi\pi$, and daily duration of stomatal opening were noted on leaf samples taken during heading and grain filling. Varieties showing less water stress, such as Pitic 62, appeared to keep their stomates open for a longer period during the day (Kaul and Crowle, 1971). The variety Manitou was consistently under higher internal water stress and its stomates closed earlier in the day. In all three studies, however, no unequivocal relation between yield and degree of internal water stress was found in the cultivars tested.

Sojka (1973) found a general relation between high ψ and high yield in many cultivars grown under water stress in Obregon, Mexico. The variety Yecora showed the highest yield and the least internal water stress. The variety Gabo, which is widely believed to be drought resistant, had the highest internal water stress along with the lowest yield. Cook and Papendick (1973) studied ψ, $\psi\pi$, and ψp in winter wheat varieties grown under water stress conditions in eastern Washington. The variety Moro avoided stress by maintaining a high internal water status. Luke appeared to tolerate a low internal water status while Nugaines neither avoided nor tolerated high water stress. Inability to adapt to high soil water stress is related to susceptibility to Fusarium culmorum, a root rot disease common in dry areas of eastern Washington and Oregon. They contended that by breeding for drought resistance, tolerance to Fusarium root rot would be obtained simultaneously.

Breeding for Drought Resistance

Hurd (1969, 1971) described a method of breeding for high yield in semiarid climates. Parents used in crossing should be well adapted to dry growing conditions. If a parent is only moderately adapted to drought, but has a particular desirable characteristic, it should be used in a three-way or double cross with adapted cultivars. Parental material should be carefully evaluated for field performance under semiarid climates and for characteristics which contribute to drought resistance. Large F_2 populations should be grownwhich give 1,000 or more selected individuals to insure selection of plants which combine all the desirable genes for yield. Certain morphological traits which may contribute to adaptation to drought are selected such as earliness, awns, and limited tillering. The F_3 generation should be grown in a yield trial to obtain an early estimate of yield. Head selections in F_3 lines which are harvested for yield are then increased. The F_5 yield nursery is grown at two locations. Head selections from desirable lines are increased, and the F_7 generation is grown in replicated yield trials at three or four locations. The large number of lines grown in the F_3, F_5, and F_7 generations are considered especially important in breeding for high yield in semiarid climates in order to select lines which combine the relatively large number of yield genes each having a small effect.

Roy and Murty (1970) described a successful selection procedure for wheat to be grown in stress environments. F_2 populations from a large number of crosses with parents of diverse origin were grown under maximum yield conditions (irrigation, high fertility). Selection in the F_2 under such conditions were proven to be more successful than under water stress conditions because the former permits maximum expression of certain developmental traits which contribute to dryland adaptability. Such traits include seedling vigor, sychronous tillering, days to heading, and ear length. F_3 seed from selected F_2 plants were screened for quality and coleoptile development _in vitro_. The desirable selections were then planted in an irrigated location and in as many dryland locations as the amount of seed available permits. Data from visual scoring and actual yield over all the locations were used to aid in F_3 selection at the irrigated site. This cycle was repeated until adequate line purity was attained. In all generations, selection was made for traits which contribute to drought resistance, as well as for yield and stability over several dryland locations.

Yield and Adaptability as a Measurement of Drought Resistance

In crop plants, drought resistance can be defined as a plant's ability to (1) endure drought without injury or (2) make efficient use of the water (Arnon, 1972). Another trait which has been related to adaptation to dry climates is the ability of a plant to escape drought, wholly or in part. The ability to grow, develop, and reproduce normally under drought conditions has long been considered as true drought resistance. Therefore, a plant least affected by water stress has been considered to be drought resistant.

The ratio of yield under dry conditions to yield under optimal conditions of water supply was considered a valuable criterion in determining relative drought resistance. However, this can be misleading. Harrington (1935), using variety trials grown in semi-arid Saskatchewan over a period of ten years, found the wheat variety Marquis was less affected by drought than the variety Reliance. Using the above criterion, Marquis could be considered more drought resistant. However, during five of the ten years, there was a favorable moisture supply. Reliance outyielded Marquis in these years by an average of 129 kg/ha per year; while during the five dry years, the difference in favor of Reliance was 8.2 kg/ha per year. Even though the yield of Reliance was reduced by drought more than that of Marquis, over the period of ten years Reliance outyielded Marquis by an average of 343 kg/ha per year. As a result, many varieties considered to be drought resistant may give poor yields in dry seasons but will not respond maximally in seasons with favorable moisture conditions. In this case, a farmer would be better off with only moderately "resistant" varieties that give good returns in good seasons, even if they are relatively disappointing in dry seasons.

Varieties which produce the highest yields in all seasons, whether with good or poor moisture, will have maximum water use efficiency (Arnon, 1972). With this in mind, the assessment of drought resistance should include adaptability to the range of environments encountered as well as yield in the driest seasons. Therefore, genotype-environment interactions are important in the assessment of adaptability of particular cultivars to a wide range of environmental conditions. These interactions have been commonly assessed using the analysis of variance of variety yields over a number of years and locations. Significant cultivar x environment interactions indicate that varieties do not respond the same in all environments. Under conditions of high locational and seasonal variability, it is often extremely difficult to discriminate between varieties when averaged over all environments (LeClerg, et al., 1962). Although the variance technique is used extensively in estimating genotype-environment interaction, it fails to measure the stability of a given cultivar over the different environments.

Baker (1968) studied genotype-environment interactions for yield of wheat grown in Western Canada. He proposed that stability of a given cultivar is inversely proportional to the sum of squares for genotype-environment interaction attributed to that variety. Kaltsikes (1971) assessed the stability of wheat and triticale cultivars over six locations for two years in eastern Manitoba. The contribution of a cultivar to genotype-environment interaction sum of squares was used as a measure of its phenotypic stability. The variety Pitic 62 had the maximum stability and highest yield within the common wheats. Hercules, a durum wheat, had the highest overall yield but the highest instability.

Finlay and Wilkinson (1963) introduced a technique to measure varietal adaptation over environments by use of linear regression. Cultivar mean yield was regressed on the mean yield of all cultivars for each site (location within a season). Site mean yields provided a numerical grading of the environment effect over locations and seasons. Computations of means and regressions were based on log-transformed yields to achieve a high degree of regression linearity and to induce a degree of homogeneity of experimental errors for the sites.

The regression coefficient (b) provided a measure of phenotypic stability. A regression coefficient of 1.0 indicated average stability. A cultivar with $b < 1.0$ had above average stability, and $b > 1.0$ indicated below average stability. Regression coefficients and cultivar mean yields over environments were used to classify cultivars adapted specifically to high and low yielding environments and those with general adaptability to all environments. The ideal variety was described as having maximum yield potential in the most favorable environment with maximum phenotypic stability.

The utility of this technique in assessing adaptability in cereals has been amply demonstrated. Finlay and Wilkinson (1963) analyzed yield and stability of 277 diverse barley genotypes over two dryland locations for three years in which rainfall was the primary factor affecting yield. Wide variation was found in yield and stability among these varieties. They were able to group varieties of common geographical origin into certain adaptation schemes. For instance, European varieties tended to show specific adaptation to high-yielding environments. Varieties from Bolivia and North Africa tended to have high yields with average stability. Varieties from Northwest U. S. and Australia tended to give average yields along with average stability, while a group of varieties from the Southwest U. S. gave specific adaptability to low-yielding environments (low yield, high stability). However, the ideal variety with high yield and above average stability was not found.

Finlay (1968) analyzed spring wheat varieties in the International Spring Wheat Yield Nursery over 15 locations. He found that many of the newly developed Mexican wheat varieties, particularly Pitic 62, had wide adaptability (high yield and high stability). This adaptability was attributed, in part, to the range of environments in which these varieties were selected.

Progeny of barley crosses with parents having a wide range of adaptability were found to exhibit an even wider range of yield and stability than the parents (Finlay, 1963, 1971). This indicated the possibility of successful selection toward more ideal types.

Johnson, et al. (1968) and Schmidt, et al. (1972) used Finlay and Wilkinson's regression technique to analyze adaptability of winter wheat varieties grown in the Southern and Northern Great Plains of the U. S. The coefficient of determination ($\underline{r}^2$) was used as an indicator of predictability of varietal yield on the nursery mean performance. An $\underline{r}^2$ approaching 1.0 gives confidence that $\underline{b}$ along with the nursery mean performance can accurately predict a cultivar's mean performance at that location. Graphic representation of $\underline{b}$ for the varieties gave a vivid representation of their relative performance and response to the array of environments.

Eberhart and Russell (1966) proposed the use of two stability parameters to describe the performance of a variety over an array of environments. The regression of variety yield on an environmental index (non-log basis) and the sum of squared deviations from this regression provide useful measures of varietal stability. The environmental index is the deviation of each environment from the average of all environments. These parameter estimates are defined in the following model:

$$Y_{ij} = M_i + B_i I_j + d_{ij},$$

where Y_{ij} is the mean of the $\underline{i}$th cultivar at the $\underline{j}$th location, M_i is the mean of the $\underline{i}$th cultivar over all environments. B_i is the regression coefficient that measures the response of the $\underline{i}$th cultivar to varying environments, I_j is the environmental index obtained as the mean of the jth environment minus the grand mean, and d_{ij} is the deviation from regression of the ith cultivar at the jth environment.

A stable cultivar was defined as having a high mean yield, a regression coefficient of 1.0, and a small deviation mean square. They used this model in analyzing stability of 10 x 10 diallel crosses of maize over a number of locations (Eberhart and Russell, 1966, 1969). The deviation mean square was found to be a very important measure of cultivar stability in maize.

Joppa, et al. (1971) used the Eberhart and Russell model for analyzing varieties from a uniform spring wheat nursery from 1959 to 1968. The regression coefficient indicated predictable genotype-environment interactions such as adaptability to high or low-yielding environments. Specific genotype-environment interaction was defined as one which is due to a specific cause, such as disease susceptibility. The deviation mean square ($s^2 d$) provided a good indicator of specific genotype-environment interactions which could usually be related to specific causes. However, certain high-yielding varieties, such as Fletcher, Red River 68, and Era, had consistently high deviation mean squares which could not be attributed to a specific cause.

Stroike and Johnson (1972) used the Eberhart and Russell model in analysis of 28 varieties from the International Winter Wheat Performance Nursery for two years. A number of agronomic and nutritional quality traits, as well as yield, were analyzed. Bezostaia, a widely adapted cultivar, had the highest overall mean yield and responded strongly to more favorable environments (large regression coefficient). Certain varieties, such as Sturdy and Parker, showed high mean yields, an average regression coefficient, and a low deviation mean square indicating their wide adaptability.

Daaloul (1973) analyzed four winter wheat varieties for yield and stability in three relatively high-yielding locations over two years in Oregon. Pullman Selection 101 was found to have high yield along with a low b and low s^2d. These values indicated that P-101 had wide adaptability to the environments in which it was grown. Corvallis Selection 55-1744, had high yield, low b, and a high s^2d. The high s^2d was considered to be due to its high shattering in the drier environments. Brevor, a poorly adapted cultivar, was indicated by low yield and average stability. Moro, with low yield, high b and high s^2d, was shown to be poorly adapted, and very sensitive because of changes in environment. The high s^2d was attributed to lodging under higher yielding environments.

Environmental index or site mean yield may be biased estimates of the environment (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). There is a tendency to underestimate b because the assumption that the independent variable (site mean or environment index) is measured without error, may not always be true (Hardwick and Wood, 1972). The magnitude of this bias depends on the number of genotypes estimating the environment and the ratio of the environment mean square to the error mean square. Therefore, a larger number of genotypes or variance component due to environments will give a relatively smaller bias, although it may not be negligible. Hardwick and Wood (1972) proposed a model in which varietal means were regressed on environmental variables. The main restriction to the model is the complexity of measuring and computing the environmental effects and therefore, the model is of little practical use in most situations.

The techniques as proposed by Finlay and Wilkinson (1963) and Eberhart and Russell (1966) have been shown to be of practical use in analyzing adaptability of cultivars to a wide, as well as a more restricted, range of environments. It is important to define the range of environments as to the major factors limiting yield before assessing varieties as to their adaptability. By defining a range of environments in a geographic region where the major yield limiting factor is moisture, one would be able to adequately assess the varieties as to their drought resistance or dryland adaptability.

III. ANALYSIS OF YIELD RESPONSE TO ENVIRONMENTS

Materials and Methods

Ten wheat cultivars were analyzed for grain yield at six locations over a period of four years. The cultivars included six common soft white winter wheats and one hard red winter wheat, *Triticum aestivum* L. em. Thell, ssp. *vulgare*, and three white winter club wheats, *T. aestivum* L. em. Thell, ssp. *compactum* (Appendix Table 1). The cultivars selected for use in this study represent wide genetic diversity. Except for Rew and McDermid, the cultivars are at present or have previously been grown under commercial production in the Pacific Northwest. McDermid has recently been released for commercial production, while Rew is an advanced line under consideration for release. Golden and Omar represent long term check varieties.

Data were provided from yield trials managed by the personnel at the Sherman Experiment Station, in Moro, Oregon and the Pendleton Experiment Station near Pendleton, Oregon. The yield trials were grown in randomized complete block designs on summer-fallow rotation. Four rows, with 30 cm spacings between rows, and five m long were planted. From this, the two center rows, 2.5 m long (0.74 m^2) were harvested for grain yield. Four replications per location were used in the analysis.

The locations selected represent a range of soil and climatic conditions characteristic of the dry wheat-growing regions of eastern Oregon (Appendix Table 2).

Analysis of variance was used to evaluate grain yield within and among locations (LeClerg, et al., 1966). The F-test was used to determine the significance of the cultivar, location, and interaction mean squares. Duncan's new multiple range test was used to determine significant differences between cultivars. The Bartlett chi-square test was used to test the homogeneity of the error mean squares among sites.

Regression techniques described by Finlay and Wilkinson (1963) and Eberhart and Russell (1966) were used to analyze stability of yields across locations. Statistical significance of each regression coefficient from 1.0 was determined by use of the t-test.

Results and Discussion

Climatic Conditions

The climatic conditions during the 1970 crop season were generally good for winter wheat production (Appendix Table 3). Good stands were established in the fall, although fall growth was limited because of late seeding. High precipitation with little runoff during the winter months provided a large reserve of soil moisture.

However, grain yields in the shallow soil areas, such as Pilot Rock and Arlington, suffered from low precipitation from April through June. June temperatures throughout the area were high enough to cause premature ripening and depressed test weights in certain cultivars. Winterkill and stripe rust appeared not to have an effect on grain yields.

Climatic conditions for the 1971 crop season were very favorable. Stands were well established, however, minimal fall growth occurred. There was little runoff from the fall rains and good soil moisture conditions resulted. High precipitation, low evaporation, and low temperatures in June gave favorable crop growth which was represented by record high average yields. Winterkill did not occur, and only trace amounts of stripe rust were evident.

Conditions during the 1972 crop season were less than favorable for winter wheat production. Because of poor fall moisture conditions in the drier areas, seeding was late. Stripe rust was not a problem, but some winterkilling occurred in certain areas because of lack of snow cover. However, winterkilling was not observed in the trials used in this analysis.

Poor moisture conditions existed throughout the 1973 growing season. Cold temperatures in December caused extensive winterkilling in regions where there was inadequate snow cover. High evaporation and high soil moisture stress in late spring and early summer caused decreased test weights and low yields. The trial at Arlington was severely affected by a combination of severe winterkill and moisture stress and therefore, was not harvested. The other trials were little affected by winterkill.

Yield Response to Environment

Yields for the sites (location-years) were variable within a location as well as across locations within a year (Table 1). The Pendleton location had the highest yields across the four years and represented the upper end of the yield spectrum. The other locations represented a wide range of yield levels but all yielded less than the Pendleton sites. Because this study is basically concerned with yield

Table 1. Mean grain yields in tons per hectare for each location within each year.

	Site Mean Yield				
Location	1970	1971	1972	1973	Location Mean
Pendleton	4.30	4.82	4.73	3.45	4.32
Pilot Rock	0.94	2.73	1.70	1.70	1.77
Rew	2.22	3.09	1.85	1.67	2.21
Moro	3.20	2.48	2.85	1.03	2.39
Heppner	3.19	2.27	1.95	1.37	2.20
Arlington	1.86	2.63	2.06	-	2.18
Year Mean	2.62	3.00	2.52	1.84	2.53 Overall Mean

response under drought stress, the favorable conditions for yield at the Pendleton location may not typify drought stress conditions. Therefore, yield stability analysis was conducted for the group of sites with the Pendleton sites excluded as well as with all sites included.

The coefficients of variation for the sites ranged from 6.94 to 20.41 percent (Tables 2, 3, 4, and 5). Cultivar mean squares were not significant (5% level) for seven of the 23 locations. However, the Duncan multiple range test indicated statistical differences between some cultivars in 20 of the 23 locations. Rew was excluded from the analysis across sites because it was not represented in some sites in 1970.

The error mean squares for all the sites were found to be non-homogeneous. Therefore, combined analysis over all sites was not valid because the underlying assumption of homogeneity among variances was not met. Because the error mean squares appeared to be dependent on site means, the yield data were transformed to $\log_{10}$ data to remove such dependency. However, homogeneity among error mean squares was not obtained by using log transformation. Therefore, locations with extremely high or low error mean squares (non-log basis) were eliminated until homogeneity among the remaining error mean squares was obtained. Seventeen sites had homogeneous error mean squares and were used in a combined analysis of variance

Table 2. Mean yields (tons/ha) of cultivars grown at six locations in Oregon for the 1970 crop season.

Cultivar	Pendleton	Pilot Rock	Rew	Moro	Heppner	Arlington
Golden	3.00 e[1]	1.04 ab	1.71 d	2.71 e	2.70 b	1.66 cd
Omar	3.84 d	0.69 cd	1.92 cd	2.92 de	3.41 ab	1.58 d
Wanser	4.23 bcd	1.04 ab	2.06 bcd	3.17 bcd	3.12 ab	2.09 ab
Moro	3.75 d	0.97 bc	2.03 bcd	3.01 de	2.75 ab	1.59 d
Nugaines	4.77 ab	0.59 d	2.52 ab	3.67 a	2.98 ab	1.93 abc
McDermid	4.11 a	1.13 ab	2.36 abc	3.43 abc	3.67 ab	2.01 ab
Yamhill	4.05 cd	1.13 ab	2.33 abc	3.23 bcd	3.30 ab	2.17 a
Paha	4.49 a	0.63 d	2.45 ab	3.48 ab	2.84 b	1.16 bcd
Hyslop	4.89 a	1.27 a	2.60 a	3.32 abcd	3.97 a	1.96 abc
Rew	4.52 abc	-	-	3.09 bcde	-	-
Site Mean	4.30	0.94	2.22	3.20	3.19	1.86
Coefficient of Variation	8.43	20.41	13.53	7.98	19.15	11.13
Cultivar[2] Significance	<.01	<.01	<.01	<.01	n. s.	<.01

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[1] Duncan multiple range test - means in a column followed by the same letter are not significantly different at the 5% probability level.

[2] Significance level of the mean square for cultivars in the analysis of variance.

Table 3. Mean yields (tons/ha) of cultivars grown at six locations in Oregon for the 1971 crop season.

Cultivar	Pendleton	Pilot Rock	Rew	Moro	Heppner	Arlington
Golden	3.28 d	2.55 ab	2.82 c	1.81 c	2.42 ab	2.27 c
Omar	4.24 c	2.81 ab	2.94 bc	2.37 b	2.15 abc	2.49 c
Wanser	4.27 c	2.80 ab	2.95 abc	2.38 b	2.11 bc	2.54 bc
Moro	4.04 c	3.01 a	3.00 abc	2.31 b	2.24 abc	2.58 bc
Nugaines	5.48 a	2.42 b	3.19 abc	2.44 b	2.30 abc	3.01 a
McDermid	5.97 a	2.90 ab	3.40 a	2.62 b	2.29 abc	2.91 ab
Yamhill	5.39 a	2.59 ab	2.85 c	2.59 b	2.04 c	2.66 abc
Paha	4.59 c	2.85 ab	3.26 abc	2.30 b	2.40 ab	2.64 abc
Hyslop	5.64 a	2.77 ab	3.17 abc	2.74 ab	2.31 abc	2.60 bc
Rew	5.27 ab	2.57 ab	3.34 ab	3.22 a	2.43 a	2.56 bc
Site Mean	4.82	2.73	3.09	2.48	2.27	2.63
Coefficient of Variation	9.20	10.86	8.91	13.53	8.43	9.3
Cultivar Significance	< .01	n.s.	< .05	< .01	n.s.	< .05

Table 4. Mean yields (tons/ha) of cultivars grown at six locations in Oregon for the 1972 crop season.

Cultivars	Pendleton	Pilot Rock	Rew	Moro	Heppner	Arlington
Golden	3.74 e	1.50 c	2.15 a	2.23 c	1.80 a	1.96 a
Omar	4.29 d	1.64 bc	1.63 bc	3.14 ab	1.95 a	2.26 a
Wanser	4.59 cd	1.82 ab	1.93 abc	2.79 bc	2.00 a	2.04 a
Moro	4.69 bcd	1.66 bc	1.64 bc	2.39 c	1.81 a	2.02 a
Nugaines	5.33 a	1.71 bc	2.02 ab	3.09 ab	1.92 a	1.93 a
McDermid	4.62 bcd	1.96 a	1.95 abc	3.28 ab	2.01 a	2.29 a
Yamhill	4.72 bcd	1.58 c	1.75 bc	2.23 c	1.83 a	1.95 a
Paha	5.00 abc	1.61 bc	1.55 c	2.92 abc	2.02 a	2.16 a
Hyslop	5.15 ab	1.75 b	1.91 abc	2.81 abc	2.20 a	2.11 a
Rew	5.12 ab	1.71 bc	1.94 abc	3.51 a	1.94 a	1.87 a
Site Mean	4.73	1.70	1.85	2.85	1.95	2.06
Coefficient of Variation	6.94	8.01	13.18	15.30	14.68	12.72
Cultivar Significance	<.01	<.05	<.05	<.01	n.s.	n.s.

Table 5. Mean yields (tons/ha) of cultivars grown at five locations in Oregon for the 1973 crop season.

Cultivar	Pendleton	Pilot Rock	Rew	Moro	Heppner
Golden	2.50 d	1.71 a	1.49 bc	0.94 bcd	1.34 abc
Omar	2.89 cd	1.59 a	1.30 c	1.07 abc	1.19 c
Wanser	2.80 cd	1.90 a	1.69 b	1.03 abcd	1.49 ab
Moro	2.45 d	1.69 a	1.62 b	1.15 ab	1.25 bc
Nugaines	4.13 a	1.56 a	1.74 ab	0.87 cd	1.50 ab
McDermid	4.02 a	1.72 a	2.03 a	0.83 d	1.51 a
Yamhill	3.37 bc	1.90 a	1.67 b	1.24 a	1.40 abc
Paha	3.76 ab	1.68 a	1.64 b	1.14 ab	1.24 bc
Hyslop	4.35 a	1.48 a	1.80 ab	1.02 abcd	1.40 abc
Rew	4.18 a	1.81 a	1.71 ab	0.99 bcd	1.36 abc
Site Mean	3.45	1.70	1.67	1.03	1.37
Coefficient of Variation	11.28	16.95	12.37	13.41	11.38
Cultivar Significance	< .01	n.s.	<.05	<.01	n.s.

(Table 6). Highly significant mean squares for environments (sites), genotypes and genotype x environment interactions were present.

McDermid had the highest mean yield for the 17 sites used in the combined analysis of variance. McDermid and Hyslop were significantly higher than all other cultivars except Nugaines. Paha, Wanser and Yamhill were all statistically in the same yielding group. Though Moro and Omar were low yielding, Golden was significantly the lowest yielding cultivar in the analysis.

Although differences were evident in overall cultivar yields, a significant genotype x environment interaction indicated that the cultivars did not respond the same across all environments. This was evident when examining relative differences within each of the sites. Regression techniques were, therefore, used to ascertain the response of each cultivar to the range of environments.

Values were computed for all sites (group A) and for sites excluding Pendleton (group B) using the Eberhart and Russell method (1966) (Table 7). The Finlay and Wilkinson method (1963) (log basis) was also used to compute values for all sites (group C) and for sites excluding Pendleton (group D) (Table 8).

The means and regression coefficients (b) for the cultivars were similar in relative magnitude whether the Finlay and Wilkinson or Eberhart and Russell models were used or whether the Pendleton sites were included or excluded (Figures 1, 2, 3 and 4). The cultivars

Table 6. Analysis of variance and cultivar means over 17 sites having homogeneous error mean squares.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Probability Level
Total	611	635.81			
Environments[1]	16	546.69	34.168	101.84	<.001
Error (a)	51	17.11	0.336		
Genotype	8	13.53	1.692	23.69	<.001
Genotype X Environment	128	29.35	0.229	3.21	<.001
Error (b)	408	29.13	0.971		

Cultivar	Mean T/Ha	DMRT[2]
McDermid	2.60	a
Hyslop	2.57	a
Nugaines	2.52	ab
Paha	2.47	bc
Wanser	2.41	c
Yamhill	2.40	c
Moro	2.31	d
Omar	2.23	d
Golden	2.13	e
Grand Mean	2.41	
Coefficient of Variation	11.20	

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[1] Includes Pendleton 1970, 1972; Pilot Rock 1970, 1971, 1973; Rew 1970-1973; Moro 1970, 1971; Heppner 1971-1973; and Arlington 1970-1972.

[2] Duncan Multiple Range Test, means followed by the same letter are not significantly different at the 5% level.

Table 7. Yield and stability parameters obtained using the Eberhart and Russell method (non log) for nine cultivars over environments including and excluding the Pendleton sites.

	Group A - All Sites Included			Group B - Pendleton sites excluded		
Cultivar	Mean	Regression Coefficient	Deviation Mean Square	Mean	Regression Coefficient	Deviation Mean Square
McDermid	2.78 a[1]	1.16*[2]	0.054	2.33 a	1.12	0.018
Hyslop	2.75 a	1.17**	0.057	2.27 a	1.07	0.044
Nugaines	2.66 b	1.20**	0.046	2.17 b	1.13	0.046
Paha	2.56 c	1.09*	0.047	2.14 bc	1.08	0.031
Yamhill	2.52 c	0.99	0.053	2.13 bc	0.87	0.034
Wanser	2.47 c	0.88**	0.025	2.16 b	0.90**	0.010
Omar	2.36 d	0.91*	0.048	2.06 c	1.08	0.033
Moro	2.33 d	0.85**	0.059	2.04 c	0.90	0.027
Golden	2.15 e	0.62**	0.056	1.93 d	0.77**	0.045

* Significant at the 5% level
** Significant at the 1% level

[1] Duncan multiple range test at the 5% level - may be too sensitive because the error mean squares were not homogeneous for all the locations

[2] Regression of cultivar means on site means. Significance from $\beta = 1.0$

Table 8 . Yield and stability parameters obtained using the Finlay method (log basis) for nine cultivars over environments including and excluding Pendleton sites.

	Group C - All Sites Included			Group D - Pendleton Sites Included		
Cultivar	Mean	Regression Coefficient	Deviation Mean Square	Mean	Regression Coefficient	Deviation Mean Square
McDermid	1.573 a	1.06	1.43	1.513 a	1.05	1.47
Hyslop	1.568 a	1.03	1.80	1.500 a	0.96	1.76
Nugaines	1.543 b	1.21**	2.26	1.472 bc	1.24**	2.61
Yamhill	1.539 b	0.91	1.56	1.483 b	0.83**	1.34
Wanser	1.534 b	0.89**	0.66	1.486 b	0.89**	0.46
Paha	1.533 b	1.13*	2.04	1.470 bcd	1.15	2.24
Moro	1.507 c	0.90*	1.49	1.460 cde	0.92	1.00
Omar	1.504 c	1.04	2.00	1.453 de	1.14*	1.79
Golden	1.480 d	0.77**	2.05	1.438 e	0.85	2.21

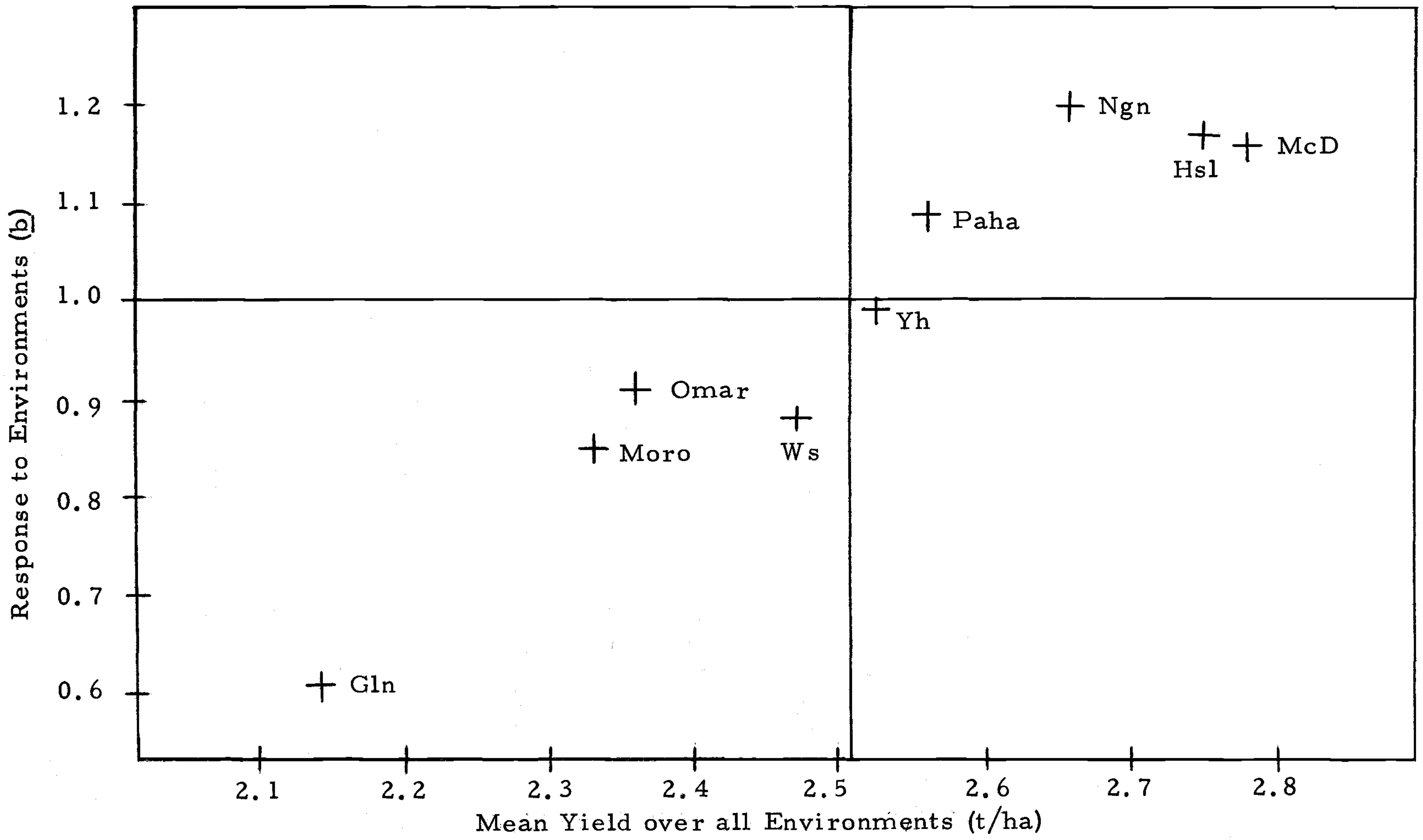

Figure 1. Relationship of overall mean yield to the stability response to all environments using the Eberhart and Russell model for the wheat cultivars, Hyslop (Hsl), McDermid (McD), Nugaines (Ngn), Yamhill (Yh), Wanser (Ws), Golden (Gln), Paha, Omar and Moro.

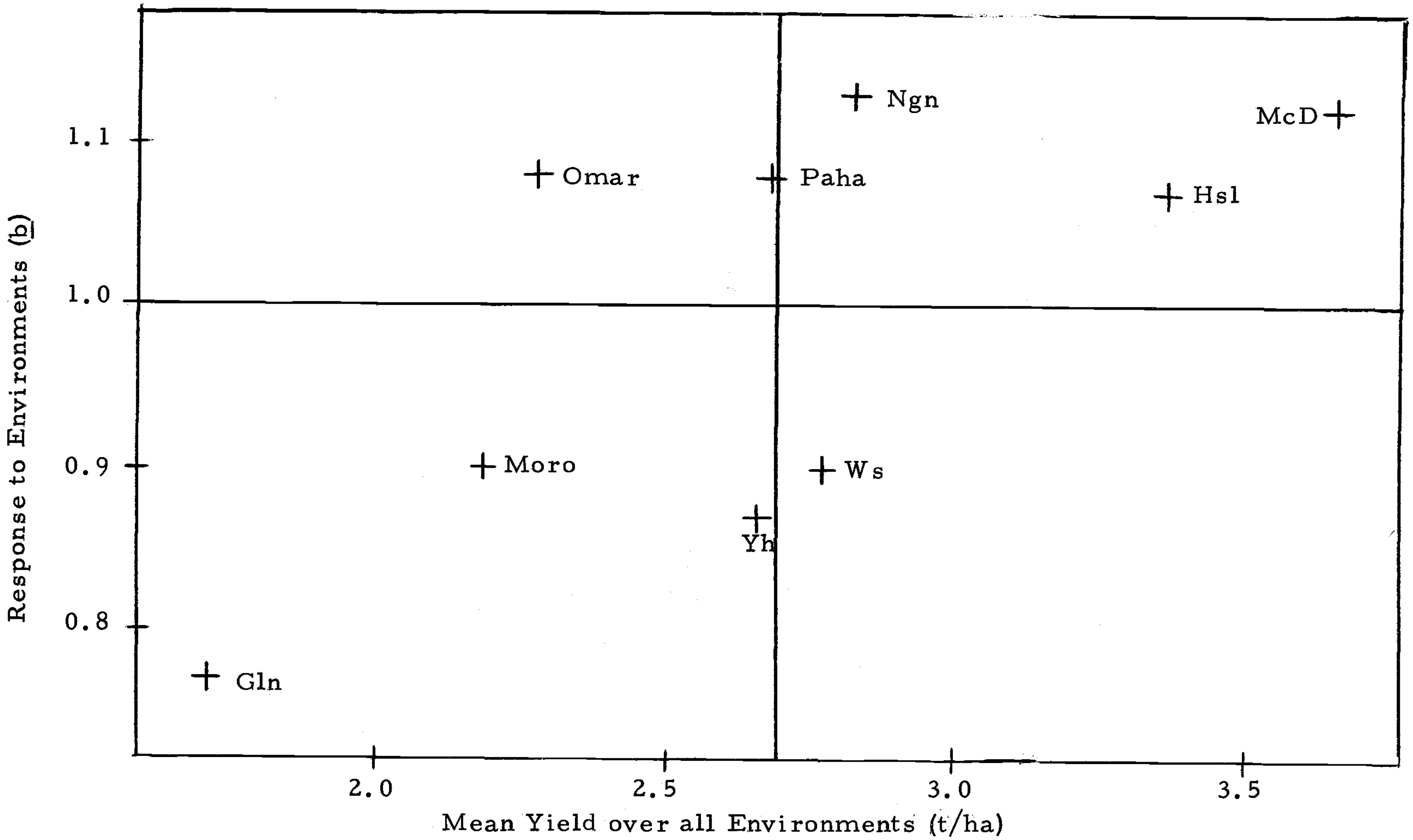

Figure 2. Relationship of overall mean yield to the stability response to environments, Pendleton sites excluded, using the Eberhart and Russell model for the wheat cultivars, Hyslop (Hsl), McDermid (McD), Nugaines (Ngn), Yamhill (Yh), Wanser (Ws), Golden (Gln), Paha, Omar and Moro.

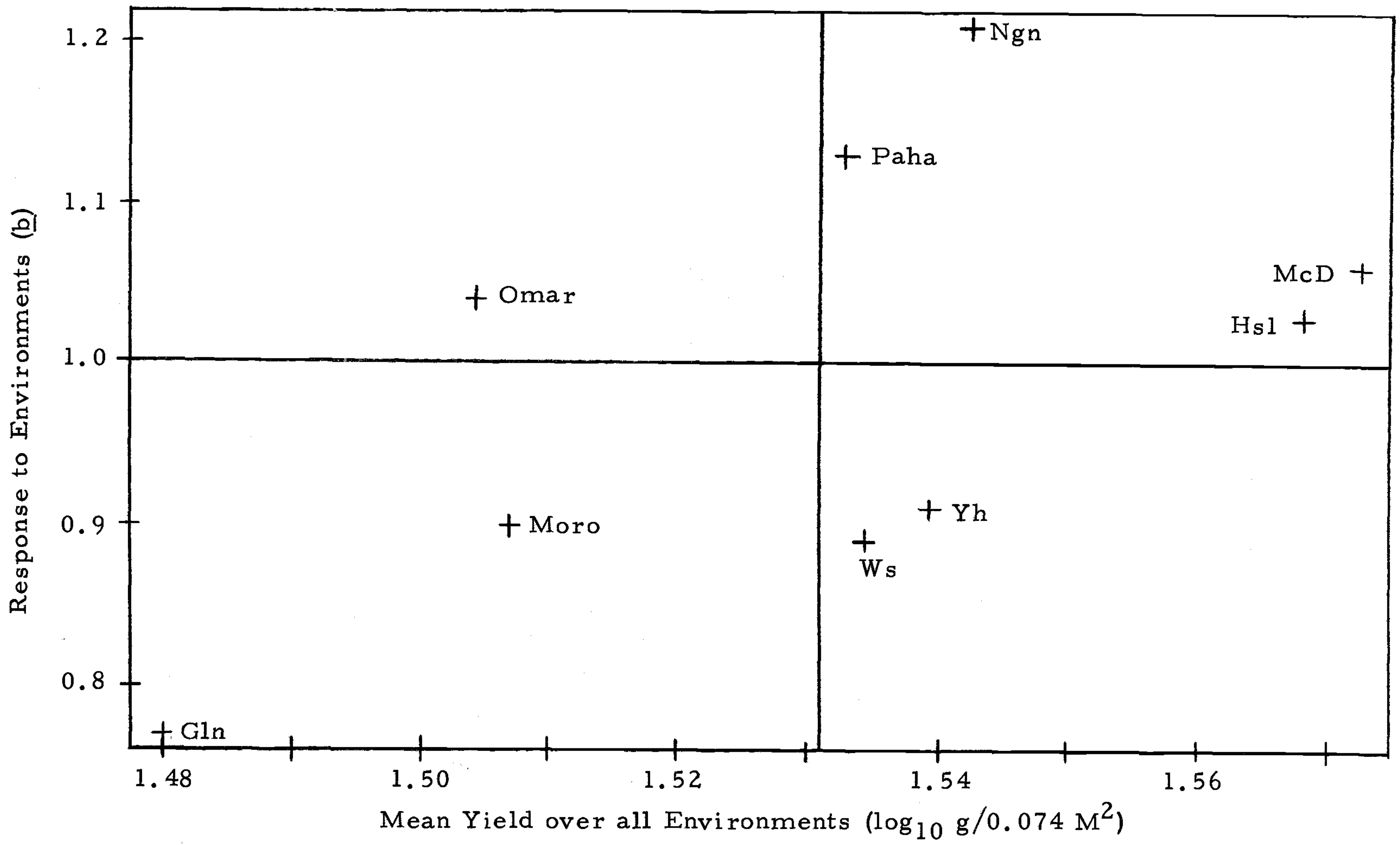

Figure 3. Relationship of overall $\log_{10}$ mean yield to the stability response to all environments using the Finlay and Wilkinson model for the wheat cultivars, Hyslop (Hsl), McDermid (McD), Nugaines (Ngn), Yamhill (Yh), Wanser (Ws), Golden (Gln), Paha, Omar and Moro.

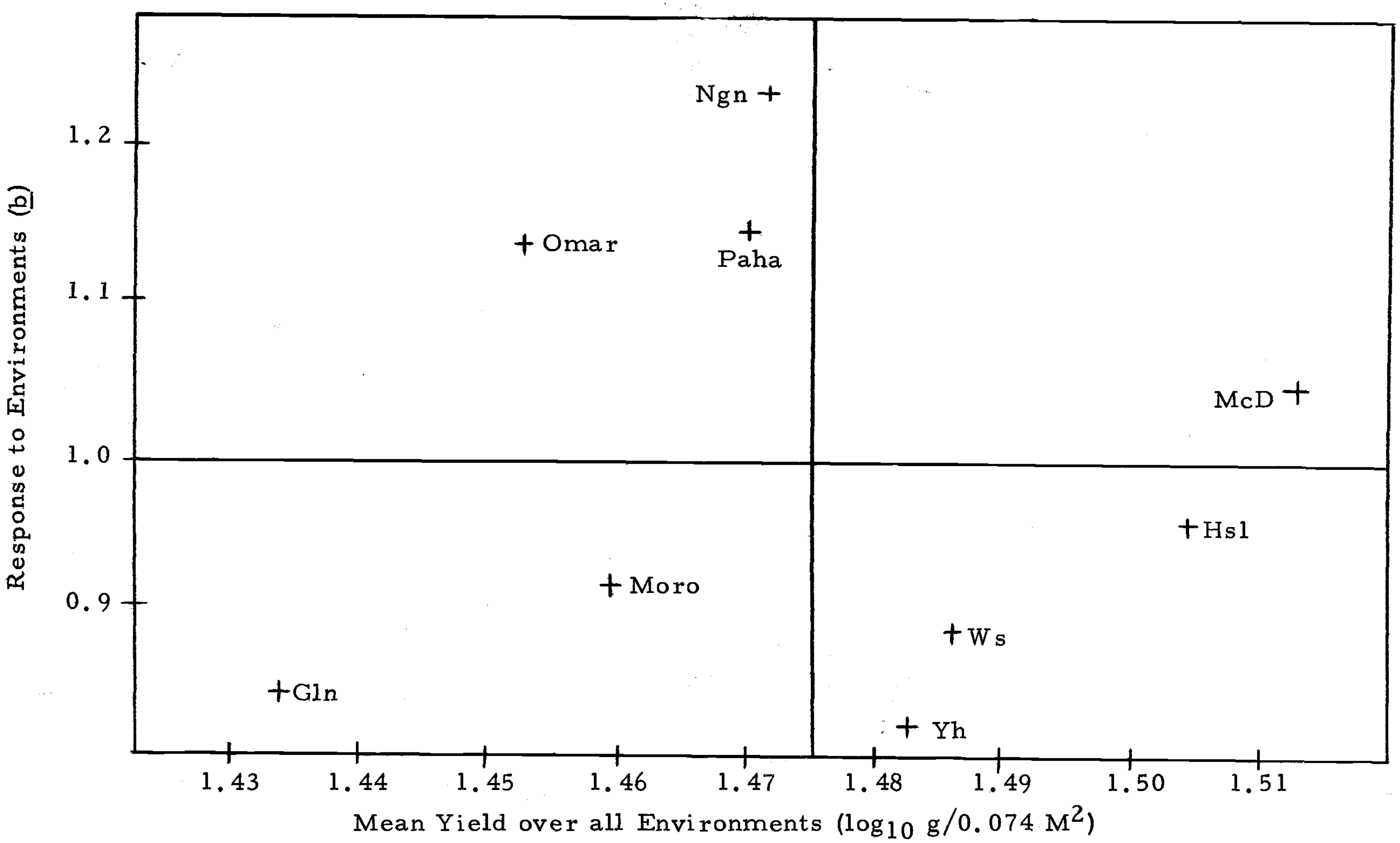

Figure 4. Relationship of the overall $\log_{10}$ mean yield to the stability response to environments, Pendleton sites excluded, using the Finlay and Wilkinson model for the wheat cultivars, Hyslop (Hsl), McDermid (McD), Nugaines (Ngn), Yamhill (Yh), Wanser (Ws), Golden (Gln), Paha, Omar and Moro.

McDermid and Hyslop had the highest overall yields and average or above average responses to change in environments ($\underline{b} \geq 1.0$). This indicated that the cultivars generally yield well in all the environments. In fact, Hyslop was either the highest yielder or not significantly different from the highest yielder in 21 out of the 23 sites. McDermid held this distinction in 20 out of the 23 sites. Nugaines had above average yields and the greatest response to changes in environments (largest $\underline{b}$). Nugaines was in the highest yielding group in only 18 of the 23 sites.

Paha, Wanser and Yamhill had near average yields but they differed widely in their environmental responses. Wanser had a stable response to environments ($\underline{b} < 1.0$), while Yamhill had an average or below average response ($\underline{b} \leq 1.0$). However, Paha had an average or above average response to environments ($\underline{b} \geq 1.0$). Moro and Omar had low mean yields, and Moro had a more stable environmental response than Omar. Golden had the lowest mean yield as well as the most stable response to changing environments.

Using the Eberhart and Russell model, the deviation mean squares (s^2d) for group A (nonlog, all sites included) were generally larger than those where the Pendleton sites were excluded (Table 7). This indicated that the cultivar means at the Pendleton sites had relatively large deviations about the regression line which contributed to a larger s^2d. This is illustrated for some cultivars whose s^2d

decreased when the Pendleton sites were excluded (Figures 5, 6, and 7). However, Nugaines and Wanser did not have decreased s^2d values, and the deviations of the means at the Pendleton sites about the regression line were small (Figures 8 and 9). Because s^2d affects the predictability of the regression slope, a more accurate prediction of cultivar yields would be possible when the Pendleton sites were excluded. Use of the Pendleton sites also caused some changes in the slope of the regression line for some cultivars which may have affected the accuracy of predictions in the lower yielding environments. Therefore, further assessment of cultivar adaptability by use of the Eberhart and Russell model was restricted to the group of environments with the Pendleton sites excluded.

When using the Finlay and Wilkinson method, the s^2d values did not decrease to a large extent and, in some cases, increased when the Pendleton sites were excluded. Therefore, the predictability of this method with all sites included was considered adequate. Further assessment of cultivar adaptability by use of the Finlay and Wilkinson method was restricted to the group where all sites were included.

Eberhart and Russell (1966) stressed the importance of the deviation mean square in assessing adaptability. Even though Wanser and McDermid had low s^2d values (nonlog, Pendleton sites excluded) and Hyslop, Nugaines and Golden had relatively high values, the range of s^2d was not large in relation to those found in other studies with

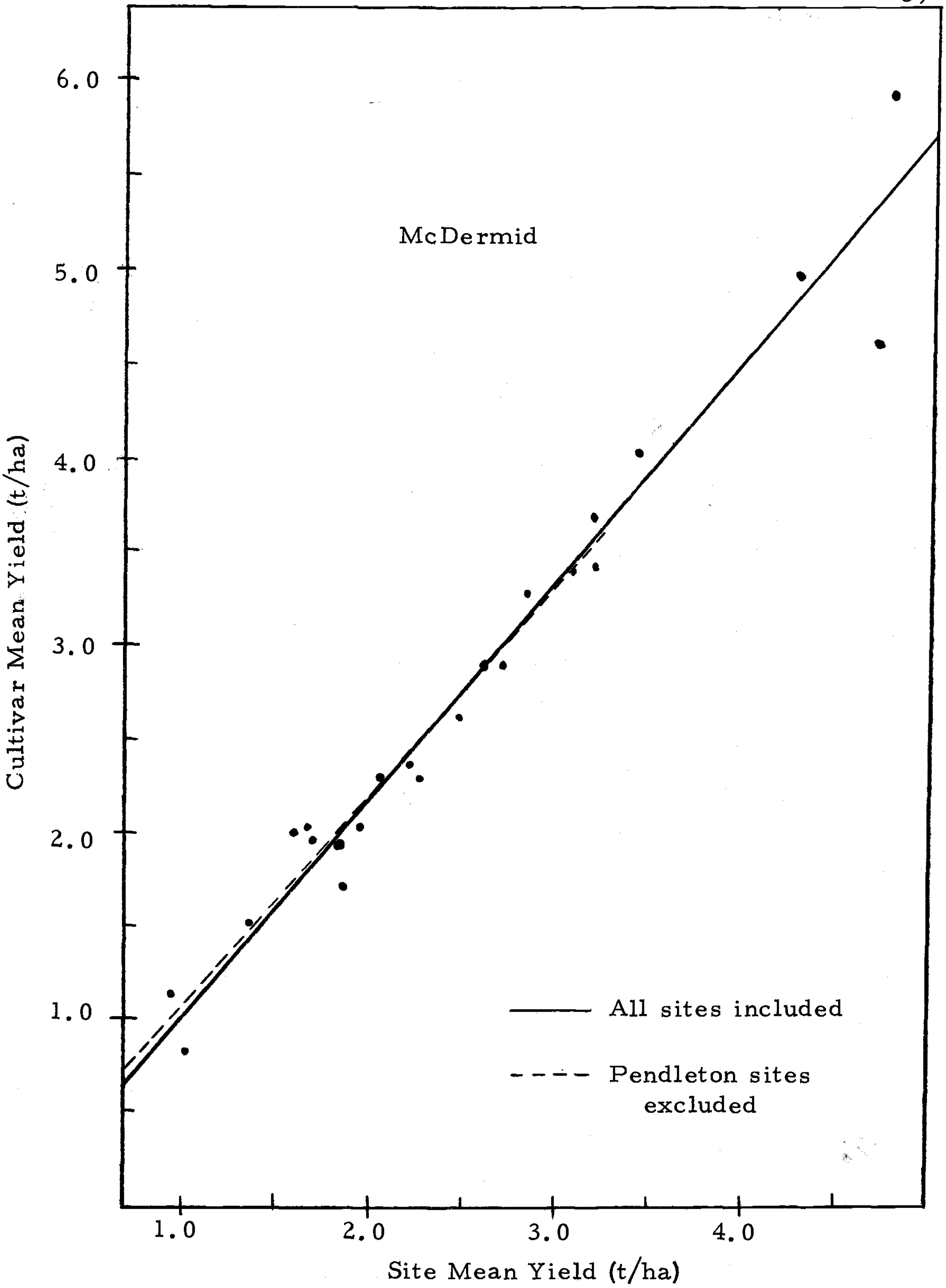

Figure 5. Regressions of cultivar means for McDermid on the site means, Pendleton sites included and excluded, using the Eberhart and Russell model.

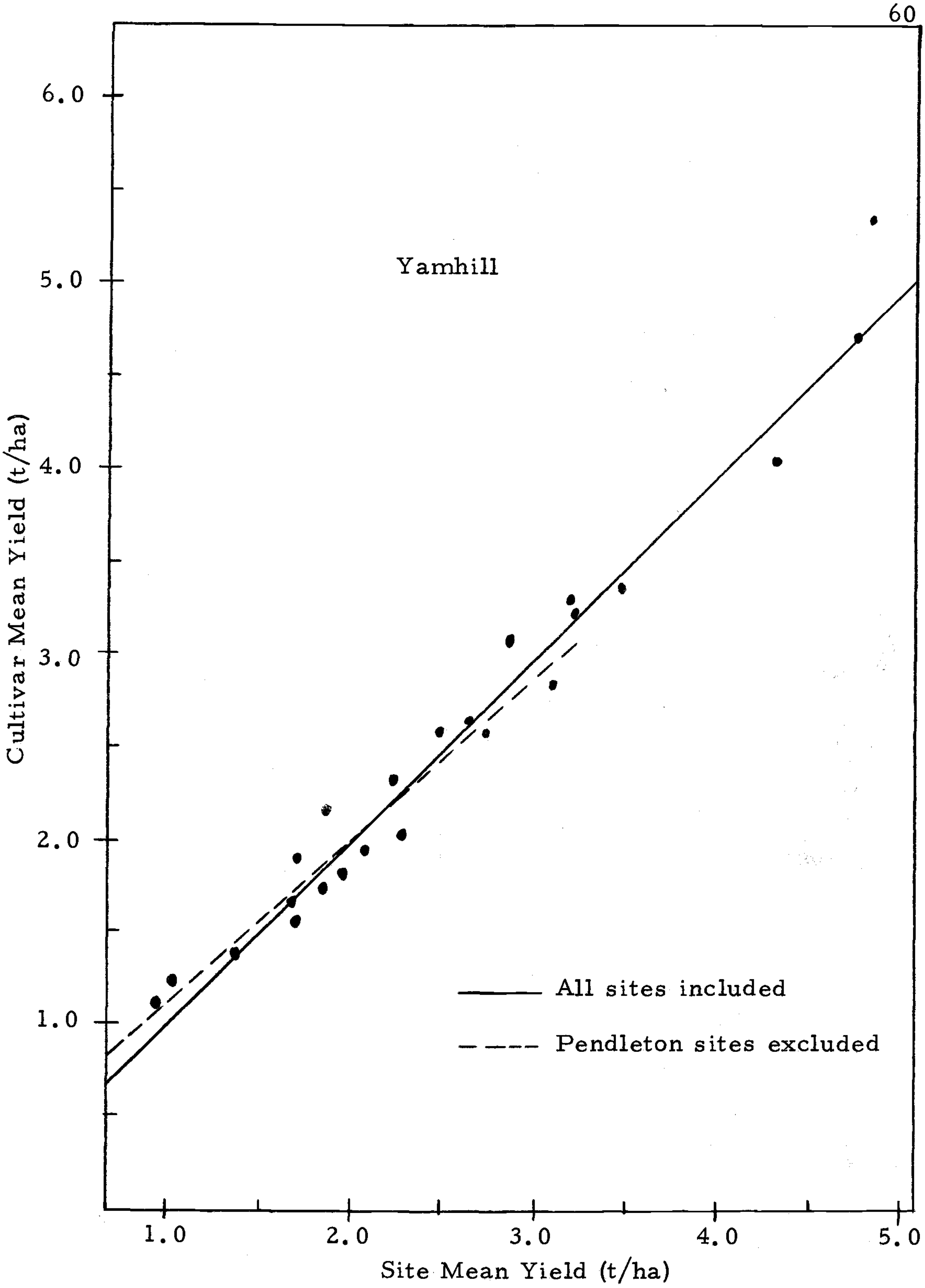

Figure 6. Regressions of cultivar means for Yamhill on site means, Pendleton sites included and excluded, using the Eberhart and Russell model.

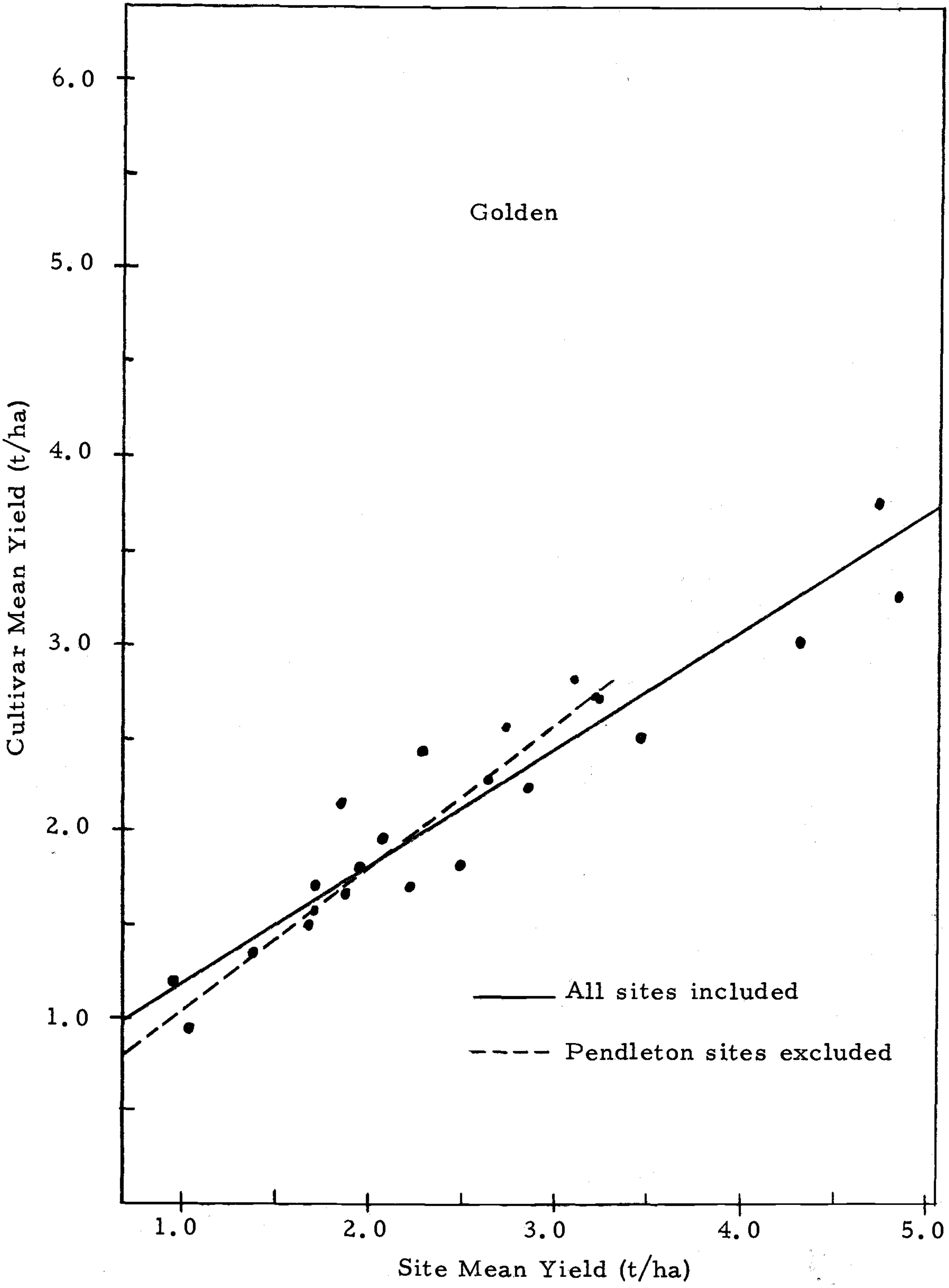

Figure 7. Regressions of cultivar means for Golden on site means, Pendleton sites included and excluded, using the Eberhart and Russell model.

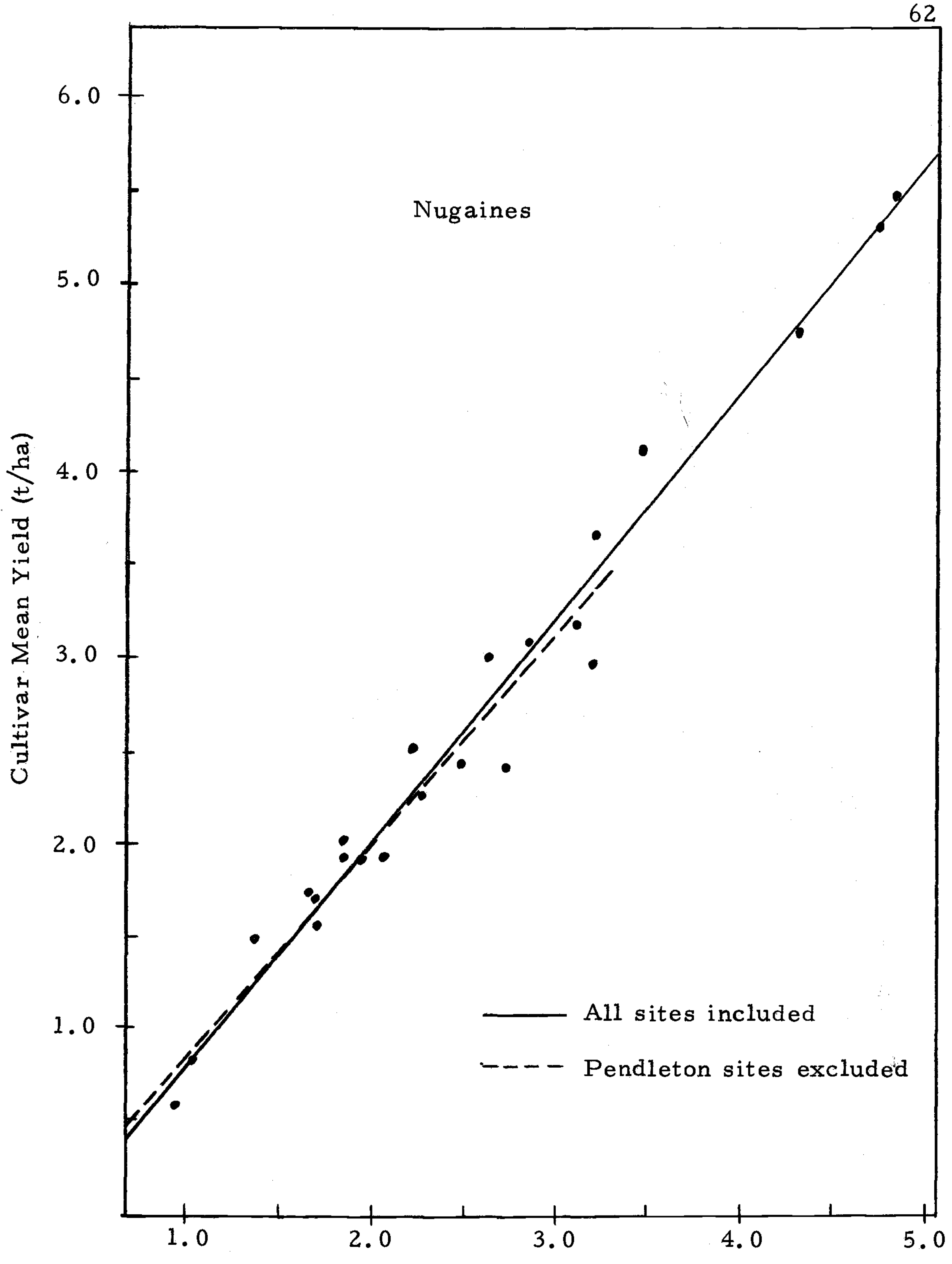

Figure 8. Regressions of cultivar means for Nugaines on site means, Pendleton sites included and excluded, using the Eberhart and Russell model.

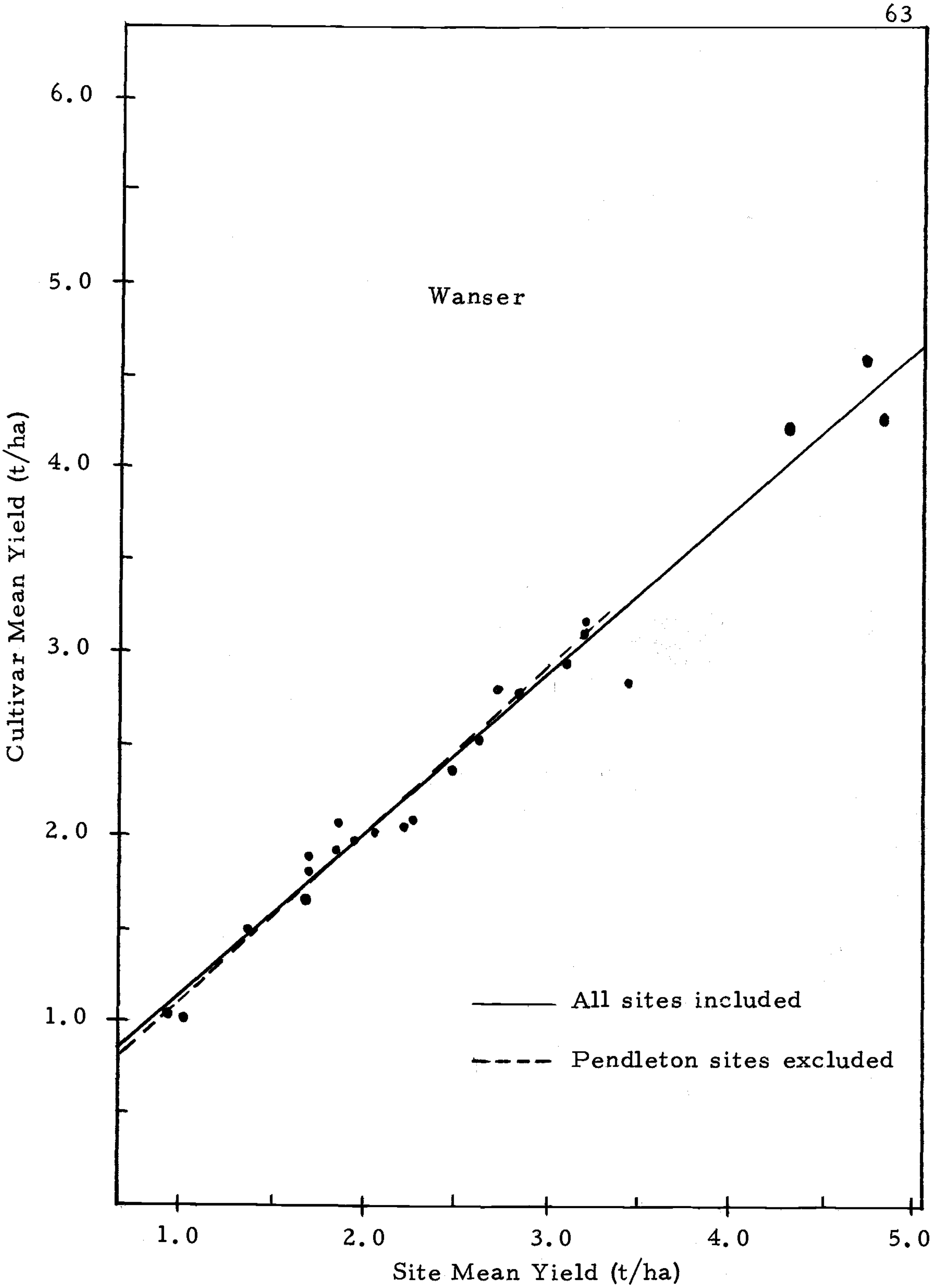

Figure 9. Regressions of cultivar means for Wanser on site means, Pendleton sites included and excluded, using the Eberhart and Russell model.

wheat (Joppa, *et al.*, 1971; Stroike and Johnson, 1972). High deviation about the regression line is ascribed to specific genotype-environment interactions from unpredictable causes. Because of the relatively low s^2d values in the present study, there appeared to be no major factors such as diseases, winterkill or stand establishment problems which could have caused specific responses of certain cultivars. The high predictability of the regression coefficients was also supported by the high coefficients of determination present which ranged from 0.87 to 0.98 for the cultivars. Therefore, the slope of the regression line was considered the most important factor used in assessing the adaptability of the cultivars in this study.

Before assessing the drought resistance and adaptability of these cultivars to dryland conditions, some ideal parameters must be developed. Certainly, a cultivar that yields the highest in all sites would be considered the most widely adapted. However, this is rarely the case if the environments represent a wide diversity. Finlay and Wilkinson (1963) proposed that an ideal, widely adapted cultivar would have maximum yield potential in the most favorable environment with maximum phenotypic stability. However, an instance can be visualized where the most widely adapted cultivar may be highest yielding in the maximum yielding in the maximum yielding site but can still be relatively unstable (high *b*). Eberhart and Russell (1966) proposed that an ideal cultivar would have a high mean yield, a regression coefficient of 1.0, and a small s^2d. Stroike and Johnson (1972) described widely adapted cultivars as having a strong response to more favorable conditions.

Drought resistance is defined as the ability to produce the highest yields under the most severely stressed conditions. Therefore, relative yields at the lowest expected environmental yield level is of major importance in assessing dryland adaptability. However, a widely adapted, drought resistant cultivar must have the genetic potential to respond maximally to more favorable environmental conditions in order to have the highest total production across all environments. Therefore, an ideal cultivar in terms of dryland adaptability is described as having (1) the highest yield under the most severely stressed condition and (2) the greatest response to more favorable moisture conditions (largest b).

The regression lines of the cultivars McDermid, Yamhill, Nugaines, and Golden were compared using both regression methods (Figures 10 and 11). At a very low environmental index (EI) which corresponds to 1.0 t/ha, Yamhill was predicted to yield the highest. McDermid and Golden were predicted to yield the same and Nugaines had the lowest predicted yield. McDermid began to outyield Yamhill when site yields were over 1.41 t/ha. McDermid was predicted to yield better than Nugaines in all environments and better than Golden when the EI was greater than -1.1 or 1.0 t/ha. Paha and Omar had

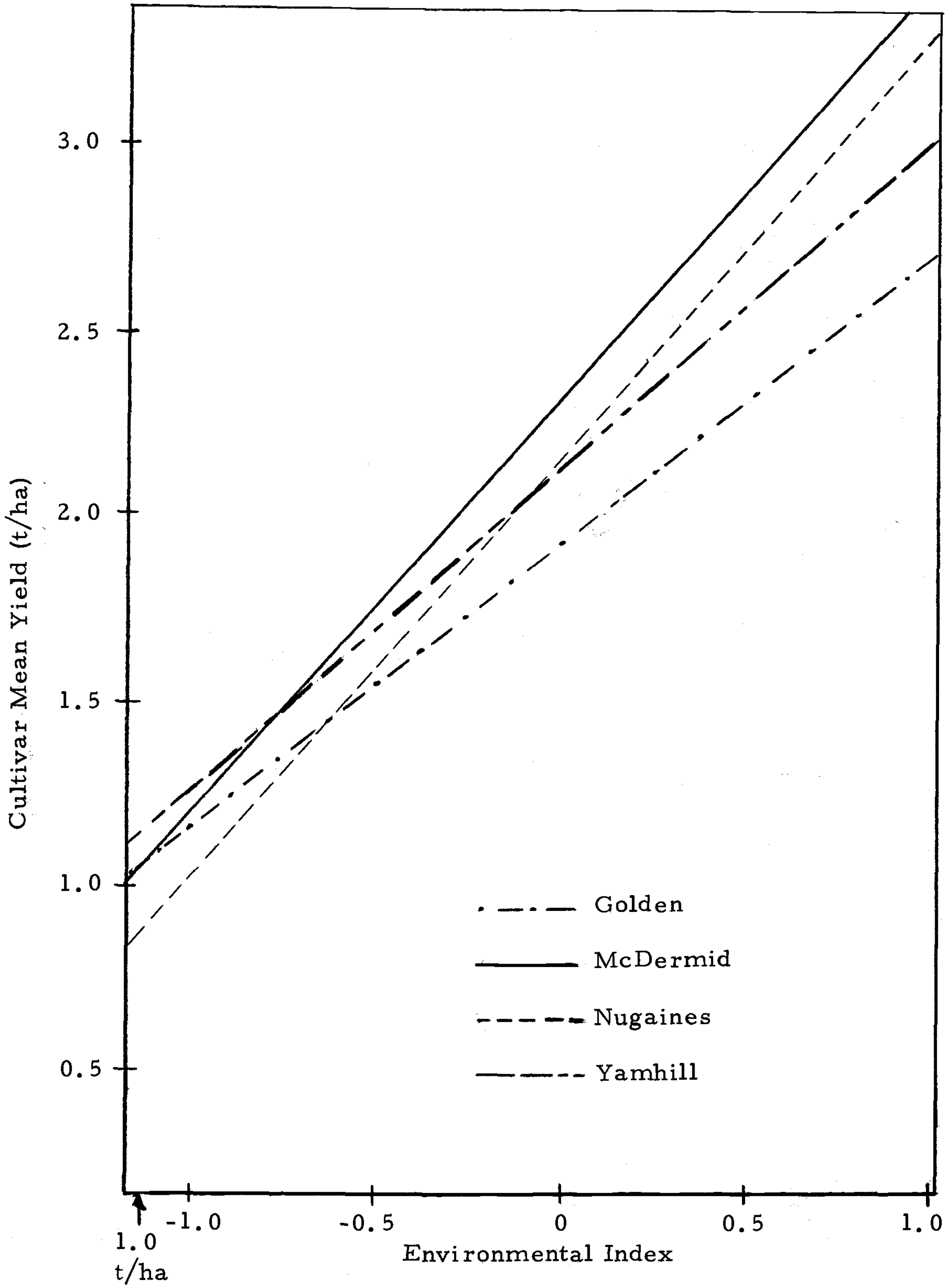

Figure 10. Regression of cultivar means of McDermid, Nugaines, Yamhill, and Golden on environmental index, Pendleton sites excluded.

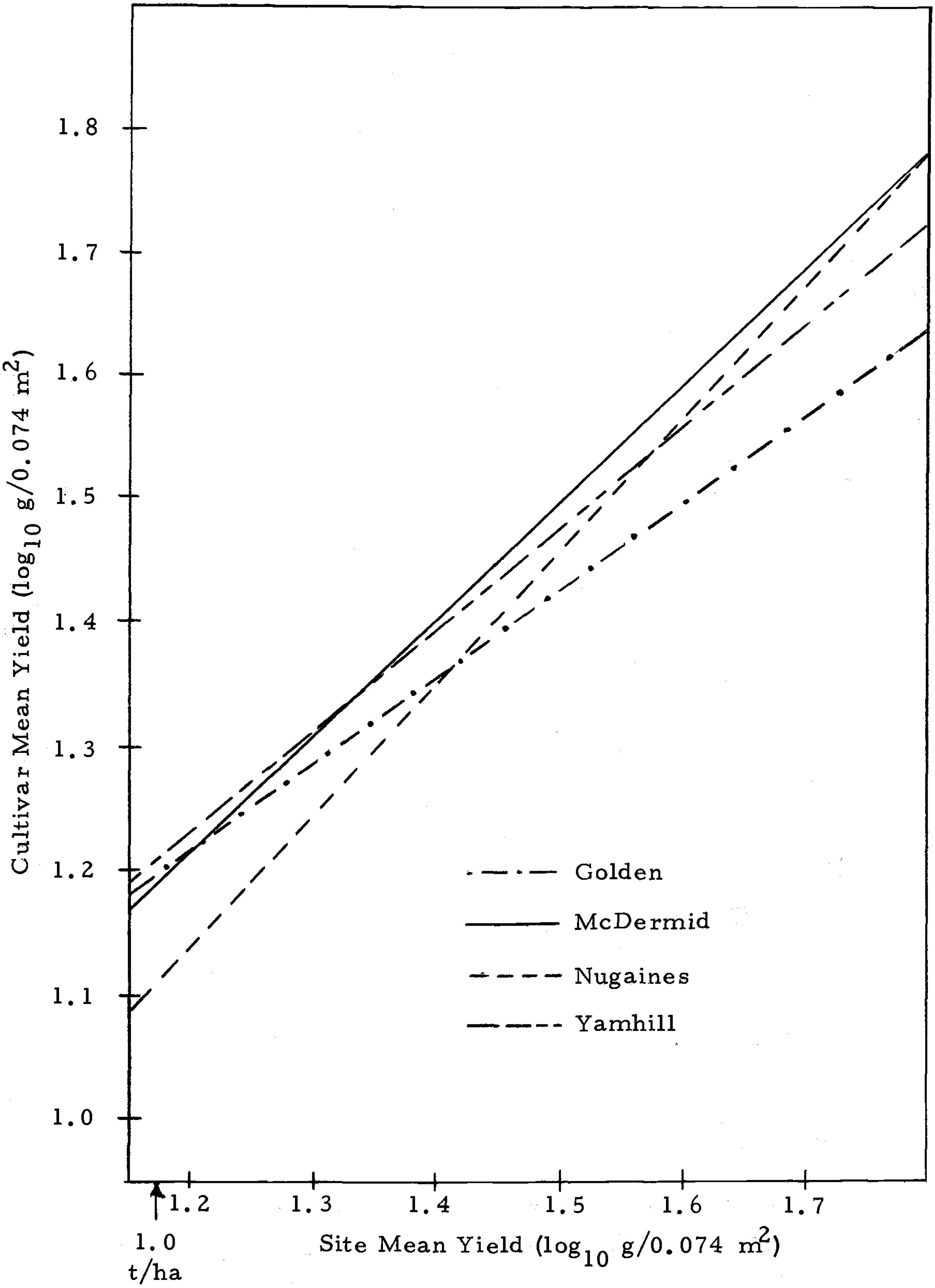

Figure 11. Regression of log$_{10}$ cultivar means of McDermid, Nugaines, Yamhill, and Golden on log$_{10}$ site means with all sites included.

much the same response as Nugaines although at lower yield levels throughout the range of environments (Figure 12). Moro showed a more stable response than Nugaines and was predicted to yield just below McDermid at an EI corresponding to 1.0 t/ha. Hyslop responded much like McDermid, and Wanser responded to environmental change much like Yamhill (Figure 13).

To test the accuracy of prediction under the most severely stressed condition (1.0 t/ha) the predicted cultivar yields were compared with the actual combined means at the two lowest yielding sites (Table 9). These sites, Pilot Rock in 1970 and Moro in 1973, had an overall combined yield of 0.97 t/ha. The predicted values had high correlations with the actual yields with the Finlay and Wilkinson method (Pendleton sites included) having the highest degree of accuracy in prediction.

No single cultivar analyzed in this study had both of the attributes of the ideal cultivar. Nugaines had the largest response to environments but this was in part due to its more negative response to lower yielding sites (Figure 10). Nugaines had low yields under the least favorable environment and, therefore, cannot be considered drought resistant or adapted to the whole range of conditions. Hyslop and McDermid had relatively good yields under very stressed conditions with the exception that McDermid had a low yield at Moro in 1973. The two cultivars also had sufficient response to better

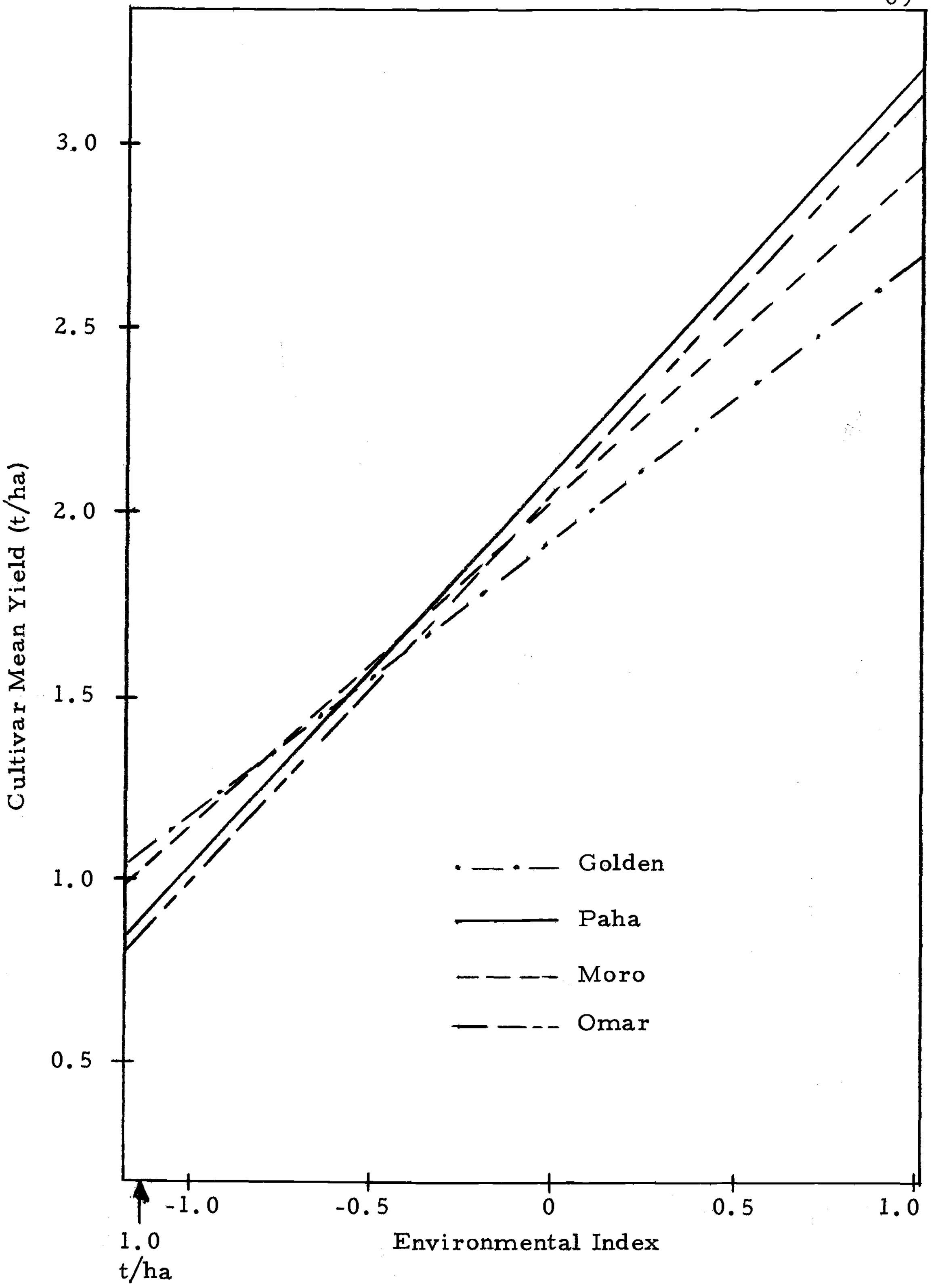

Figure 12. Regressions of cultivar means of Paha, Omar, Moro, and Golden on environmental index, Pendleton sites excluded.

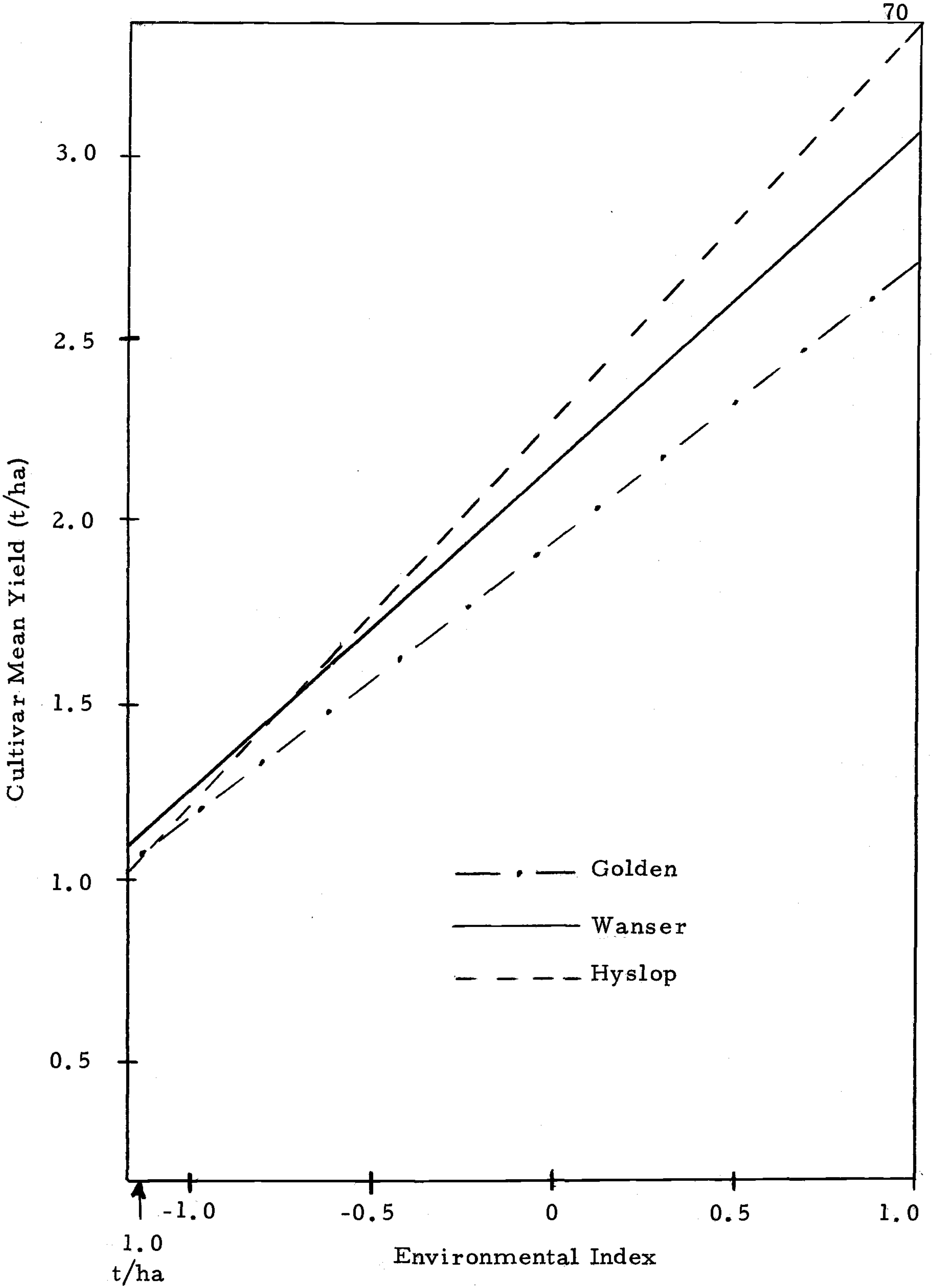

Figure 13. Regression of cultivar means for Hyslop, Wanser and Golden on environmental index, Pendleton sites excluded.

Table 9 . Predicted cultivar yields based on regression and a site mean of 1.0 ton per hectare and correlation of these predicted yields with the average cultivar yields at the two lowest yielding sites.

Cultivar	Combined[1] Means	B Predicted Mean	C Predicted Log Mean
Golden	.99	1.06	1.20
Omar	.88	.83	1.13
Wanser	1.04	1.13	1.21
Moro	1.06	1.02	1.18
Nugaines	.73	.88	1.11
McDermid	.98	1.05	1.19
Yamhill	1.19	1.14	1.21
Paha	.88	.91	1.13
Hyslop	1.14	1.06	1.23
Correlation Coefficient		0.83	0.91

[1] Cultivar means combined for Pilot Rock in 1970 and Moro in 1973 with an overall mean of 0.97 t/ha.

B = Excluding Pendleton sites - Eberhart and Russell method.

C = All sites included - Finlay and Wilkinson method.

conditions in order to yield well throughout the whole range of environments encountered. Therefore, McDermid and Hyslop were considered to be the most widely adapted cultivars.

The club wheats did not appear to be particularly adapted to these moisture limited wheat-growing areas, assuming the sites used in this study are representative. Moro and Omar had low overall yields as well as low predicted yields at the low yielding environment. These two cultivars had either the highest yield or were not significantly different from the highest yielder in only eight out of the 23 sites. Paha, a short club wheat, had a better overall yield record but tended to yield relatively lower in the low yielding environments. However, the club wheats have the ability to establish good stands in the fall, and they are important in dry areas where this can be a problem with other cultivars (Donaldson and Nagamitsu, 1973).

Golden may be considered to be least affected in yield by higher stress because it had the most stable response to environments. But this was due mainly to its inability to respond with higher yields to more favorable environments.

Yamhill and Wanser yielded well in the lowest yielding environments. However, they lacked the phenotypic response to better conditions in order to yield well in all environments. Wanser was the most predictable of all cultivars in its response to changing environments. Yamhill and Wanser may have some particular mechanisms which enable them to do well under the driest conditions. However, these cultivars are very unlike according to their parentage (Appendix Table 1), phenotype and area of commercial production. Yamhill is a mid-tall, awnless cultivar with large leaves and a large semi-compact head. Wanser is a tall, awned cultivar with smaller head and leaf size. Yamhill is currently grown in the high-yielding areas of the Willamette Valley in western Oregon. But Wanser is grown in some of the driest wheat-growing regions of eastern Oregon. Therefore, the cultivars cannot be assigned their drought resistance or dryland adaptability simply by knowledge of their phenotype or area of commercial production. Certain aspects of a cultivar's response to drought must be studied to ascertain the specific traits which enable it to yield well under dry conditions.

The fact that McDermid and Hyslop are widely adapted to moisture-limited conditions is of interest when taking into consideration the conditions under which these genotypes were selected. Early generation selection was conducted under essentially nonlimited moisture conditions of the Willamette Valley. The selections were later tested under a wide range of conditions throughout Oregon before their release. These facts are in support of the breeding program for water stressed environments as proposed by Roy and Murty (1970). They contend that initial selection should be conducted under maximum yielding conditions so as to permit maximum expression of developmental traits which contribute to dryland adaptability. Later selection and yield testing should be conducted under a wide range of conditions to insure wide adaptability of the genotypes.

IV. CULTIVAR RESPONSE TO WATER STRESS

Knowledge of how certain adapted cultivars respond to water stress conditions during development and with regard to grain yield and the components of yield would be useful. This would establish a basis for ascertaining mechanisms which enable a genotype to withstand stress. This knowledge would also be useful to the plant breeder in selecting for certain agronomic traits which contribute to drought resistance. The purpose of this study was to establish a basis for the expression of drought resistance by field study of cultivar responses to moisture stress in terms of plant water status, growth and development, grain yield and yield components.

Materials and Methods

1972 Study

Fifteen cultivars were grown at the Ryan Farm in Wasco County, Moro and Pilot Rock in 1972. The cultivars included were Yogo, Tendoy, Golden, Triplet, McDermid, Hyslop, Yamhill, Coulee, Brevor, Gaines, PI 178383 and Pullman Selection 101. The club wheats Moro, Paha and Omar/1854-1 were also included.

At Ryan Farm and Moro, nurseries consisted of randomized complete block designs with two replications, and each plot consisted of six rows, 61 cm long with 30 cm spacing between rows. Plants were space-planted at 10 cm intervals within the row. At Pilot Rock, nursery consisted of a randomized complete block design with four replications. Each plot consisted of one row, 2.7 m long, with plants spaced at 15 cm intervals.

Two, three-leaf samples were obtained from plants of each cultivar within each replication on 27 April and 9 June for osmotic potential determination. Yield and components were determined on a single plant basis for all equally competing plants in each plot. Plot means were used in the analysis of variance.

1973 Yield Trial Study

Ten cultivars (Appendix Table 1) were analyzed for yield and the components of yield at Pilot Rock, Pendleton and Heppner in 1973. Osmotic potential and water potential on each plot were determined once on 6 or 7 June during the grain filling period. Four replications of the randomized complete block experiments were analyzed. Plot means were used in the analysis.

Analysis of variance for each trait was conducted for each location and combined across the three locations. Correlation coefficients were calculated for all trait combinations.

Path-coefficient analysis (Dewey and Lu, 1959) was used to determine the pathways of association of the traits with grain yield.

The path-coefficient, a standarized partial-regression coefficient was obtained by the formula:

$$b' = b\frac{S_y}{S_i}$$

where b is the partial-regression coefficient determined by multiple regression analysis and S_y and S_i are the standard deviations of yield and the trait being considered, respectively.

Growth Analysis Study

Five cultivars, Yamhill, Hyslop, Nugaines, Moro and Wanser were sampled at time intervals from the jointing stage until maturity to obtain growth measurements under stress conditions. A plant tissue sample (0.093 m^2) was taken from each of four replications in a yield trial at Pilot Rock. Plant samples were obtained on 14 April, 12 May, 27 May and 7 July, 1973.

The samples were analyzed for number of tillers, total dry matter, leaf moisture content, leaf area, specific leaf weight, and leaf area ratio. Leaf samples for osmotic potential determination were also obtained.

Net assimilation rate ($\overline{NAR}$), crop growth rate ($\overline{CGR}$), and relative growth rate ($\overline{RGR}$) values were calculated using the following formulae (Radford 1967):

$$\overline{NAR} = \frac{W_2 - W_1}{A_2 - A_1} \cdot \frac{(\log_e A_2 - \log_e A_1)}{t_2 - t_1} = \text{mg dm}^{-2}\ \text{day}^{-1}$$

$$\overline{CGR} = \frac{W_2 - W_1}{t_2 - t_1} = \text{mg day}^{-1}$$

$$\overline{RGR} = \frac{\text{loge } W_2 - \text{loge } W_1}{(t_2 - t_1)} = \text{mg g}^{-1} \text{ day}^{-1}$$

where W, A and t are the total dry weight, photosynthetic area and time of sampling, respectively.

Total dry matter, grain yield, and yield components were obtained at harvest. Associations among traits and path-coefficient analysis were determined for grain yield, yield components, and the osmotic potentials which were obtained on 27 May and 6 June.

Determination of Plant and Soil Water Status

Three flag leaves or three of the youngest, fully developed leaves were removed at random from plants in each plot. The leaves were immediately placed in a sample holder made of clear vinyl tubing of 1.27 cm diameter and 10 cm long, sealed at both ends with rubber stoppers. Samples were placed in an ice chest containing dry ice in the field. Samples were kept frozen until they were used for osmotic potential determination in the laboratory.

Osmotic potential measurements were determined by use of a sample chamber psychrometer (C 51, Wescor Inc., Logan, Utah) in conjunction with at dew point microvoltmeter (HR 33, Wescor, Inc.).

Samples were warmed to room temperature. Sap was extracted from the tissue by squeezing the sample holder in a vise. A 6.4 mm diameter filter disk was soaked in the cell sap and placed in the psychrometer. Two minutes were allowed for vapor pressure equilibrium to occur within the chamber before passing a cooling current of 8.0 milliamperes through the themocouple junction for ten seconds. After cooling, the dew point temperature of the sample was maintained at the thermocouple by the dew point microvoltmeter. The dew point reading was determined and converted directly to bars of pressure by a factor calculated from the readings of KCl solutions with known osmotic potentials at a given temperature. Two readings were taken on each sample of expressed cell sap.

Water potential of the flag leaves was determined in the field by use of a pressure bomb apparatus (PMS Instruments, Corvallis, Oregon). The leaf blade was cut from the leaf sheath just above the collar. The leaf was inserted into a slit rubber stopper which was placed in the head of the pressure cylinder. This was locked on the pressure chamber with the blade inside the chamber except for the cut portion extending through the opening in the cylinder head. Pressure was slowly applied by use of pressured nitrogen gas. The pressure at which the leaf water began to exude from the cut-end portion of the blade was determined by means of a pressure gauge.

This was read directly in atmospheres and was later converted to bars. The negative value of this was taken to be the water potential of the leaf at the time of sampling. Three leaves from each plot were used in separate water potential determinations and the mean of the three were used in the analysis.

Soil samples were taken at depths of 30.5 cm intervals throughout the soil profile for moisture determination. Soil were sampled to a depth of 0.61, 0.91, and 1.14 m in the Heppner, Pilot Rock, and Pendleton yield trials, respectively on 7 June, 1973. Soil was sampled to a depth of 0.61 m in the growth analysis study at Pilot Rock at each plant sampling date in 1973. Each sample was placed in a small metal can which was then placed in a plastic bag. The sample was weighed and then dried in an oven until a constant dry weight was obtained. The moisture was calculated as a percentage of the dry soil weight. This value was converted to soil water potential by use of a soil moisture retention curve for each of the soil types sampled.

Results and Discussion

Plant Water Status in Relation to Yield and Component Responses

Osmotic potentials taken on 6 June, 1972, indicated that the plants at Pilot Rock were under the most severe water stress (Table

10). Plants at Ryan Farm appeared to be under less severe water stress than those at Moro (Tables 11 and 12). Soil water potentials did not indicate differences between locations as all samples had values lower than -15.0 bars.

Differences existed between cultivars in the osmotic potential readings at the three locations. The $\psi\pi$ measurement taken on 6 June during the grain filling period showed larger and more consistent differences than those taken on 27 April. Analysis of variance indicated no significant differences existed between cultivars for the $\psi\pi$, 27 April readings at Moro. The cultivar Yamhill had the highest (least negative) $\psi\pi$, values taken on 6 June at all locations, indicating that it maintained a relatively high internal water status. The club wheats, Paha, Moro and Omar/1854-1, had high $\psi\pi$ values, also. The cultivars, Yogo, Tendoy and Triplet were under relatively high stress as indicated by their low $\psi\pi$ values at the three locations. The remaining cultivars fluctuated between the extremes delineated by the previously mentioned cultivars. McDermid had a consistently lower $\psi\pi$ than its sister selection, Hyslop.

Grain yield and spike number per plant were characterized by high coefficients of variation. Except at Pilot Rock, the high error mean squares negated the possibility of finding significant yield differences between cultivars. Coefficients of variations were lower

Table 10. Cultivar means for yield, yield components, height, and osmotic potential from a nursery grown at Pilot Rock, Oregon in 1972.

Cultivar	Yield[1] (g)	Spike[1] Number	Kernels Per Spike	Kernel Weight	Osmotic[2] Potential	Height (cm)
Yogo	11.6	12.1	33.0	29.4	-28.1	92.8
Tendoy	11.9	11.7	31.9	32.0	-28.5	87.3
P-101	15.3	12.9	40.1	30.8	-26.0	66.7
Om/1854-1	16.4	11.3	52.8	28.0	-23.9	61.6
Golden	16.7	12.9	42.0	30.9	-25.1	84.1
Triplet	14.9	12.9	39.9	28.7	-28.3	83.2
McDermid	15.5	12.2	39.6	32.6	-26.0	70.4
Hyslop	14.9	10.9	45.5	32.4	-25.1	64.8
Yamhill	15.2	9.4	44.0	37.5	-23.7	55.9
Paha	16.1	9.9	59.1	26.8	-24.2	64.7
Coulee	12.5	13.7	32.6	29.4	-26.9	64.6
PI 178383	13.4	16.2	32.2	26.6	-25.0	83.5
Moro	15.9	11.6	53.8	25.6	-24.4	76.8
Brevor	10.7	8.8	33.2	38.0	-25.9	75.2
Gaines	14.6	15.8	33.6	28.4	-27.9	62.8
Mean	14.4	12.2	40.9	30.5	-25.9	73.0
Coefficient of Variation	16.4	16.0	9.8	5.7	5.4	5.4
Lease Significant Difference 5%	3.4	2.8	5.7	2.5	2.0	5.7

[1] Per plant

[2] Determined from the flag leaf during the grain filling period (9 June)

Table 11. Cultivar means for yield, yield components, height, and osmotic potential from a nursery grown at Ryan Farm in Wasco County, Oregon in 1972.

Cultivar	Yield (g)	Spike Number	Kernels Per Spike	Kernel Weight	Osmotic Potential 9 June	Osmotic Potential 27 April	Height (cm)
Yogo	10.3	8.6	35.8	32.6	-16.7	-21.5	103.4
Tendoy	10.3	8.9	32.9	35.8	-15.9	-20.4	92.3
P-101	15.1	10.6	39.1	35.5	-16.6	-20.8	71.5
Om/1854-1	13.9	6.3	60.4	36.9	-14.8	-19.9	69.7
Golden	10.7	8.8	37.1	32.8	-15.5	-20.6	88.5
Triplet	14.0	9.3	41.3	35.3	-16.6	-21.8	88.1
McDermid	15.8	9.6	41.6	38.4	-16.6	-20.0	70.1
Hyslop	13.7	8.1	43.4	38.7	-14.5	-20.7	66.4
Yamhill	13.5	5.9	56.0	41.1	-12.6	-19.8	72.1
Paha	14.1	5.9	66.9	35.1	-14.1	-20.9	73.8
Coulee	13.2	9.9	35.8	36.1	-16.7	-19.7	67.2
PI 178383	13.8	12.6	29.9	35.2	-14.8	-18.3	92.4
Moro	10.9	6.0	55.4	32.6	-14.6	-19.4	84.0
Brevor	10.0	7.8	32.8	39.0	-16.3	-18.6	74.3
Gaines	12.8	9.5	37.2	36.4	-16.6	-20.2	65.6
Mean	12.8	8.5	43.0	36.1	-15.5	-20.2	78.6
Coefficient of Variation	28.7	22.8	12.0	4.2	6.5	5.4	5.5
Least Significant Difference 5%	-	4.2	11.1	3.2	2.2	2.4	9.3

Table 12. Cultivar means for yield, yield components, height, and osmotic potential from nursery grown at Moro, Oregon in 1972.

Cultivar	Yield (g)	Spike Number	Kernels Per Spike	Kernel Weight (mg)	Osmotic Potential		Height (cm)
					9 June	27 April	
Yogo	4.3	7.8	24.1	24.0	-25.0	-18.5	70.9
Tendoy	4.6	6.7	24.8	26.8	-26.0	-20.4	67.6
P-101	4.6	6.9	28.1	23.7	-23.7	-22.6	55.0
Om/1854-1	4.4	4.3	42.2	24.9	-20.6	-20.4	47.9
Golden	5.6	6.3	31.4	28.2	-22.9	-20.2	62.4
Triplet	5.1	7.2	28.0	25.6	-23.6	-19.9	69.1
McDermid	5.2	6.2	30.1	27.6	-23.2	-19.1	56.2
Hyslop	4.4	4.4	35.1	29.2	-20.8	-20.0	55.5
Yamhill	5.4	4.9	34.9	31.0	-18.0	-19.3	51.7
Paha	6.2	4.4	54.4	26.2	-19.7	-20.2	52.4
Coulee	5.2	6.9	27.2	26.6	-20.7	-19.9	50.0
PI 178383	5.3	8.4	29.6	22.7	-18.2	-20.0	65.4
Moro	5.5	5.0	43.8	25.1	-18.1	-18.4	58.5
Brevor	4.9	5.9	24.2	32.9	-21.0	-20.7	58.4
Gaines	5.0	6.0	29.1	28.9	-21.7	-22.7	51.0
Total	5.0	6.1	32.4	26.9	-21.5	-20.2	58.1
Coefficient of Variation	33.5	26.5	18.2	7.0	12.5	13.0	7.7
Least Significant Difference 5%	-	3.5	12.7	4.1	5.8	-	9.6

and cultivar differences were found for kernels per head, kernel weight, and plant height.

PI 178383 had the largest spike number per plant at the three locations while Yamhill and Paha generally had low spike numbers. The club wheats, Paha, Moro and Omar/1854-1, were characterized as having a large number of kernels per spike at all locations and low kernel weights at Pilot Rock and Moro. Yamhill and Brevor had the highest kernel weights at all three locations. Yogo and Tendoy were the tallest cultivars and Nugaines was the shortest at all locations.

Correlations among all the traits were calculated (Table 13). Spike number and kernels per head had significant positive associations with yield indicating their major role in contributing to yield differences. Kernels per head and kernel weight, except at Ryan Farm, were negatively associated with spike number.

There was a significant positive association of yield and $\psi\pi$ taken on 6 June at Pilot Rock and Moro. The significant correlation between kernel weight and $\psi\pi$ taken on 6 June at Moro suggested that the relation of $\psi\pi$ and yield was mainly through kernel weight. At Pilot Rock, the association of $\psi\pi$ and yield appeared to be related to the positive association of $\psi\pi$ and kernel number per head. This was evident with Yamhill and the club wheats which had high $\psi\pi$ values, high kernel numbers and high yields and with Yogo and Tendoy which had low yields, low $\psi\pi$ values and low kernel numbers per spike.

Table 13. Phenotypic correlations among all traits measured at Pilot Rock, Moro, and Ryan Farm, Oregon in 1973.

	Yield	Spike Number	Kernels/ Spike	Kernel Weight	Osmotic Potential 9 June	Osmotic Potential 27 April
			Pilot Rock[1]			
Spike No.	0.59**					
Kls./Sk.	0.35*	-0.37*				
Kl. Wt.	-0.20	-0.45**	-0.23			
Osmotic Potential 9 June	0.31*	-0.17	0.56**	0.05		
Height	0.03	0.31*	-0.35*	-0.19	-0.36*	
			Moro			
Spike No.	0.36**					
Kls./Sk.	0.39**	-0.53**				
Kl. Wt.	0.16	-0.29*	-0.07			
Osmotic Potential 9 June	0.36**	-0.15	0.07	0.45**		
Osmotic Potential 27 April	-0.10	-0.01	0.02	-0.05	-0.08	
Height	0.11	0.52**	-0.32*	-0.21	-0.29*	0.12
			Ryan Farm			
Spike No.	0.65**					
Kls./Sk.	0.32*	-0.45**				
Kl. Wt.	0.24	-0.08	0.10			
Osmotic Potential 9 June	0.07	-0.28*	0.47**	0.22		
Osmotic Potential 27 April	0.06	0.18	-0.13	0.20	-0.11	
Height	-0.13	0.24	-0.30*	-0.49**	-0.08	-0.12

[1] Three replications only

* Significant at the 5% level

** Significant at the 1% level

At Ryan Farm which was under the least water stress, there was no association between $\psi\pi$ and yield. However, a negative association of $\psi\pi$ with spike number and a positive association with kernel number existed. The association of spike number and $\psi\pi$ was partially due to the low spike numbers and high $\psi\pi$ values of the club wheats and Yamhill.

The significant correlations of plant height with spike number and kernels per head indicated that the taller cultivars had larger tiller numbers and lower kernel numbers per spike. The negative association of kernel weight and plant height was evident with PI 178383, Yogo, Yamhill, Brevor, McDermid and Hyslop. The first two cultivars were tall and had low kernel weights, whereas the latter four cultivars were shorter and had relatively high kernel weights.

The early $\psi\pi$ measurements (27 April) appeared to be of little value in determining cultivaral differences and associations among traits because water stress was probably a less limiting factor in the earlier part of the growing season.

The major limit to this preliminary study was that it was conducted under space-planted conditions. Under solid-seeded conditions where there is enhanced competition among plants for a limited moisture supply, yield, yield component and $\psi\pi$ differences and association among the traits may change.

Cultivar differences existed in internal water status during the grain filling period. Although water stress varied among the locations, relative differences between cultivars remained stable. Yamhill and the club wheats, Paha, Moro and Omar/1845-1, appeared to be least affected by severe water stress in terms of yield and kernel number per head. Their high osmotic potential values indicated that they may avoid stress by maintaining a high internal water status. The space-planted conditions limit the extension of these conclusions to normal growing conditions. But the results established the need for further investigation into the response of wheat cultivars to water stress.

Although adequate soil moisture reserves from the fallow period were available to the 1973 wheat crop (Appendix Table 3), the exceptionally dry winter and spring severely limited crop yields throughout the dryland wheat growing regions of eastern Oregon. In the shallow soil areas such as Heppner and Pilot Rock, the available moisture was depleted early in the spring leaving little available for later crop development. At the locations with deep soils such as Pendleton, moisture depletion occurred later in the development of the crop.

Soil moisture samples taken on 7 June at Pendleton, Pilot Rock and Heppner had water potentials below -15.0 bars. This indicated that the crops were under high soil moisture stress during the grain filling period. Based on leaf water potential (ψ), the trial growing in the shallow soils at Heppner was under the most severe water stress of the three locations (Tables 14, 15, and 16). The crop at Pendleton was under the least stress as indicated by its high water potential and osmotic potential ($\psi\pi$) values.

The cultivar mean square for grain yield at Pilot Rock was nonsignificant. The high coefficient of variation for this trait indicated that a large amount of variation existed in the trial which could not be accounted for by the cultivar or replication effects. Although a nonsignificant cultivar mean square for yield existed at Heppner, significant differences between some cultivars were detected by use of the Duncan multiple range test. The cultivar mean squares for ψ at Pendleton and for $\psi\pi$ and kernels per spikelet at Heppner were also nonsignificant. Statistical analysis for kernel weight was not possible at Heppner because kernel weight was determined on a sample of the four replications bulked together. All other traits at the three locations had significant cultivar mean squares.

The locations were combined for analysis of variance for all traits except kernel weight (Tables 17 and 18). The locations did not have homogeneous error mean squares for grain yield and ψ. Therefore, tests of significance for these two traits may indicate differences which, in fact, may not exist. Significant location, cultivar and cultivar x location mean squares were evident for all traits except kernels

Table 14. Cultivar means for yield, yield components, osmotic potential and water potential from the yield trial at Pendleton, Oregon in 1973.

Cultivar	Yield	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic[2] Potential	Water[2] Potential
Golden	2.50 d[1]	498	21.6	16.0	1.35	23.4	-25.8	-20.5
Omar	2.89 cd	428	31.1	18.8	1.65	21.8	-27.8	-21.0
Wanser	2.80 cd	551	22.4	12.6	1.78	22.9	-32.5	-21.2
Moro	2.45 d	465	28.4	17.6	1.61	18.6	-28.2	-22.2
Nugaines	4.13 a	691	24.2	15.4	1.58	24.6	-26.9	-20.8
McDermid	4.02 a	680	26.4	14.9	1.77	22.3	-29.0	-22.6
Yamhill	3.37 bc	435	28.4	16.3	1.74	27.2	-22.7	-21.7
Paha	3.76 ab	441	37.8	19.4	1.94	22.7	-26.4	-21.9
Hyslop	4.35 a	599	28.5	16.3	1.75	25.6	-24.9	-21.2
Rew	4.18 a	496	32.5	17.1	1.90	25.9	-25.2	-21.3
Mean	3.45	529	28.1	19.0	1.71	23.5	-26.9	-21.4
Coefficient of Variation	11.3	9.1	8.4	3.5	9.3	6.4	11.5	7.8
Least Significant Difference 5%	0.6	70	3.4	1.0	0.23	2.2	4.5	-

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[1] Duncan's new multiple range test at the 5% level

[2] Determined from the flag leaf during the grain filling period

Table 15. Cultivar means for yield, yield components, osmotic potential and water potential from the yield trial at Pilot Rock, Oregon in 1973.

Cultivar	Yield	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential
Golden	1.71	264	20.8	15.4	1.35	31.4	-30.8	-40.8
Omar	1.59	241	21.2	17.2	1.24	29.5	-31.5	-35.8
Wanser	1.90	338	17.3	12.0	1.45	32.3	-34.8	-40.0
Moro	1.69	273	22.8	16.4	1.39	27.6	-32.0	-38.5
Nugaines	1.56	295	17.0	13.1	1.30	31.4	-33.6	-37.8
McDermid	1.72	328	17.1	13.0	1.32	30.6	-35.9	-38.9
Yamhill	1.90	233	22.6	16.2	1.39	36.3	-27.8	-33.6
Paha	1.68	243	23.4	17.6	1.33	29.4	-31.7	-35.4
Hyslop	1.48	254	18.1	14.1	1.29	32.3	-35.7	-35.4
Rew	1.81	242	21.0	13.7	1.53	35.8	-31.4	-41.4
Mean	1.70	271	20.1	14.9	1.36	31.6	-32.5	-37.8
Coefficient of Variation	17.0	11.7	14.1	4.3	14.4	3.7	7.6	8.8
Least Significant Difference 5%	-	46	4.1	0.9	-	1.7	3.6	4.8

Table 16. Cultivar means for yield, yield components, osmotic potential and water potential from the yield trial at Heppner, Oregon in 1973.

Cultivar	Yield	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential
Golden	1.34 abc	257	22.1	13.5	1.64	23.7[1]	-32.7	-47.5
Omar	1.19 c	201	27.4	15.2	1.80	21.8	-30.4	-44.6
Wanser	1.49 ab	277	19.5	10.8	1.80	27.7	-34.6	-46.6
Moro	1.25 bc	214	26.5	14.4	1.84	22.0	-31.3	-43.2
Nugaines	1.50 ab	275	20.0	12.2	1.64	27.0	-30.3	-43.7
McDermid	1.51 a	285	20.4	11.9	1.72	26.3	-30.8	-49.4
Yamhill	1.40 abc	208	22.6	14.5	1.56	30.1	-28.6	-43.4
Paha	1.24 bc	202	26.1	14.5	1.79	23.8	-32.0	-42.4
Hyslop	1.40 abc	222	23.3	13.1	1.79	27.2	-33.2	-44.8
Rew	1.36 abc	218	23.5	12.8	1.86	26.8	-26.7	-44.2
Mean	1.37	236	22.6	13.3	1.74	25.6	-31.1	-45.0
Coefficient of Variation	11.4	11.1	10.1	5.7	10.2	-	10.8	4.7
Least Significant Difference 5 %	-	38	3.3	1.1	-	-	-	3.1

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[1] Sampled from four replications. No statistical analysis possible

Table 17. Mean squares from the combined analysis of variance for seven traits measured on the ten cultivars grown at Pendleton, Pilot Rock and Heppner, Oregon in 1973.

Source of Variation	df	Yield[1]	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Osmotic Potential	Water[1] Potential
Location	2	10995.36**	1020924**	653.47**	99.857**	1.8183**	338.25*	5822.25**
Error (a)	9	140.98	2549	11.50	1.154	0.7553	71.86	18.12
Cultivars	9	172.14**	33231**	111.94**	35.179**	0.1028**	52.01**	22.86**
Cult. x Loc.	18	167.19**	7865**	20.15**	1.650**	0.0423	11.00	12.58*
Error (b)	81	19.00	1321	6.32	0.464	0.3180	8.78	5.93
Total	119							
Coefficient of Variation		13.5	10.5	10.6	4.6	11.1	9.8	7.0

[1] Error mean squares for the individual locations were not homogeneous

*Significant at the 5% level

**Significant at the 1% level

Table 18. Combined means for yield, yield components, osmotic potential and water potential for the ten cultivars grown at Pendleton, Pilot Rock and Heppner, Oregon in 1973.

Cultivar	Yield	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential
Golden	1.73	340	21.5	15.0	1.45	26.2	-29.8	-36.3
Omar	1.77	290	26.5	17.1	1.57	24.4	-29.9	-33.8
Wanser	1.93	389	19.7	11.8	1.68	27.6	-34.0	-35.9
Moro	1.68	317	25.9	16.2	1.62	22.8	-30.5	-34.6
Nugaines	2.24	420	20.4	13.6	1.50	27.7	-30.3	-34.1
McDermid	2.26	431	21.3	13.3	1.60	26.3	-31.9	-37.0
Yamhill	2.07	292	24.6	15.7	1.57	31.2	-26.4	-32.9
Paha	2.08	296	29.1	17.2	1.69	25.3	-30.0	-33.3
Hyslop	2.25	358	23.3	14.5	1.61	28.4	-31.3	-33.8
Rew	2.29	319	25.7	14.5	1.77	29.5	-27.8	-35.6
Mean	2.03	345	23.8	14.9	1.60	26.9	30.2	34.7
Coefficient of Variation	13.5	10.5	10.6	4.6	11.1	-	9.8	7.0
Least Significant Difference 5%	0.22	29	2.0	0.6	0.14	-	2.4	2.0

per spikelet and $\psi\pi$ which had nonsignificant cultivar x location mean squares.

As in 1972, Yamhill had $\psi\pi$ values which were the highest or among the highest at all locations indicating that its response was relatively stable across years and seeding conditions. The cultivar Rew had the highest $\psi\pi$ at Heppner as well as above average values at the other locations. The club wheats, Paha, Moro and Omar, had above average $\psi\pi$ values at Pilot Rock but had about average or below values at Heppner and Pendleton. As a group, their relative response in terms of $\psi\pi$ did not seem to be as high as it was under the space-planted conditions of 1972. Wanser had among the lowest $\psi\pi$ values at all the locations. Hyslop and McDermid had the lowest $\psi\pi$ values at Pilot Rock. The insignificant cultivar x location interaction mean square indicated that the cultivars responded the same in terms of $\psi\pi$ at the three locations.

There was no significant differences in water potential between cultivars at Pendleton. At Pilot Rock and Heppner, Yamhill had high ψ values. The club wheats, except for Moro at Pilot Rock also had high ψ values. Hyslop had above average ψ values at Pilot Rock and Heppner. Golden, McDermid and Wanser at Heppner and Pilot Rock, and Rew at Pilot Rock were under high moisture stress at the time of sampling as indicated by their low ψ values. At Heppner and Pilot Rock, cultivars with high $\psi\pi$ values generally had high ψ values although at Pilot Rock, Rew and Golden had high $\psi\pi$ but had the lowest ψ values.

In terms of grain yield, the cultivars responded differently at the three locations. At Pendleton, Hyslop gave the highest yield, although it was not significantly different from Rew, Nugaines, McDermid and Paha. Golden had the lowest yield but it was not significantly lower than yields of Moro, Omar and Wanser. Although cultivar yields were not different statistically at Pilot Rock, Yamhill and Wanser yielded the highest with Hyslop having the lowest yield. McDermid, Nugaines and Wanser had the highest mean yields at Heppner while Omar had the lowest grain yield.

Wanser, Nugaines and McDermid had the highest number of spikes per square meter at the three locations. Yamhill and the club wheats, Moro, Paha and Omar, had the lowest number of spikes. The club wheats and Yamhill had the highest spikelet numbers per spike. Wanser had the lowest spikelet numbers at the three locations.

Rew had the highest spikelet fertility (kernel number per spikelet) at all the locations, although the cultivar mean squares for this trait were nonsignificant at Pilot Rock and Heppner. The nonsignificant interaction mean square in the combined analysis of variance indicated that the cultivars responded relatively the same for this trait across locations.

Positive association existed for yield and spike number at all locations and for kernels per spikelet and yield at Pendleton and Pilot Rock (Table. 19). Kernel weight was significantly associated with yield at Pendleton and Heppner. Kernels per spike was positively associated with its two components, kernels per spikelet and spikelets per spike at all locations. Spikelets per spike were negatively associated with spike number at all locations. Kernel weight was negatively associated with spikelets per spike at Pilot Rock and Heppner. These negative correlations among the yield components were indicative of yield component compensation which is defined as the competition among sinks (yield components) during development for a limited source supply (photosynthates).

Although the association of $\psi\pi$ and grain yield was significant, the relationship was not absolute. Yamhill did not yield well at Pendleton even though it had a high $\psi\pi$, and Hyslop, Rew, Nugaines and McDermid yielded much higher, although they had lower $\psi\pi$ values. At Pilot Rock, Yamhill and Wanser yielded the highest even though their $\psi\pi$ values were very high and very low, respectively. At Heppner, where no relations were evident for $\psi\pi$ and ψ with yield, McDermid had the highest yield, even though it was under the most severe water stress. This study, therefore, supports the work of Kaul (1967, 1969) and Kaul and Crowle (1971) which found no unequivocal relationship between internal water status and yield in

Table 19. Associations among traits for cultivars grown at Pendleton, Pilot Rock and Heppner, Oregon in 1973.

	Spikes/m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential
			Pendleton				
Yield	0.49**	0.33*	-0.05	0.51**	0.68**	0.49**	0.03
Spikes/m^2		-0.50**	-0.54**	-0.19	0.13	-0.11	-0.12
Kls. /Spk.			0.73**	0.70**	0.04	0.24	0.02
Splts. /Spk.				0.03	-0.21	0.14	-0.02
Kls. /Splt.					0.27	0.21	0.07
Klwt.						0.66**	0.16
Osmotic Potential							0.09
			Pilot Rock				
Yield	0.44**	0.49**	-0.18	0.73**	0.30	0.45**	-0.03
Spikes/m^2		-0.43**	-0.63**	0.07	-0.12	-0.09	-0.17
Kls. /Spk.			0.55**	0.66**	-0.06	0.38*	0.14
Splts. /Spk.				-0.24	-0.35*	0.27	0.24
Kls. /Splt.					0.23	0.21	0.06
Klwt.						0.32*	0.00
Osmotic Potential							-0.06
			Heppner				
Yield	0.72**	-0.25	-0.30	-0.05	0.46**	0.05	-0.04
Spikes/m^2		-0.70**	-0.50**	-0.44**	0.23	-0.16	-0.29
Kls. /Spk.			0.63**	0.66**	-0.53**	0.15	0.33*
Splts. /Spk.				-0.16	-0.46**	0.17	0.44**
Kls. /Splt.					-0.22	0.08	0.02
Klwt.						0.11	-0.06
Osmotic Potential							0.29

*Significant at the 5% level

**Significant at the 1% level

spring wheat, even though consistent genotypic differences were evident for ψ and $\psi\pi$.

Osmotic potential had significant positive correlations with kernel weight at Pilot Rock and Pendleton. This is evident in cultivars, such as Yamhill and Rew, which had high $\psi\pi$ and kernel weights. This association was nonsignificant at Heppner. The positive association with kernels per spike and $\psi\pi$ was significant at Pilot Rock.

No association with ψ and any of the other traits occurred at Pilot Rock and Pendleton. At Heppner, positive correlations of ψ with kernels per spike and spikelets per spike were evident. This association was expressed in the cultivars McDermid and Wanser which had low ψ values and low spikelet numbers.

Path-coefficient analysis at each location gave an insight as to the direct and indirect relationships of the yield components, $\psi\pi$, and ψ with grain yield (Tables 20, 21, and 22). Spike number had the largest direct effect on yield. This effect was largest at Heppner and smallest at Pendleton. However, the total association of the two traits was smaller at Heppner as a result of negative indirect effects through some of the other yield components, mainly spikelet number but also kernels per spikelet.

A large positive direct relationship of spikelet number with yield existed at Pilot Rock and Heppner and to a smaller extent at Pendleton. But a negative total association was present at these

Table 20. Path-coefficient analysis of factors influencing yield of the ten wheat cultivars at Pendleton, Oregon in 1972.

Relationships of Yield and:	Direct Effect	Indirect Effects via: Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential	Total (r)
Spks. /m^2	0. 7735		-0. 1145	-0. 1514	-0. 0641	0. 0618	-0. 0104	-0. 0023	0. 4926
Kls. /Spk.	0. 2300	-0. 3852		0. 2046	0. 2403	0. 0186	0. 0235	0. 0004	0. 3322
Splts. /Spk.	0. 2811	-0. 4167	0. 1674		0. 0096	-0. 1000	0. 0135	-0. 0004	-0. 0455
Kls. /Splt.	0. 3423	-0. 1449	0. 1615	0. 0079		0. 1248	0. 0202	0. 0013	0. 5131
Kl. Wt.	0. 4703	0. 1017	0. 0091	-0. 0597	0. 0909		0. 0632	0. 0030	0. 6785
Osmotic Potential	0. 0964	-0. 0837	0. 0561	0. 0394	0. 0717	0. 3085		0. 0016	0. 4900
Water Potential	0. 0186	-0. 0938	0. 0047	-0. 0062	0. 0232	0. 0747	0. 0084		0. 0296

R^2 = 0. 9872

Residual = 0. 0128

Table 21. Path-coefficient analysis of factors influencing yield of the ten wheat cultivars at Pilot Rock, Oregon in 1973.

		Indirect Effects via:							
Relationships of Yield and:	Direct Effect	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential	Total (r)
Spks. /m^2	0.9277		-0.1137	-0.3453	0.0340	-0.0566	0.0030	0.0008	0.4439
Kls. /Spk.	0.2637	-0.4001		0.3028	0.3397	-0.0296	0.0120	-0.0007	0.4878
Splts. /Spk.	0.5491	-0.5834	0.1454		-0.1253	-0.1710	0.0085	-0.0012	-0.1779
Kls. /Splt.	0.5123	0.0615	0.1748	-0.1343		0.1103	0.0065	0.0003	0.7314
Kl. Wt.	0.4888	-0.1074	-0.0160	-0.1922	0.1156		0.0100	0.0000	0.2988
Osmotic Potential	0.0316	-0.0868	0.0997	0.1478	0.1056	0.1551		0.0003	0.4533
Water Potential	-0.0049	-0.1571	0.0368	0.1333	-0.0319	-0.0002	-0.0019		-0.0259

R^2 = 0.9780

Residual = 0.0220

Table 22. Path-coefficient analysis of factors influencing yield of the ten wheat cultivars at Heppner, Oregon in 1973.

Relationships of Yield and:	Direct Effect	Indirect Effects via:							Total
		Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential	Water Potential	(r)
Spikes/m^2	1.3035		0.1423	-0.4684	-0.4201	0.1616	0.0057	-0.0088	0.7158
Kls./Spk.	-0.2022	-0.9174		0.5965	0.6349	-0.3713	-0.0055	0.0100	-0.2550
Splts./Spk.	0.9412	-0.6482	-0.1281		-0.1486	-0.3193	-0.0062	0.0131	-0.2953
Kls./Splt.	0.9588	-0.5711	-0.1339	-0.1460		-0.1547	-0.0028	0.0007	-0.0490
Kl. Wt.	0.7014	0.3004	0.1070	-0.4288	-0.2114		-0.0040	-0.0018	0.4628
Osmotic Potential	-0.0362	-0.2054	-0.0305	0.1605	0.0734	0.0765		0.0088	0.0470
Water Potential	0.0300	-0.3828	-0.0677	0.4117	0.0224	0.0428	-0.0106		-0.0398

R^2 = 0.9811

Residual = 0.0189

locations as a result of a strong indirect relationship of the two traits via spike number and smaller indirect effects through kernels per spikelet and kernel weight.

A large direct effect of kernels per spikelet on grain yield existed at Heppner. However, the total association of these traits was very small because of a large negative indirect effect of kernels per spikelet via spike number and smaller negative effects through the other yield components. However at Pendleton and Pilot Rock, the direct relationship of kernels per spikelet with grain yield was enhanced by positive indirect relationships through kernels per spike and kernel weight.

The relationship of kernel weight with grain yield at Pendleton was primarily a result of a positive direct effect. At Heppner, the association of kernel weight and yield was a result of a large positive direct effect, a positive indirect effect via spike number and negative indirect effects through spikelet number and kernels per spikelet.

The negative indirect relationships of the yield components with yield through other yield components were lower at Heppner than at Pendleton and Pilot Rock. This indicated that a more intense yield component compensation had occurred at the more severely stressed location. Tillering made a contribution to yield but the effect was offset by the association of high tillering with smaller head size. Small head size is a pronounced characteristic of Wanser and Nugaines which have a high tillering capacity. The opposite case of low tillering capacity in relation to large head size is a characteristic of the club wheats and Yamhill. These cultivaral relationships were the most pronounced at Heppner which was under the most severe water stress.

The association of $\psi\pi$ with yield at Pendleton was primarily due to a positive indirect effect through kernel weight. This suggested that the high water stress only became a yield-limiting factor during the grain filling period when kernel weight was being established. At Pilot Rock, the significant association of $\psi\pi$ and yield was due to small positive indirect effects through all the yield components except spike number. This suggested that water stress became yield-limiting earlier in the development of the plant when spikelet number and fertility were being established. This was indicated at Heppner, also, by the small positive indirect effects of $\psi\pi$ as well as ψ, on yield via spikelet number, kernels per spikelet, and kernel weight. However, the total associations were very small because of the overriding effect of the negative indirect relationship of $\psi\pi$ and ψ with yield through spike number. These negative indirect relationships, although smaller were also found at Pendleton and Pilot Rock. This relationship indicated that high tillering capacity which had a large direct effect on yield was also related to a higher degree of water stress.

Therefore, the role of plant water status on final yield depends on the importance of spike number in contributing to yield differences as shown by the direct effect of spike number with yield. This determined the size of negative indirect effect of plant water status on yield via spike number.

Tillering is established presumably under better moisture conditions than the later-developed yield components. A cultivar which could develop a large number of spikes would in a sense escape drought during the development of the yield component which gives a high contribution to final grain yield. This escape characteristic could be assigned to Wanser, McDermid, and Nugaines, all of which depend on a large number of spikes for grain yield.

The negative relationship of tillering and plant water status supports the premise that excessive tillering causes earlier soil moisture depletion which contributes to higher stress in later stages of plant development (Hurd, 1971). Small late tillers which contribute almost nothing to final grain yield transpire valuable water which contributes to a higher soil moisture stress (Chinoy, 1961). Therefore, a restricted tillering capacity may be useful in conserving soil moisture. Few spike numbers are not necessarily detrimental to final yield under severe stress conditions, if the cultivar is able to avoid or tolerate stress during the later development and thus make adequate contributions to yield via the other components of yield.

However, under better moisture conditions, as shown at Pendleton, the inability to develop a large number of spikes appeared to cause the low yield in Yamhill.

The major effect of water stress on the final kernel weight is the decrease in the length of the grain filling period (Fisher, 1970; Asana, 1961). This is evident when low kernel weights are caused by hastened maturity in a crop under severe moisture stress. Presumably, a cultivar's ability to extend its photosynthetic activity during grain filling under stress could be a decided advantage in kernel weight and grain yield. Although the length of the grain filling period was not measured in this study, the relative maturity on 27 June was observed (Table 23). Large differences were not evident at Pilot Rock because most of the crop had reached maturity at this time. Yamhill, which was under the least internal stress at Heppner and Pendleton, had the highest number of green culms on 27 June which was indicative of a more prolonged grain filling period. This may be partially responsible for Yamhill's high kernel weights. At Pendleton, Wanser and McDermid were almost completely mature by 27 June. McDermid had the highest number of dry culms at Heppner which was also indicative of a shortened grain filling period. However, Wanser and McDermid appeared to tolerate to some extent a severe internal stress by maintaining average kernel weights at all locations.

Table 23. Relative maturity of ten cultivars expressed as percent of dry culms determined on 27 June at three locations in eastern Oregon.

	Percent Dry Culms on 27 June		
	Pendleton	Pilot Rock	Heppner
Golden	45	95	12
Omar	40	88	10
Wanser	86	95	24
Moro	55[1]	100	30
Nugaines	52	99	10
McDermid	92	100	51
Yamhill	29	98	2
Paha	40	99	11
Hyslop	79	100	50
Rew	50	100	20

[1] Three replications only

The relationship of grain filling period and kernel weight was not absolute as the club wheats matured relatively late but had low kernel weights. The length of the grain filling period deserves further study as to its importance. This along with kernel weight, as determined by large, plump kernels, are easily identifiable traits which may enable the breeder to select plants which maintain high tissue water status under stress conditions. Upon further study, these traits may also be useful in genetic studies of plant responses to water stress. Of particular interest, would be genetic analysis of crosses between McDermid or Wanser and Yamhill, and between Yamhill and cultivars not particularly adapted to stress conditions, such as Nugaines.

The yielding ability of Hyslop and Rew was related to their lack of a strong dependence on a single yield component for the final grain yield. This balance among the components enabled the genotypes to express a higher yield through a combination of small increases in each component. Therefore, Hyslop and Rew may utilize a combination avoidance, tolerance and escape characteristics in contributing to final yield under stress conditions. The moderate tillering capacity of Hyslop enabled partial escapement during development of this major yield component. The average or above average values for the later-developed components indicated that Hyslop could partially tolerate a moderate to high internal water stress. Rew tended to partially avoid severe internal stress during later development by maintaining a relatively high osmotic potential.

The general poor yields of the club wheats under stress conditions appeared to be related to a number of characteristics. They did not completely avoid stress as indicated by their moderate plant water stress and did not particularly tolerate this internal stress as indicated by their consistently low kernel weights. Because of the restricted tillering capacity of the club wheats they were also unable to compensate for the effect of stress on the later-developed components.

Response in Growth and Development to Water Stress

Soil moisture was available to the crop at Pilot Rock until the latter part of April when the moisture became depleted in the shallow soil (Table 24). The crop was under high soil moisture stress from the period of floral development through maturity. The growth measurements on the cultivars after the 14 April sampling were taken while the crop was under high soil moisture stress.

Table 24. Soil water potentials (bars) from soil moisture samples taken in the growth analysis study at Pilot Rock, Oregon in 1972.

	Soil Depth	
	0 - 30.5 cm	30.5 - 60 cm
14 April	-4.8	-3.5
12 May	<-15.0	<-15.0
27 May	<-15.0	<-15.0
8 June	<-15.0	<-15.0

The first sampling (14 April) occurred just before head initiation (jointing stage). The second sampling was made during the early boot stage, while the third sampling (27 May) was taken during the later part of anthesis. The 7 July sampling of dry matter and tiller number was done when maturity had been reached. No difference between cultivars in stage of development was observed at any of the sampling dates.

There were high coefficients of variation for dry matter, leaf area, and tiller number on the 14 April sampling date (Table 25). Dry matter increased over time while green leaf area increased to a point and then decreased. Tiller number was dramatically reduced between the first and second sampling dates, presumably at the onset of high moisture stress. Further reduction occurred from 12 May to 27 May.

Sampling date x cultivar mean squares for dry matter, leaf area and tiller number were not significant (Table 26) indicating that the cultivars responded in the same relative manner over time. Nugaines showed the highest tiller reduction primarily because it had more tillers at the onset of stress (Figure 14). This cultivar showed a reduction between all sampling dates. Wanser had the highest tiller number at maturity and had very little reduction in tiller number after anthesis. Yamhill had a high tiller reduction from 14 April to 12 May and had the lowest tiller number at maturity.

Yamhill maintained the highest leaf area ratio (leaf area/total dry weight) from jointing through anthesis (Table 26) while Hyslop maintained the lowest leaf area ratio at each sampling date. Wanser and Yamhill had low specific leaf weights (leaf weight per cm^2) while Hyslop and Nugaines had high values.

Osmotic potential and leaf moisture content decreased throughout the season (Table 27). No significant differences for leaf moisture content occurred during the later stages of development. Wanser

Table 25. Cultivar means for dry matter, leaf area and number of tillers from samples (0.093 m^2) taken at time intervals in the growth analysis study at Pilot Rock, Oregon in 1973.

	Dry Matter				Leaf Area (cm^2)			Tiller Number			
Cultivar	14 April	12 May	27 May	7 July	14 April	12 May	27 May	14 April	12 May	27 May	7 July
Yamhill	10.3	27.8	36.1	45.2	1150	1772	1070	63.2	27.5	21.2	18.5
Hyslop	10.3	28.5	30.6	47.3	994	1286	671	61.2	33.0	22.2	22.8
Nugaines	8.4	27.3	30.2	38.9	849	1465	856	90.5	48.0	32.2	26.5
Moro	7.9	29.3	29.9	35.9	779	1608	817	55.8	35.8	23.0	23.2
Wanser	8.1	29.9	31.5	44.0	903	1551	890	69.0	43.2	31.5	29.0
Mean	9.0	28.6	31.6	42.3	935	1536	861	68.0	37.5	26.0	24.0
Coefficient of Variation	23.1	14.0	12.8	14.5	23.7	17.6	18.5	23.5	16.6	16.8	16.6
Least Significant Difference 5%	-	-	-	-	-	-	-	-	6.8	6.8	6.1

Table 26. Cultivars means and significance of mean squares for traits measured over time in the growth analysis study at Pilot Rock, Oregon in 1973.

Cultivar	Total Dry Matter	Leaf Area	Number of Tillers	Leaf Area Ratio	Specific Leaf Weight	Percent Leaf Moisture	Osmotic Potential
Yamhill	29.9	1331	32.6	68.3	5.86	305	-27.7
Hyslop	29.2	984	34.8	54.7	6.40	261	-24.5
Nugaines	26.2	1057	49.3	61.4	6.54	291	-24.7
Moro	25.7	1067	34.4	60.2	6.05	277	-26.3
Wanser	28.4	1115	43.2	63.5	5.90	271	-30.8
Mean	27.9	1111	38.9	61.6	6.15	281	-25.6
Least Significant Difference 5%	4.3	184	9.1	3.5	0.25	18	2.9
Time Mean Square	**	**	**	**	**	**	**
Cultivar Mean Square	*	**	**	**	**	**	**
Time x Cultivar Mean Square	n. s.	n. s.	n. s.	*	n. s.	n. s.	**
Coefficient of Variation	15.5	20.0	23.3	6.9	5.0	7.7	11.3

* Significant at the 5% level
** Significant at the 1% level

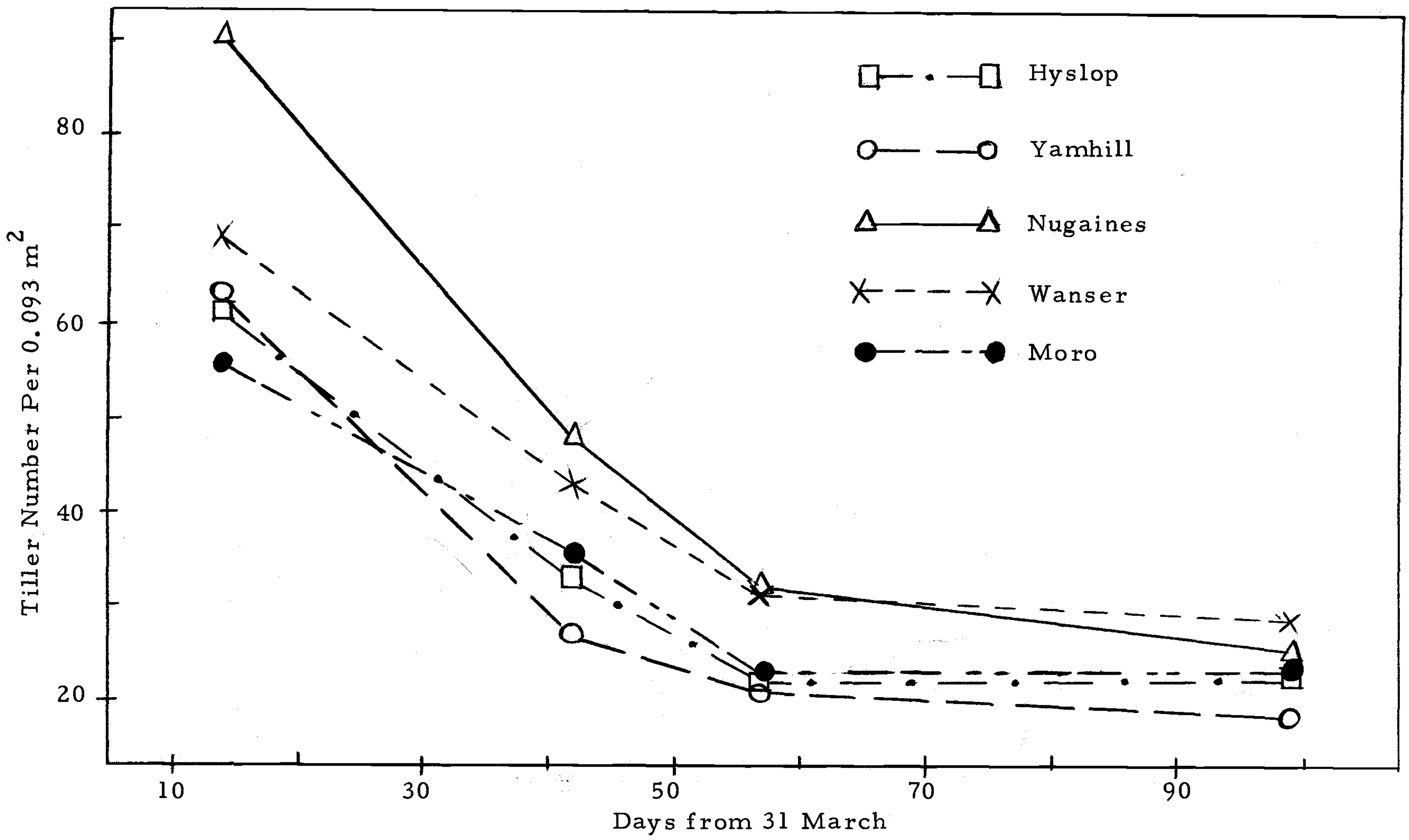

Figure 14. Change in number of tillers over time for the cultivars Hyslop, Yamhill, Nugaines, Wanser and Moro, sampled at Pilot Rock, Oregon in 1973.

Table 27. Cultivar means for leaf moisture percent (dry weight basis) and osmotic potential taken at time intervals in the growth analysis study at Pilot Rock, Oregon in 1973.

	Percent Leaf Moisture			Osmotic Potential			
Cultivar	14 April	12 May	27 May	14 April	12 May	27 May	6 June
Yamhill	445	283	188	-16.2	-21.7	-21.8	-27.3
Hyslop	374	240	170	-17.8	-24.3	-24.1	-31.9
Nugaines	409	272	191	-17.2	-24.2	-25.1	-32.3
Moro	404	241	174	-16.0	-26.4	-27.4	-35.6
Wanser	393	237	182	-18.1	-29.4	-31.9	-43.8
Mean	407	255	181	-17.1	-25.2	-26.1	-31.8
Coefficient of Variation	5.7	9.8	8.6	5.0	10.9	7.8	14.6
Least Significant Difference 5%	35.7	-	-	1.3	4.2	3.1	7.1

maintained the lowest $\psi\pi$ from jointing through the grain filling period while Yamhill had high $\psi\pi$ values (Figures 15). The significant cultivar x xampling date interaction was primarily due to the response of Moro between the first and second sampling dates.

Net assimilation rate was high from 14 April to 12 May (Stage 1) but was reduced from the boot stage through anthesis (Stage 2) (Table 28). NAR became larger during the period of grain filling (Stage 3). Crop growth rate (CGR) followed the same trend but relative growth rate (RGR) did not increase after anthesis. The increased NAR during grain filling was mainly due to a gradually decreasing leaf area while dry matter was continuing to increase. This study did not take into consideration the spike and awns as photosynthetic sources which contributed to dry matter increases during grain filling. The lack of increase in overall RGR during the grain filling period may have been due to an increase in dry matter which was not contributing to the source size or photosynthetic capacity, although cultivar differences were evident.

The cultivars showed dramatic differences in NAR changes (Figure 16). Yamhill had a low NAR during Stage 1 but it had high NAR relative to the other cultivars during Stage 2 because of the slight decrease in NAR from the first to the second time intervals. The NAR for Yamhill had only a small increase from Stage 2 to Stage 3 thus giving it a relatively low NAR during the grain filling stage.

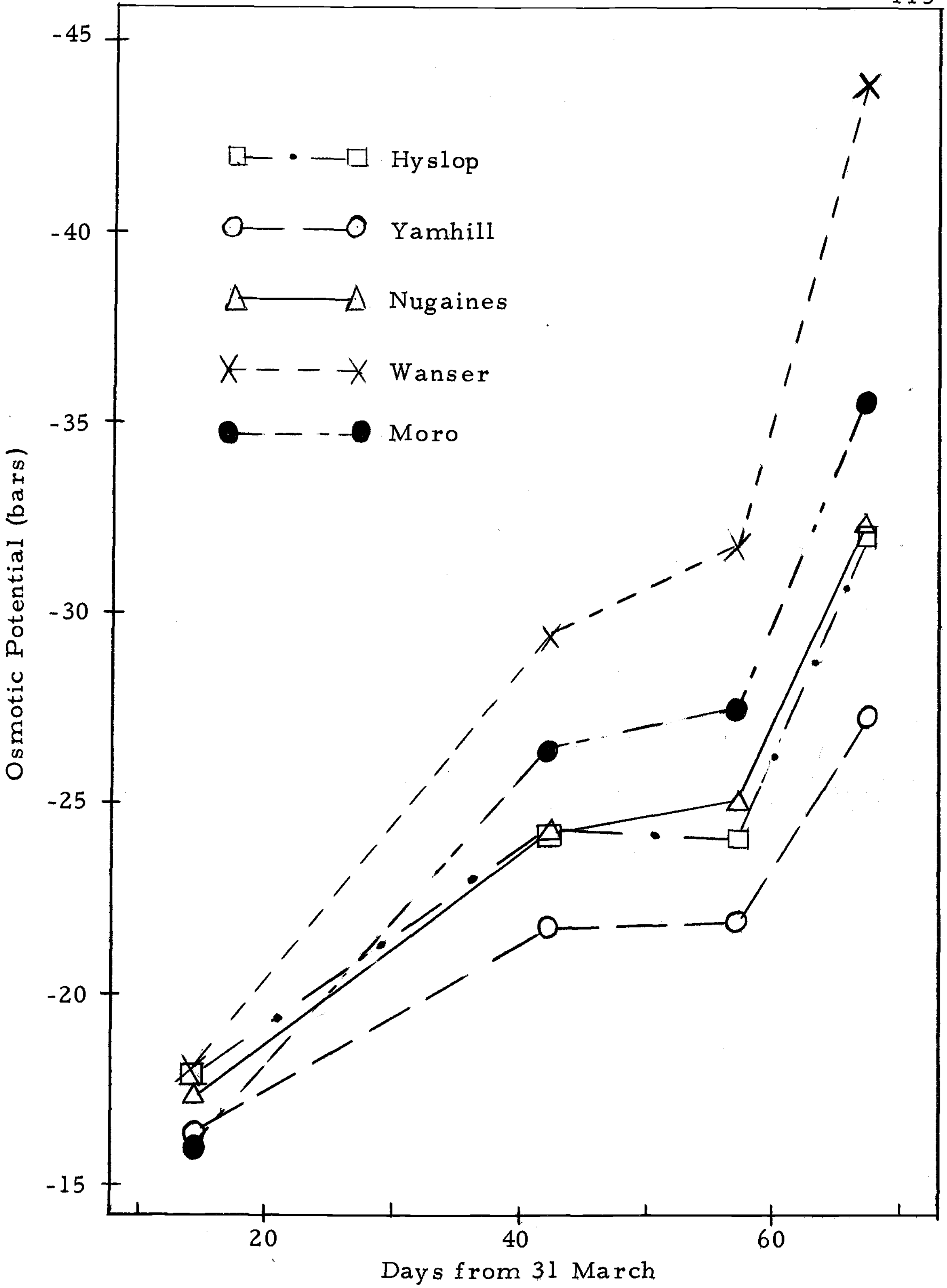

Figure 15. Change in osmotic potential over time for the cultivars, Hyslop, Yamhill, Nugaines, Wanser and Moro sampled at Pilot Rock, Oregon in 1973.

Table 28. Cultivar means for net assimilation rate, crop growth rate and relative growth rate for the three time intervals in the growth analysis study at Pilot Rock, Oregon in 1973.

	Net Assimilation Rate $mg\ dm^{-2}\ day^{-1}$			Crop Growth Rate $mg\ day^{-1}$			Relative Growth Rate $mg\ g^{-1}\ day^{-1}$		
Cultivar	14 April to 12 May	12 May to 27 May	27 May to 7 July	14 April to 12 May	12 May to 27 May	27 May to 7 July	14 April to 12 May	12 May to 27 May	27 May to 7 July
Yamhill	42.1	39.4	49.4	627	548	223	35.6	17.2	5.5
Hyslop	55.6	14.2	116.2	652	134	410	36.5	4.5	10.7
Nugaines	60.0	16.8	53.3	677	191	212	42.2	6.6	6.2
Moro	67.1	3.1	37.6	768	36	146	47.1	1.2	4.4
Wanser	65.1	15.8	75.3	780	103	306	46.8	3.4	8.2
Mean	57.9	17.4	64.9	701	203	260	41.4	6.7	7.1

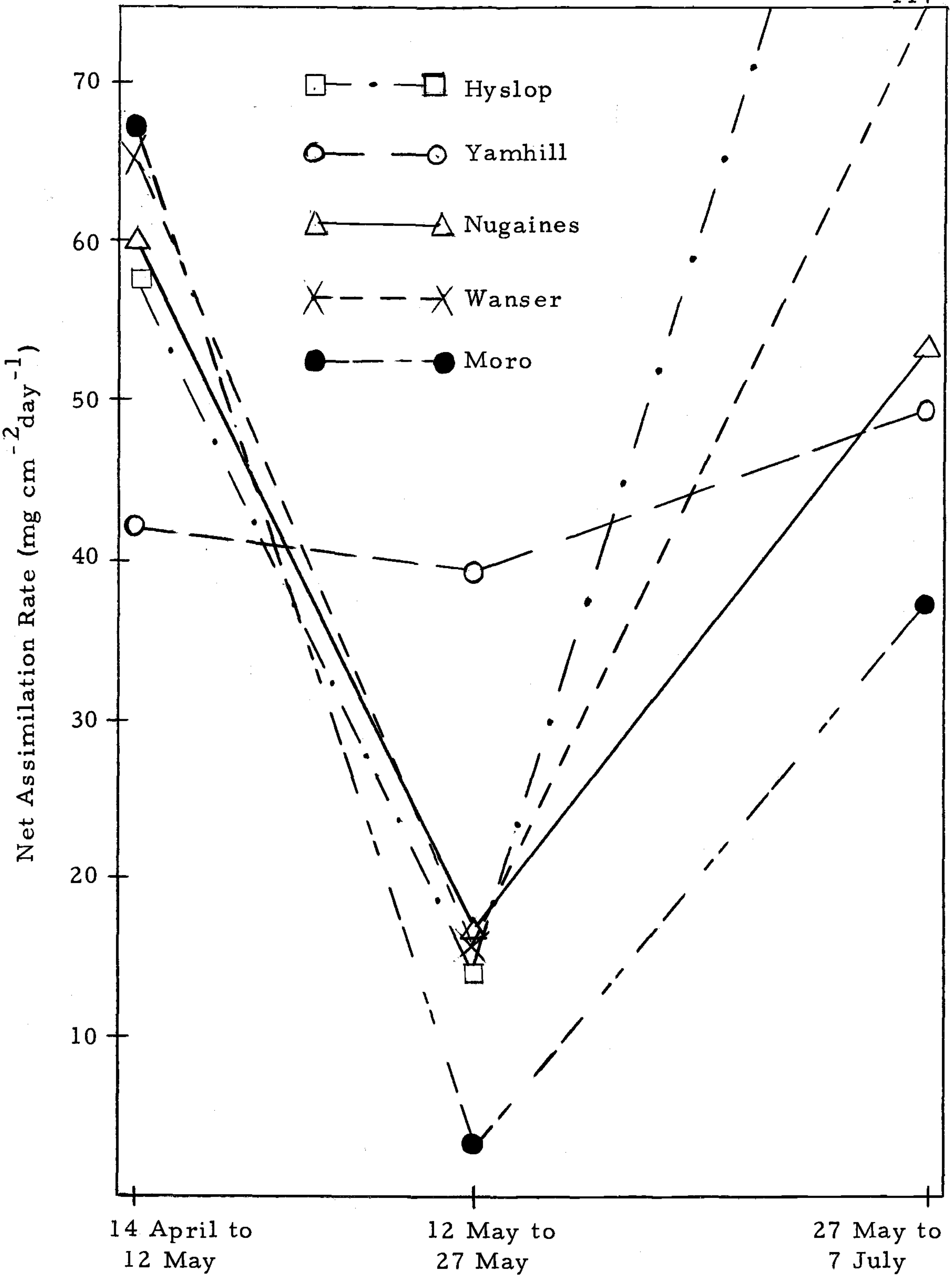

Figure 16. Change in net assimilation rate over three time intervals for the cultivars Hyslop, Yamhill, Nugaines, Wanser and Moro sampled at Pilot Rock, Oregon in 1973.

Moro had the most dramatic decrease in NAR from Stage 1 to Stage 2 and had the lowest NAR during grain filling. Hyslop was shown to have the highest NAR in Stage 3 indicating a high contribution per unit of photosynthetic area during the grain filling period. Cultivar differences were also evident in crop growth rate (Figure 17). All cultivars except Yamhill had a dramatic decrease in CGR from Stage 1 to Stage 2. Yamhill had a very high CGR relative to the other cultivars in the period from boot through anthesis. The crop growth rate for Yamhill decreased from Stage 2 to Stage 3 while all other cultivars had an increase in crop growth rates. Hyslop, Wanser, and Moro had an increased CGR in Stage 3 over those in Stage 2. The CGR for Nugaines did not change from Stage 2 to Stage 3. The relative cultivar responses were the same for RGR and CGR.

The results showed that under these stress conditions Yamhill had a different growth response during the period from boot stage through anthesis. While the other cultivars were making very small contributions to dry matter production during this stage, Yamhill was making a large contribution. This may be related to Yamhill's ability to avoid internal dessication. Hyslop and Wanser had large contributions to dry matter production during grain filling which appeared to compensate for their low contributions during the earlier stage. This indicated that Wanser may be relatively tolerant of its severe internal stress during the later stages of development. Moro had the lowest

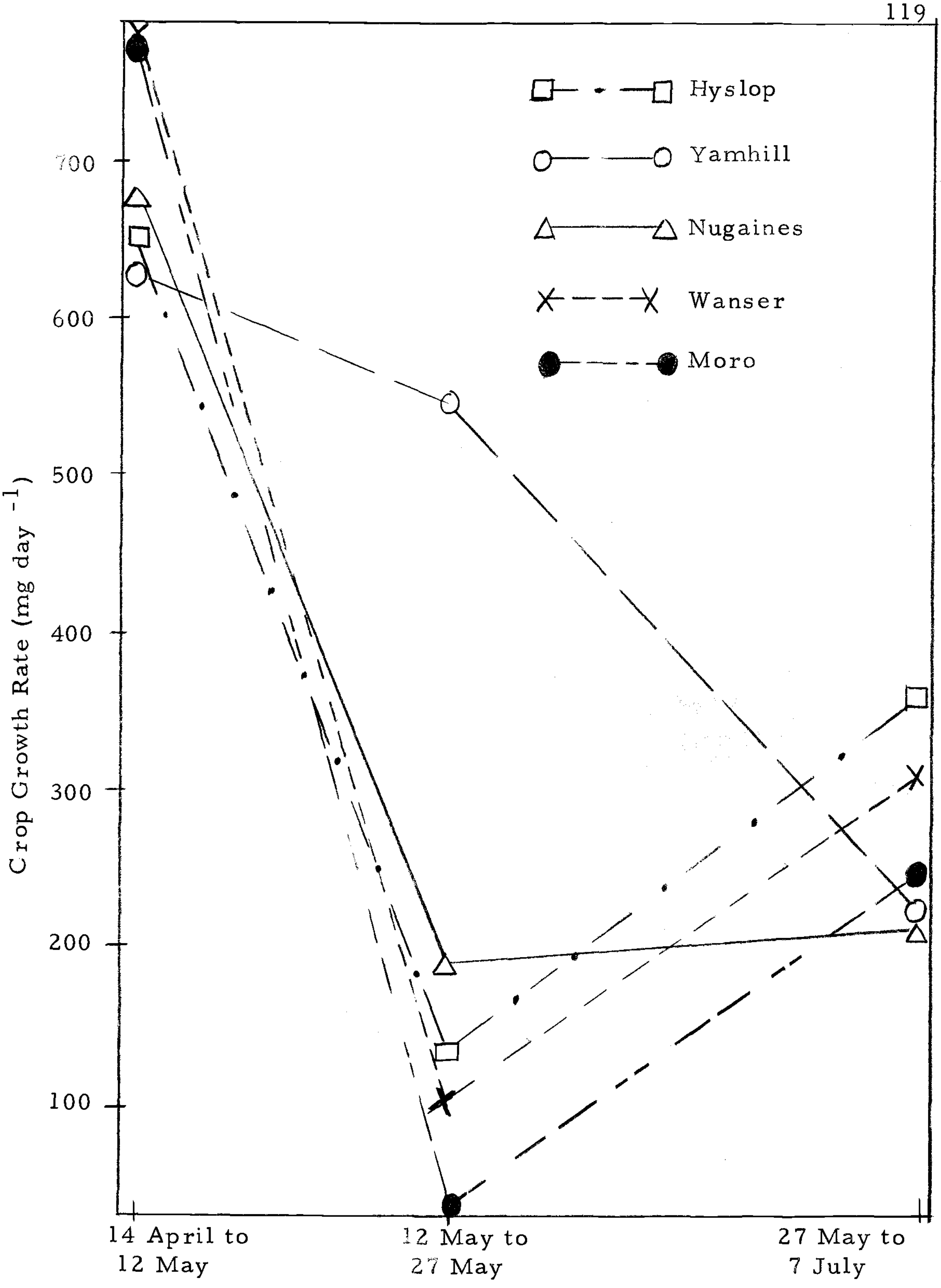

Figure 17. Change in crop growth rate over three time intervals for the cultivars, Hyslop, Yamhill, Nugaines, Wanser and Moro sampled at Pilot Rock, Oregon in 1973.

rate of dry matter accumulation from boot stage through grain filling which was indicative of an intolerance to a high internal water stress.

A high coefficient of variation was present for final grain yield (Table 29). The cultivar mean square for yield was nonsignificant. However, significant cultivar differences in grain yield were found (Duncan multiple range test). Hyslop and Yamhill were the highest yielding but were not significantly higher than Wanser and Nugaines. Moro had the lowest grain yield but was not significantly lower than Nugaines and Wanser. Wanser and Nugaines had the highest spike numbers and Yamhill, the lowest. Yamhill and Moro had high numbers of spikelets per spike while Nugaines had the lowest number. Yamhill and Hyslop had the highest numbers of kernels per spikelet. Yamhill had the highest kernel weight.

Total dry matter and grain yield had a very high positive association (Table 30). Kernel number per spikelet was highly correlated with grain yield and dry matter production. Spike number was negatively associated with spikelet number and $\psi\pi$ taken on 27 May. Kernel weight was significantly associated with $\psi\pi$ taken on 6 June.

Path coefficient analysis of the yield components (Table 31) indicated that spike number had a large direct effect on yield, but the total association was reduced by negative indirect effects through the other yield components. Because tillering capacity is determined

Table 29. Cultivar means for total dry matter, grain yield and yield components in the growth analysis study at Pilot Rock, Oregon in 1973.

Cultivar	Total Dry Matter	Grain Yield	Spikes/ m^2	Kernels/ Spike	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight
Yamhill	3.95 ab[1]	1.66 a	171.5	26.1	15.4	1.70	36.8
Hyslop	4.06 a	1.67 a	193.8	26.0	13.8	1.88	33.2
Nugaines	3.64 ab	1.35 ab	244.9	16.7	12.0	1.38	32.7
Moro	3.09 b	1.18 b	183.4	20.7	15.2	1.38	31.2
Wanser	3.45 ab	1.32 ab	239.6	17.0	12.2	1.39	32.2
Mean	3.64	1.44	206.4	21.3	13.7	1.55	33.2
Coefficient of Variation	15.0	19.8	11.8	12.4	5.3	13.0	4.8
Least Significant Difference 5%	-	-	37.6	4.1	1.1	0.31	2.5

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[1] Duncan multiple range test at the 5% level

Table 30. Correlations among grain yield, yield components, total dry matter, and osmotic potentials in the growth analysis study at Pilot Rock, Oregon in 1973.

	Spikes/ m^2	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Total Dry Matter	Osmotic Potential ($\psi \pi$)	
						27 May	6 June
Yield	0.27	0.26	0.74**	0.41	0.90**	0.22	0.21
Spks. /m^2		-0.50*	0.20	0.29	0.35	-0.47*	-0.42
Spklts. /Spk.			0.13	0.26	0.13	0.40	0.38
Kls. /Spklt.				0.30	0.58**	0.37	0.30
Kl. Wt.					0.44	0.31	0.46*
T. D. M.						0.24	0.19
Osmotic Potential 27 May							0.66**

*Significant at the 5% level

**Significant at the 1% level

Table 31. Path-coefficient analysis on yield of yield components and osmotic potential for five cultivars in the growth analysis study at Pilot Rock, Oregon in 1973.

Relationships of Yield and:	Direct Effect	Indirect Effects via:						Total (r)
		Spikes/ m^2	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight	Osmotic Potential ( )		
						27 May	7 June	
Spks. /m^2	0.7382		-0.2297	-0.1493	-0.0836	-0.0227	0.0190	0.2719
Splts. /Spk.	0.4557	-0.3721		0.0956	0.0757	0.0191	-0.0174	0.2566
Kls. /Splt.	0.7404	-0.1489	0.0589		0.0855	0.0180	-0.0137	0.7402
Kl. Wt.	0.2885	-0.2138	0.1196	0.2193		0.0151	-0.0209	0.4078
Osmotic Potential 27 May	0.0483	-0.3461	0.1801	0.2759	0.0902		-0.0299	0.2185
Osmotic Potential 6 June	-0.0455	-0.3092	0.1742	0.2235	0.1319	0.0318		0.2067

early in plant development, these negative indirect effects may be the result of a reduced source capacity (leaf area) per tiller. Kernel number per spikelet also had a high direct effect on grain yield which was expressed in the large final association of these two traits. Therefore, spikelet fertility was shown to be most important in determining grain yield in this study. The positive association of kernel weight and yield was due to a small positive direct effect, and indirect effects through spikelet number and kernel number per spikelet. The positive indirect associations among spikelet number, spikelet fertility and kernel weight suggested that there was no component compensation or competition for available assimilates when these yield components were being developed. If this were the case, the source capacity would not have been limiting at this time, and the major effect of an early stress on yield would have been through a reduced sink capacity (Fischer, 1970).

The small association of $\psi\pi$ and yield was due to small positive indirect effects through spikelets per spike, kernels per spikelet and kernel weight and a high negative indirect effect through spike number. These relationships indicated that the association of low spike numbers with high $\psi\pi$ values was more than compensated for by the positive associations of $\psi\pi$ with the other yield components. The cultivar Moro was an exception to this relationship because of its low spike number as well as a relatively low $\psi\pi$.

Moro had a relatively low growth rate during the later stages of development which was finally revealed in low total dry matter and low grain yield. The low grain yield was a combined result of low spike number, low spikelet fertility and low kernel weight. These poor values may be related to the high degree of internal water stress which Moro experienced from early boot through anthesis and during the grain filling period when these traits were being developed.

Wanser was under the highest degree of water stress throughout development. However, its high tillering capacity, established before stress occurred, compensated somewhat for the negative effect of water stress on the other components of yield. The high tillering capacity of Nugaines was not related to a severe internal water stress, as was the case with Wanser. However, Nugaines appeared to be intolerant to an even moderate internal stress during the spike development and grain filling because of its low values for spikelet number, spikelet fertility and kernel weight as compared to values for Hyslop which was under the same level of stress.

Hyslop was under a moderate internal stress during development and was the top yielder. This cultivar had a moderate tillering capacity and was relatively tolerant to stress during spikelet development, anthesis and grain filling. This was illustrated by a high NAR during grain filling and a high spikelet fertility.

Although Yamhill had a low spike number, it was able to yield well because of the combined compensation of its high spikelet number, spikelet fertility and kernel weight for its relatively low tillering capacity. The high values for these traits seem to be related to Yamhill's ability to avoid stress by maintaining a high internal water status during the periods of inflorescence development, anthesis and grain filling when these traits were being established. This was also evidenced by the high growth rate for Yamhill from the boot stage through anthesis.

Mechanisms which enable Yamhill to maintain high plant water status under stress should be the subjects of future drought study. This should include analysis of root growth and distribution; stomatal size, frequency and distribution; the importance of synchronous tillering; and the role of awns.

Based on the results of this experiment, avoidance of water stress during inflorescence development and grain filling, when some of the major yield components are being developed is important in contributing to final grain yield. Relative tolerance during the later stages of development is also important in genotypes not having the ability to avoid stress. A high tillering capacity may compensate for the effect of water stress on the later developed components.

The ability to yield well under stress conditions has been shown in this study to be expressed through yield components by different genotypic characteristics which contribute to drought resistance. This has implications in breeding for high in stress environments. Certainly, a breeder should use in his crossing program genotypes which have proven adaptation to stress conditions. However, he should not necessarily limit himself to these genotypes when breeding for drought resistance. More exotic plant types which have not necessarily been proven under stress should be incorporated into the germplasm pool to expand the breadth of variability and possibly increase the chances of ultimate success. For instance, Yamhill has many characteristics of the Swedish-type wheats which have been shown to yield well in moist climates of western Europe. However, this cultivar was shown to yield well under stress because of characteristics which contribute to drought avoidance. Also, selection in segregating generations should not be restricted to a specific ideotype because final yield under stress was shown in genotypes with widely different morphological characteristics.

V. SUMMARY AND CONCLUSIONS

The objective of this study was to characterize the expression of drought resistance in winter wheat grown under field stress conditions. Cultivars were evaluated for (1) their adaptability to moisture-limited areas of eastern Oregon and (2) their response to water stress in terms of plant water status, growth and development, yield and the components of yield.

Ten winter wheat cultivars were evaluated for yield and adaptability to limited moisture wheat-growing areas of eastern Oregon. The stability of cultivar yields across six locations and four years was assessed by regression of the cultivar mean for a site on the site mean. The mean of a given site was considered an estimate of the total effect of the environment. Regression coefficients were also calculated on $\log_{10}$ transformed data. The regression coefficient, the overall cultivar mean and the predicted mean at a low yielding environment of 1.0 t/ha were used to assess the adaptability to the wide range of environments and specific adaptability to drought stressed conditions.

McDermid and Hyslop yielded well under low moisture conditions and also had an adequate response to more favorable conditions which enabled them to yield well in all environments. Yamhill and Wanser yielded well under the least favorable conditions and were, therefore, considered to be relatively drought resistant. However, their high stability was due to an inability to respond adequately to more favorable environments. Nugaines and Paha had adequate overall yields but their instability across environments was due to their relatively poor grain yields under less favorable conditions. Golden had the lowest overall yield as well as the most stable response to environmental change. This cultivar yielded adequately under the least favorable conditions but lacked the genetic potential to respond adequately to more favorable environments.

Cultivars were evaluated under field conditions for their response to water stress in terms of internal plant water status, plant growth and development, grain yield and the components of yield. Osmotic potential of the cell sap expressed from previously frozen leaf samples was determined by use of sample chamber psychrometer. Total water potential was determined from detached flag leaves by the use of a pressure bomb apparatus.

Fifteen cultivars were evaluated for osmotic potential, yield, and yield components under space-planted conditions at three dryland locations in 1972. Consistent differences in plant water status during the grain filling period were found in some cultivars. Yamhill and the club wheats had high osmotic potentials. Associations of plant water status and some yield components were evident but this varied with locations. This preliminary study pointed to the need of further study of cultivar responses to water stress under solid-seeded conditions.

Ten cultivars were evaluated under solid-seeded conditions at three locations in 1973 for yield, the components of yield and plant water status during the grain filling period. Yield component compensation was most intense at the location under the most severe water stress. Spike number had the largest direct effect on yield but the final association with yield was reduced because of the association of large spike numbers with fewer kernels per spike. The direct effects of spikelet number and fertility were large at the location under the most severe stress but their total associations with yield were negative because of large negative indirect effects through the other yield components. Kernel weight had a large direct effect on yield at the most severely stressed location but its final association with yield was reduced somewhat because of negative indirect relationships through spikelet number and fertility.

Plant water status had positive indirect relationships with yield through spikelet number, kernels per spikelet, and kernel weight. However, a negative relationship through spike number reduced the total association of water status and yield. This was evident in McDermid and Wanser which were under the highest internal water stress but yielded well at the most severely stressed locations because of their large spike numbers. Yamhill consistently maintained a high internal water status. The yield of Yamhill was primarily due to its high kernel weight, as well as spikelet number and fertility. The high kernel weight of Yamhill appeared to be related to a longer grain filling period. The club wheats did not maintain a high internal water status under solid-seeded conditions. Their poor yield performance was related to the restricted tillering capacity as well as to their low kernel weights. Nugaines was under moderate stress, and its yield was related to a high tillering capacity and an average kernel weight. Hyslop was under moderate to severe stress and its yield was related to an average spike number, spikelet number and fertility, and an above average kernel weight.

Five cultivars were evaluated for growth responses and internal water status under field stress conditions for the period from head initiation to maturity. Total dry matter, yield, and yield components were determined at maturity to relate these traits to growth responses during development. The nursery came under severe soil moisture stress between head initiation and the boot stage. The tiller number was severely reduced when the nursery came under severe soil moisture stress, a period between the head initiation and boot stage. The net assimilation rate and growth rates generally showed a large reduction from head initiation to anthesis and an increase during the grain filling period, although differences occurred between some cultivars.

The cultivar Moro which was under high internal water stress had the lowest growth rates and net assimilation rates which was finally revealed in the lowest grain yield and total dry matter. The low yield was a result of low spike number along with low kernel weight and spikelet fertility. The higher yield of Wanser was related to a large amount of tillering before stress occurred which compensated somewhat for the negative effect of its severe internal water stress on later-developed yield components. Yamhill, which maintained a high internal water status throughout development, had a stable net assimilation rate and a slowly decreasing crop growth rate. The high grain yield of Yamhill may be related to a positive effect of a high internal water status during development on spikelet number and fertility and kernel weight. Hyslop, which was under moderate stress, yielded well because of its high tillering capacity as well as high spikelet fertility. Hyslop was also able to maintain a high growth rate and net assimilation rate during the grain filling period.

Based on the results of these studies the following conclusions are made:

(1) Drought resistance is the result of avoidance, tolerance and escape characteristics.

(2) Plant water status influences the components of yield, other than spike number, when their development occurs during a period of

high external stress. The contribution of plant water status to grain yield depends on the magnitude of the direct effect of spike number on yield.

(3) Drought avoidance is the ability to maintain a high plant water status when under high external stress conditions. In Yamhill, the stable growth rate during inflorescence development and the extended period of grain filling may have resulted from the ability of this cultivar to avoid drought. These characteristics also may explain the large spikelet number and the high kernel weight of Yamhill.

(4) Even though Hyslop and Wanser had a moderate and high internal water stress, respectively, they were able to tolerate stress in terms of high growth rates during the grain filling period.

(5) The high yielding ability of Wanser and McDermid under high stress conditions is primarily related to a large number of spikes. This trait was considered an escape characteristic because tillering was established before the onset of severe stress.

(6) The club wheats neither avoid or tolerate internal water stress under solid-seeded conditions nor do they have sufficient tillering capacity to compensate for the effect of stress on the later-developed components of yield.

(7) Nugaines, Hyslop and Rew maintain a moderate internal stress during later development but differ in their yield component responses. The yield of Nugaines depends primarily on a high

tillering capacity, whereas the yield of Rew and Hyslop depends on a balance of contributions from all the components of yield.

(8) Widely adapted cultivars, such as Hyslop and McDermid, not only yield well under severe stress conditions but have the genetic potential to respond adequately to more favorable moisture conditions.

(9) Cultivars specifically adapted to lower yielding environments, such as Yamhill and Wanser, are able to avoid, tolerate, or escape drought but are limited in one or more of their yield component responses to more favorable moisture conditions. Conversely, cultivars specifically adapted to higher yielding environments, such as Nugaines and Paha, lack the ability to consistently yield well under stress conditions but have a high response to more favorable moisture conditions.

(10) The cultivar best adapted to dryland cultivation should have the highest yield under stress conditions as expressed through the components of yield by one or a combination of avoidance, tolerance or escape characteristics. This cultivar should also have the maximum expression in, and balance among, the components of yield for maximum response to more favorable moisture conditions.

(11) Because high yield under stress was found to be manifested through different characteristics of the plant, the breeder should be aware of traits which contribute to drought resistance, but he should

not be restricted to a particular ideotype when breeding for yield under conditions of high moisture stress.

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APPENDIX

Appendix Table 1. Parentage and market classes of wheat cultivars analyzed for grain yield.

Cultivar	C.I. Number	Parentage	Market Class
Golden	10063	Selection From Fortyfold (C.I. 4156)	common, soft white
Nugaines	13968	Norin 10/Brevor//Orfed/Brevor'S'/3/Burt	"
Yamhill	14563	Heines VII/Redmond (Alba)	"
Hyslop	14564	Nord Desprez/2*Pullman Sel. 101	"
McDermid	14565	Nord Desprez/2*Pullman Sel. 101	"
Rew	17294	Orfed/Elgin//Elmar/3/Heines VII/4/ Orfed/Elgin//Elmar/3/P-101	"
Wanser	13844	Burt/Itana	common, hard red
Omar	13072	Elgin 19/Elmar	club, soft white
Moro	13740	P.I. 178383/2*Omar	club, soft white
Paha	14485	Suwon 92/4*Omar	club, soft white

Appendix Table 2. Locations of experiments in Oregon.

Name	Location	Soil Type
Pendleton	Experiment Station, Umatilla County 9 miles northeast of Pendleton	Walla Walla silt loam very deep
Pilot Rock	Bill and Jack Etter Farm, Umatilla County east and northeast of Pilot Rock	Pilot Rock silt loam moderately deep
Rew	Ronald Rew Farm, Umatilla County 10 miles west of Pendleton	Ritzville silt loam deep
Moro	Experiment Station, Sherman County at Moro	Walla Walla silt loam very deep
Heppner	Frank Anderson Ranch, Morrow County 12 miles southwest of Heppner	Morrow silt loam moderately deep
Arlington	Marion Weatherford Ranch, Gilliam County 10 miles south of Arlington	Ritzville silt loam deep
Ryan	Charles Ryan Farm, Wasco County 4 miles east of Dufur	Condon silt loam moderately deep

Appendix Table 3. Summary of climatic data at the Pendleton Experiment Station, Pendleton, Oregon and the Sherman Experiment Station, Moro, Oregon for the crop years 1970, 1971, 1972 and 1973.

Month	Temperature (C)				Precipitation		Evaporation		Wind Speed	
	Max.	Min.	Mean	±Normal[1]	Cm	± Normal[1]	Cm	± Normal[2]	Km/hr	± Normal[2]
					1970 Pendleton					
Sept.	25.0	7.2	16.1	0.6	1.65	-0.05	16.94	-0.18	4.5	0.5
Oct.	15.5	0.6	8.3	-1.7	3.58	0.05	-	-	3.1	-1.1
Nov.	11.7	-0.6	5.6	1.7	1.12	-3.53	-	-	3.7	-0.6
Dec.	5.0	-1.7	1.7	0.0	6.07	0.86	-	-	4.3	-0.8
Jan.	4.4	-3.3	0.6	1.1	13.28	8.26	-	-	4.3	-1.3
Feb.	8.9	0.0	4.4	1.7	3.81	0.10	-	-	4.2	-1.1
Mar	11.1	-0.6	5.6	-0.6	4.75	0.81	-	-	5.5	-0.6
Apr.	13.3	0.0	6.7	-3.3	2.67	-1.02	10.77	-1.20	6.9	1.1
May	21.6	5.0	13.3	0.0	1.57	-1.85	20.22	1.12	5.3	0.6
June	28.3	10.5	19.4	2.2	2.16	-1.30	24.51	4.39	6.0	1.4
July	32.7	12.2	22.2	1.1	0.28	-0.48	33.86	3.56	5.3	1.1
Aug.	32.2	9.4	21.1	0.6	0.13	-0.66	32.64	5.08	4.5	0.2
Total					41.07	1.19	138.94	12.78		
Previous Year					40.03	0.30	125.88	-1.65		
Crop Total (2 Years)					81.10	1.50	264.82	11.13		
					1970 Sherman					
Sept.	22.9	8.0	15.5[3]	-0.7	1.32	0.05	17.40	1.65	5.6	-1.6
Oct.	14.0	1.3	7.7	-2.7	1.32	-0.89	8.92	1.68	5.6	-0.3
Nov.	10.4	-0.2	5.2	1.4	1.35	-2.77	-	-	4.7	-1.0
Dec.	2.8	-2.9	0.0	-0.9	5.08	0.91	-	-	4.3	-1.8
Jan.	2.1	-4.3	1.1	0.2	10.06	5.51	-	-	5.1	-0.8
Feb.	7.1	0.2	3.7	2.2	3.23	0.05	-	-	5.8	-0.6
Mar.	10.0	0.2	5.1	-0.1	2.24	-0.51	-	-	7.7	-0.2
Apr.	11.6	0.2	5.9	-3.2	0.97	-0.97	13.06	0.71	9.7	0.0
May	18.6	4.4	11.5	-1.6	0.84	-1.30	31.41	3.66	8.4	-1.4
June	26.4	11.0	18.7	2.4	0.56	-1.68	28.27	6.60	6.4	-2.9
July	28.9	12.7	20.8	0.3	0.00	-0.43	33.83	5.00	6.9	-2.7
Aug.	28.8	11.3	20.0	0.3	0.00	-0.43	33.88	8.89	7.7	-1.3
Total					27.56	-2.44	156.77	28.19		
Previous Year					32.51	2.51	147.42	18.85		
Crop Total (2 Years)					60.07	0.08	304.19	47.04		

Appendix Table 3. Continued.

Month	Temperature (C)				Precipitation		Evaporation		Wind Speed	
	Max.	Min.	Mean	± Normal[1]	Cm	± Normal[1]	Cm	± Normal[2]	Km/hr	± Normal[2]
					1971 Pendleton					
Sept.	22.2	4.4	13.3	-2.8	2.59	0.89	15.70	-1.24	5.1	1.0
Oct.	16.6	1.1	8.9	-1.7	3.56	0.03	-	-	4.7	0.5
Nov.	10.5	0.0	5.0	0.6	5.64	1.07	-	-	6.0	1.4
Dec.	6.7	-2.8	1.7	0.0	2.59	-2.59	-	-	6.0	0.8
Jan.	7.8	-1.1	3.3	3.9	3.66	-1.35	-	-	6.6	1.4
Feb.	10.5	-2.2	3.9	1.1	1.96	-1.70	-	-	6.8	1.9
Mar.	10.0	-1.1	4.4	-1.7	3.25	-0.66	7.70	-	6.4	0.3
Apr.	15.5	1.7	8.3	-1.7	4.19	0.48	14.10	1.88	6.0	0.2
May	21.6	5.6	13.3	0.0	4.22	0.76	18.52	-0.51	4.3	-0.3
June	21.1	7.8	14.4	-2.8	7.98	4.42	14.76	-7.29	2.4	-1.9
July	32.2	15.0	21.1	0.0	1.60	0.81	28.78	-1.35	2.6	-1.3
Aug.	34.4	11.7	23.3	2.8	0.84	0.05	29.36	1.60	2.9	-1.3
Total					42.06	2.21	128.90	-6.91		
Previous Year					41.07	1.19	138.94	12.78		
Crop Total (2 Years)					83.13	3.40	267.84	5.87		
					1971 Sherman					
Sept.	19.7	5.4	12.6	-3.6	0.33	-0.94	19.28	3.53	7.7	0.5
Oct.	15.3	0.8	8.0	-2.3	1.73	-1.09	11.51	4.27	6.1	0.2
Nov.	8.1	0.7	3.7	-0.1	5.99	1.88	-	-	6.0	0.3
Dec.	4.3	3.2	0.6	-0.4	3.07	-1.09	-	-	5.6	-0.5
Jan.	6.8	2.3	2.3	3.6	4.14	-0.41	-	-	8.2	2.3
Feb.	8.5	1.9	3.3	1.9	0.30	-2.87	-	-	7.9	1.4
Mar.	8.2	1.8	3.2	-2.0	3.25	0.51	-	-	7.6	-0.3
Apr.	12.7	1.1	6.9	-2.2	2.13	0.20	14.83	2.49	10.0	0.3
May	19.1	6.2	12.7	-0.4	2.36	0.23	23.65	5.89	11.7	1.9
June	19.4	7.2	13.3	-3.1	2.06	-0.18	21.51	-0.15	9.5	0.2
July	29.0	12.8	20.9	0.4	0.51	0.08	34.39	5.56	7.7	-1.9
Aug.	30.6	13.6	22.1	2.4	0.23	-0.20	34.57	9.58	8.4	-0.6
Total					26.11	-3.89	159.74	31.17		
Previous Year					27.56	-2.44	156.77	28.19		
Crop Total (2 Years)					53.67	-6.32	316.51	59.36		

Appendix Table 3. Continued.

Month	Temperature (C)				Precipitation		Evaporation		Wind Speed	
	Max.	Min.	Mean	± Normal[1]	Cm	± Normal[1]	Cm	±Normal[2]	Km/hr	± Normal[2]
					1972 Pendleton					
Sept.	22.8	3.9	13.3	-2.2	0.84	0.05	16.08	-0.76	4.2	0.0
Oct.	16.6	-0.6	8.3	-2.2	4.37	1.85	8.28	-	3.2	-1.0
Nov.	10.5	0.0	5.6	1.1	7.98	0.81	-	-	3.7	-0.8
Dec.	6.1	-2.8	1.7	-0.6	9.98	3.33	-	-	6.8	1.4
Jan.	5.0	-4.4	0.0	0.6	2.92	-2.03	-	-	6.4	0.6
Feb.	6.7	-2.8	1.7	-1.1	4.31	0.64	-	-	4.8	-0.5
Mar.	13.3	1.7	7.8	1.7	5.36	1.40	8.36	-	5.5	-0.6
Apr.	15.0	0.6	7.8	-2.2	3.43	-0.28	14.00	1.60	7.1	1.1
May	22.2	5.6	13.9	0.6	3.81	0.36	19.79	0.69	4.0	-0.5
June	26.6	9.4	17.8	0.6	2.31	-1.22	25.25	2.87	5.6	1.3
July	30.5	11.1	20.5	-0.6	1.93	1.12	31.70	1.42	4.2	0.2
Aug.	31.6	11.1	21.6	1.1	0.89	0.10	28.93	2.34	3.5	-0.8
Total					48.13	6.13	152.39	8.16		
Previous Year					42.06	2.21	128.90	6.91		
Crop Total (2 Years)					90.19	8.34	281.29	1.25		
					1972 Sherman					
Sept.	20.1	5.2	12.7	-3.6	3.45	2.18	17.73	1.98	6.8	-0.5
Oct.	15.2	1.4	8.3	-2.0	1.14	-1.68	9.83	2.59	6.1	0.2
Nov.	9.0	-0.6	4.3	0.9	3.81	-0.30	-	-	6.1	0.5
Dec.	4.4	-3.3	0.6	-0.4	2.62	-1.55	-	-	7.6	1.4
Jan.	3.7	-4.0	-0.2	1.1	5.72	1.17	-	-	10.8	4.8
Feb.	5.9	-3.3	1.3	-0.1	0.66	-2.51	-	-	6.4	0.0
Mar.	11.6	1.1	6.3	1.1	3.66	0.91	-	-	6.9	-1.0
Apr.	12.0	-0.1	5.9	-3.1	1.02	-0.91	13.74	1.40	9.0	-0.6
May	20.5	5.3	12.9	-0.2	1.14	-0.99	22.73	4.98	7.7	-2.1
June	23.8	9.8	16.8	0.5	4.32	2.08	26.42	4.75	8.0	-1.3
July	28.6	11.7	20.1	-0.3	0.18	-0.25	34.14	5.31	7.4	-2.3
Aug.	29.7	12.7	21.2	1.5	1.40	0.97	31.80	6.81	7.2	-1.8
Total					29.11	-0.89	156.39	27.81		
Previous Year					26.11	-3.89	159.74	31.17		
Crop Total (2 Years)					55.22	-4.78	316.13	58.98		

Appendix Table 3. Continued.

Month	Temperature (C)				Precipitation		Evaporation		Wind Speed	
	Max.	Min.	Mean	± Normal[1]	Cm	± Normal[1]	Cm	± Normal[2]	Km/hr	± Normal[2]
					1973 Pendleton					
Sept.	23.3	4.4	13.9	-1.7	1.24	-0.51	19.23	2.13	5.5	1.1
Oct.	17.2	0.0	8.9	-1.7	1.68	-1.83	8.56	-	2.9	-1.1
Nov.	10.5	0.0	5.0	0.6	2.90	-1.73	-	-	3.4	-1.0
Dec.	1.7	-9.4	-3.9	-5.6	6.27	0.97	-	-	4.8	-0.5
Jan.	_[4]									
Feb.										
Mar.										
Apr.										
May										
June										
July										
Aug.										
Total										
Previous Year					42.06	2.21				
Crop Total (2 Years)										
					1973 Sherman					
Sept.	20.7	5.8	13.3	-2.9	1.45	0.18	17.42	1.68	6.6	-0.6
Oct.	16.5	1.7	9.1	-1.2	1.09	-1.73	9.65	2.41	5.1	-0.8
Nov.	8.3	0.6	4.4	0.7	2.11	-2.01	-	-	3.4	-2.3
Dec.	0.4	-8.2	-3.8	-4.8	4.11	-0.05	-	-	6.1	0.0
Jan.	2.6	-5.8	-1.6	-0.3	2.77	-1.77	-	-	4.7	-1.3
Feb.	6.2	-2.4	1.9	0.4	0.86	-2.31	-	-	3.9	-2.6
Mar.	11.1	19.6	5.6	0.3	1.02	-1.73	-	-	7.1	-0.8
Apr.	15.5	1.8	8.7	-0.4	0.53	-1.40	16.79	4.44	9.3	-0.3
May	20.8	5.3	13.0	-0.1	0.86	-1.27	24.33	6.58	8.2	-1.6
June	23.3	8.7	16.0	-0.3	0.64	-1.60	26.82	5.16	9.8	0.5
July	29.0	12.8	20.9	0.4	0.00	-0.43	36.96	8.13	9.5	-0.2
Aug.	26.3	10.9	18.6	-1.1	0.18	-0.25	31.57	6.58	9.8	0.8
Total					15.62	-14.38	163.55	34.98		
Previous Year					29.11	-0.89	156.39	27.81		
Crop Total (2 Years)					19.33	-15.27	319.94	62.79		

[1] Average 1929 - present

[2] Average 1963 - present

[3] Average 1931 - 1960

[4] Summarized data, not available