PHYSIOLOGICAL RESPONSES OF TRITICUM AESTIVUM L.
TO DECREASING SOIL WATER POTENTIAL

By

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TABLE OF CONTENTS

LIST OF TABLES

Table | Page

CHAPTER II

CHAPTER III

LIST OF FIGURES

Figure | Page

CHAPTER II

CHAPTER III

CHAPTER I

Introduction

This dissertation is composed of two main chapters. Each chapter is a separate paper prepared for publication in a professional journal.

There is perhaps no single factor more critical to crop production in arid and semi-arid regions than the availability of water. Water is absorbed by the plant roots, translocated to the aerial organs, and subsequently transpired. The movement of water from the soil through the plant and into the atmosphere can, therefore, be viewed as a catenary process. Under conditions of prolonged water-stress, i.e., drought, several components of this catena are altered giving rise to a cascade of events that directly affect a number of physiological and morphological characters involved in crop production potential. Moreover, the survival of the crop is ultimately affected. Since most wheat is grown in temperate areas where severe and frequent moisture deficits can occur, there has been great interest in developing genotypes that are capable of resistance to drought stress and yet high yielding under such conditions. However, the effects of drought stress on plant physiological processes is not clear and our understanding of them is, therefore, limited. Because of this, the subject of stress-physiology has received much attention and research in this direction has accelerated. This dissertation reports research on certain physiological responses of wheat to drought stress and their relationship with growth, production, and survival (resistance to drought).

A main component of the catena is the water held in the soil. As soil-water is extracted by the plant, its potential energy, the soil-water potential decreases. Under drought stress conditions, soil-water potential becomes very low and the plant must adjust its internal water status accordingly in order to continue growth and survive. Some cultivars of wheat appear to do this better than others, yet it is not understood how or to what extent soil-water potential affects the ability of different cultivars to do so. Quantification of this differential response may help breeders to identify genotypic characters that are important for survival and high yield under drought stress.

The major objective of this research was to identify the relationship between drought resistance and some physiological responses of winter wheat and the relationship of such responses to growth, productivity, and survival under drought stress conditions. The specific objective was to differentiate between these responses of cultivars with varying levels of resistance to drought stress.

CHAPTER II

The Effect of Soil-Matric Potential on Winter Wheat with Spatially Dissimilar Rooting Systems

Abstract

The purpose of this study was to measure the physiological responses of a drought resistant and a drought susceptible cultivar to varying levels of soil-matric potential. Roots were divided between soil and soil (SS), soil and nutrient solution (SN), and nutrient solution and nutrient solution (NN) in which soil had a matric potential and nutrient solution had zero matric potential. The soil was well watered for the first 39 days of the experiment. During the final 37 days of the experiment, no water was added to one side of the SS treatment or to the soil side of the SN treatment. At the end of the experiment, labelled phosphorus was added as a tracer to one soil side of the SS treatment and to the nutrient side of the SN and NN treatments in order to determine the water transfer potential of each spatially dissimilar rooting system for each cultivar. In addition, other physiological measurements included root and shoot growth, stomatal resistance, and internal plant-water relations.

The results showed that the drought resistant cultivar with roots split in SN grew taller, had greater root growth, and had a lower osmotic potential and higher turgor potential than the drought susceptible cultivar. Soil-matric potential appeared to have a strong

effect on the growth of both cultivars as indicated by the significant differences in plant height, root and shoot dry-weights, and total root length for each split-root treatment. X-ray films provided evidence that no labelled phosphorus was transferred from the labelled side to the unlabelled side by any plants regardless of the split-root treatment in which they were grown. Turgor potential was the only physiological variable that showed significant differences between cultivars, split-root treatments, and stress periods.

Introduction and Literature Review

The physiology of drought resistance is complex because plant-water deficits affect every aspect of growth. Drought reduces water absorption by roots, cell turgor, cell division, cell enlargement, stomatal opening, and consequently, decreases leaf area, root growth, and nutrient uptake (Maximov, 1929; Hsiao, 1973; Levitt, 1980). Many studies have contrasted the drought resistance of diverse species (e.g., Larcher, 1980), but few have described different cultivars, even though plant breeders have long noted that certain cultivars are able to grow in a droughty environment where others die (Kramer, 1980). Physiological reasons for the variation remain obscure. One way, therefore, to evaluate the physiology of drought resistance is to compare drought resistant and drought susceptible cultivars grown under the same conditions.

The purpose of this experiment was to compare the water status, growth, and phosphorus uptake of a drought resistant cultivar with a drought susceptible cultivar of winter wheat grown under induced water stress. We divided the roots between soil and soil (SS), soil and nutrient solution (SN), and nutrient solution and nutrient solution (NN). The split-root system allowed us to expose roots to different levels of water stress, to assess the water transfer potential of spatially dissimilar rooting systems, and determine, specifically, the effect of matric potential on the growth of the two cultivars.

Soil has a matric potential and nutrient solution has zero matric potential. Matric potential, Ψ_m, which also has been referred to as capillary potential (Hillel, 1980) is one of the two major components of the total soil-water potential, Ψ_t, in a non-saline soil where the osmotic potential, Ψ_π, is small. The gravitational potential, Ψ_g, is the other major component and the two are related as follows (Hillel, 1980):

$$\Psi_t = \Psi_g + \Psi_m$$

If plants are grown in short pots, Ψ_g is small and water moves in response to gradients in Ψ_m. Previous work (Erickson and Kirkham, 1979) showed that matric potential did affect the growth of 'Osage' winter wheat, a cultivar of unknown drought resistance. This cultivar has some drought resistance because it is adapted to the semi-arid Southern Great Plains of the U.S.A. Osage plants with roots split between soil and nutrient solution grew taller than plants with root split between soil and soil or between solution and solution, especially after water was withheld from the soil side of the soil and solution treatment. The plants were exposed to wind in addition to water stress.

In the first half of this experiment, the drought resistant and drought susceptible cultivars were well watered. During the last half, no water was added to one side of the roots split between soil and soil or to the soil side of roots split between soil and nutrient solution. Plant growth variables that were measured were plant height, shoot and root dry-weight, and root length. Leaf-water potential, osmotic potential, turgor potential, and stomatal resistance were the plant-water relation variables assessed. Labelled phosphorus, ^{32}P, was added to one side of each split-root replicate and used as a tracer to determine the potential of water to be transferred from spatially dissimilar rooting systems exposed to varying levels of Ψ_m.

Materials and Methods

This study was conducted in a growth room at Controlled Environment Research Laboratory, Oklahoma State University, Stillwater, Oklahoma. The quantum flux density of incident light, provided by white fluorescent lamps was 620 μEinsteins$\cdot$cm$^{-2}\cdot$sec^{-1}, for 12 hours per day (0600-1800 hr). The day and night temperature varied from 25° to 30° C and 20° to 25° C, respectively. Relative humidity varied between 62 and 94%.

Two cultivars of winter wheat (Triticum aestivum L. em Thell.), one considered drought resistant (cv. KanKing) and one drought susceptible (cv. Ponca) (Sandhu and Laude, 1968; Todd and Webster, 1965) were germinated in trays containing 1:1 sand-vermiculite mixture. The trays were well watered with 0.1 strength Hoagland solution for 2 weeks. Subsequently, the seedlings were extracted from the sand-vermiculite mixture and transferred for 3 weeks to 15- x 1.5 cm test tubes containing full strength Hoagland solution, which was changed every other day to reduce oxygen deficiencies.

On August 24, 1979, 54 seedlings were transferred to 18 split-root containers consisting of 1.9 liter plastic containers with lids, three seedlings per pair of containers. The containers and lids were painted black to minimize algae growth. There were three split-root treatments and two cultivar treatments, with three replications randomly arranged with a 2 x 3 factorial design (CRD). Roots were split between soil and soil (SS), soil and nutrient solution (SN), and nutrient solution and nutrient solution (NN). The crown and aerial portion of the plants were supported by #11 cork stoppers with a 1.5 cm diameter hole. Each stopper was placed on top of the paired cartons so that half of the roots from the three plants would grow in one side of the paired cartons and half of the roots would grow in the other side.

Full strength Hoagland solution (Ψ_π = -0.08 MPa) was used for roots split in nutrient solution. The nutrient solution was aerated using an air pump (Hush III Aquarium Pump, Model 83, Metaframe Aquarium Products, Maywood, NJ). The soil was a Kirkland silt loam (Udertic Paleustoll) (Gray and Roozitalab, 1976) obtained from the Agronomy Research Station, Stillwater, Oklahoma. Each container had 2167 g of soil which had been sterilized in an autoclave. Field capacity was established to be -0.03 MPa (P.I. Erickson and M.B. Kirkham, unpublished data). The soil had a solution conductivity of 1.0 mmhos (Model 5500 Salinity Bridge, Model #5000 Soil Salinity

Sensor, Soil Moisture Corp., Santa Barbara, CA).

All treatments with roots in soil were well watered for the first 39 days. During the remaining 32 days, beginning October 2, 1979, no water was added to one side of the SS treatment nor to the soil side of the SN treatments in order to induce drought stress. Therefore, there were two drought treatments employed, drought (D) and no drought (ND). However, since only the soil side of the SN treatment was dried, only the SS treatments for each cultivar was analyzed factorially (2 X 2) for this treatment effect. Nutrient solution level was maintained in containers with nutrient solution for the duration of the experiment.

Plant height measurements were made every 7 days during the experiment and are reported as the mean of three values. Total leaf-water potential (Ψ_w) measurements were made every other day during the week beginning 5 September using a Wescor HR-55 in situ thermocouple psychrometer. Osmotic potential (Ψ_π) samples were taken concurrently with Ψ_w by excising a leaf portion (2.0 cm long) from each replicated treatment and placing the samples in screen-cage psychrometers (J.R.D. Merrill Specialty Equipment, Logan, UT) (Campbell and Campbell, 1974). After 24 hours in a deep freeze chamber (-25°C) the screen-cage psychrometers were placed in a constant temperature bath (25°C) for 2 hours equilibration (Nelson et al., 1978) time and Ψ_π was determined using a Wescor Micro-Voltmeter, Wescor, Inc., Logan, UT). Turgor potential (Ψ_p) values were computed for each treatment from the mean Ψ_w and Ψ_π values. Stomatal diffusive resistance measurements (LI-COR LI-65 Autoporometer and LI-205 Diffusion

Resistance Sensor, Lambda Instrument Corp., Lincoln, NE) were made on the adaxial surface of leaves concurrently with Ψ_w. Stomatal resistance values reported are the mean of nine measurements (3 measurements per pair of containers X 3 replications).

On November 5, 1979, the nutrient solution in the containers was replaced with phosphate-free Hoagland solution. Subsequently, 1 mCi of ^{32}P (NEX-053, Orthophosphoric acid in 1 ml HCl-free solution, New England Nuclear, Boston, MA) was diluted to 18 1-ml aliquots, 0.065 mCi per split-root replicate. ^{32}P was added to the nutrient solution side of the SN treatments and to only one side of the NN treatments. In the SS treatments, ^{32}P was added to the moist soil side by inserting a syringe into a 6.35 x 0.2 cm hole. The isotype was allowed to be taken up by the plants growing in nutrient solution and soil for 24 and 48 hours, respectively, before removal of the roots for analysis. After the above time interval, plants were removed from the SS, SN, and NN treatment containers. The roots in SS and SN were carefully washed free of soil and taken to a photographic dark room where each replicate of plants was placed flat on medial X-ray film (Kodak No-Screen, Ready Pack N52T, Cat. #167-4209). After an exposure period of 10 minutes, the plants were taken to the Oklahoma State University Student Health Center, Stillwater, OK, for development. This radiographic technique was repeated twice in order to obtain quality films without excessive amounts of fog exposure. The optical density of each film was measured with a densitometer (Sakura, Model PD-81U, 0.0 - 3.5 range) in order to determine the relative amount of ^{32}P uptake for each replicate.

On November 7, 1979, root length was determined using the method of Newman (1966) and the experiment was completed after determining root and vegetative dry-weights. All materials used in the radioisotope portion of the experiment were marked with Radioactive materials signs and stored in isolation for subsequent hazardous waste disposal (burial).

Results and Discussion

Growth. During the first 39 days of the experiment when the soil was well watered, both the drought resistant and drought susceptible plants with roots split between SN were intermediate in height between those split between SS and NN (Figure 1). After water was withheld from the soil side of the SN treatment, the drought resistant plants (KanKing) grew taller, although the difference was not significant, than the drought susceptible cultivar (Ponca) with roots split between SN. The height of plants with roots split between NN remained nearly constant during the entire experiment for both cultivars. The NN plants experienced no water stress and, therefore, differences in height were not found to be significant. The height of both cultivars with roots split between SS was significantly less than the height of plants grown in SN and NN. Furthermore, highly significant differences existed between cultivars before and after water was withheld from one side of the SS containers, although there was significant stress period by cultivar interaction. This would indicate that height differences were not due solely to intrinsic differences in stage of growth and development before and after water was withheld.

The pooled analysis of variance for the six treatments showed a highly significant cultivar by SS treatment interaction averaged over both stress periods.

Significant differences for shoot dry-weight (Table I) were detected for both cultivars averaged over all split-root treatments and for all split-root treatments averaged over both cultivars. Significant cultivar shoot dry-weight by split-root treatment interaction was shown for SS but not for SN or NN. Shoot dry-weight of KanKing was greater for all split-root treatments than that of Ponca and the differences were significant except for Ponca grown in SS. This may be due to the confounding of the stress period as shoot dry-weight values were measured only at the end of the study and not before water was withheld from one side of the SS treatment. Significant differences between split-root treatments for KanKing were detected, whereas Ponca showed no significant difference in shoot dry-weight for all split-root treatments. These data would suggest that soil matric potential has a significant effect on the growth response of the drought resistant cultivar in terms of shoot dry-weight, but to a lesser extent on the drought susceptible cultivar, and that the effect is positive when differences in Ψ_m are small.

Root Growth. Root length and root dry-weight values are reported for individual sides of each split-root treatment for both cultivars (Table I). Significant differences in root length were found between cultivars averaged over all treatments. In all cases, the drought resistant cultivar had significantly greater root strength than the drought susceptible cultivar. Moreover, the SS grown drought resistant cultivar had significantly greater root length in the containers from which water was withheld than in either container to which water was added for that cultivar or both sides of the SS treatment of the drought susceptible cultivar. The stress period by cultivar interaction for the SS treatment fell just short of significance at $P<0.05$. Root length for the drought susceptible cultivar was about the same for both sides of the SS treatment, however, the water added side had slightly more root length. This large difference between cultivar root length grown under periods of water and no water (simultaneously) in SS and the near significant cultivar by stress period interaction indicates a different cultivar response to the stress period and this difference may help to characterize the differential drought response of the two cultivars. Extensive root systems have been associated with drought resistant cultivars (Hurd, 1976).

Significant differences for root dry-weight (Table I) were observed between cultivars averaged over all split-root treatments. The drought resistant cultivar showed a significantly greater root dry-weight than the drought susceptible cultivar in all comparisons except in the SS vs. SS and SS vs. Sn treatment comparisons. In these two comparisons, however, the root dry-weights were 1.7 and 2.44 times greater, respectively, for the drought resistant cultivar over the drought susceptible cultivar. As with root length, the drought resistant cultivar had a greater average root dry-weight in the soil from which water was withheld in the SS treatment than in the container of the same treatment to which water was added, although the difference was not significant. Greatest root dry-weight values were found for both cultivars with roots split between SN and the difference between cultivars was highly significant with the drought resistant cultivar having 5.7 times more root dry-weight than the drought susceptible cultivar. A highly significant cultivar by split-root treatment interaction existed which indicates a high differential root dry-weight response of the cultivars to Ψ_m.

Root dry-weight was significantly correlated with root length ($r = 0.98$, KanKing; $r = 0.96$, Ponca) for both cultivars grown under all split-root treatments. Similar positive correlations have been reported for root dry-weight and root length comparisons (Hurd, 1968; Hurd, 1974; Carrigan and Frey, 1980 Quinsberry et al., 1981).

Shoot dry-weight was correlated with root dry-weight for both cultivars grown under all split-root treatments (Figure 2). Shoot: root (S:R) ratios (Table I) provide an index for the relative performance of each organ in each split-root treatment. Significant differences existed between cultivars, Ponca having greater S:R than KanKing averaged over all split-root treatments. Plants grown in SS were significantly less in their S:R than plants grown in either SS or SN, and were not significantly different from each other.

<u>Leaf water potential</u> (Ψ_w). Significant differences in Ψ_w were not found to exist between the drought resistant and the drought susceptible cultivars averaged over all split-root treatments during the first 39 days of the experiment, when the soil was well watered, or during the final 37 days when no water was added to one side of the SS treatments (Figure 3). Significant differences between all

split-root treatments for both cultivars (average) were found. The Ψ_w of plants with root split between SN was intermediate between that of plants with roots split between SS and NN as observed in a previous experiment with the cultivar Osage (Erickson and Kirkham, 1979).

Osmotic potential (Ψ_π). The Ψ_π's of the drought resistant cultivar was significantly lower than the drought susceptible cultivar (Figure 4) average over all split-root treatments. Also, significant differences existed between all split-root treatments over both cultivars. In comparing each treatment, significant differences in Ψ_π existed between all treatment combinations except the SN Ponca vs NN KanKing comparison. Cultivar by split-root treatment interaction was not significant.

Highly significant differences in Ψ_π were found between cultivars in the SS treatment averaged over both stress periods. In the comparison of the stress periods averaged over both cultivars, no significant differences were found. However, at the end of the experiment, KanKing had a much lower Ψ_π than Ponca (-1.21 and -0.32 mPa, respectively: L.S.D. @ 0.05 = 0.07 mPa). Perhaps one reason for the drought resistance of KanKing is due to its ability to lower it Ψ_π to a greater degree than non-resistant cultivars when grown under drought stress conditions. This has been suggested previously (Maximov, 1929) as a drought resistance mechanism.

Ψ_π of plants with roots split between SN was, in general, intermediate between that of plants with roots split between SS and NN. Plants with roots split between NN had the highest Ψ_π and plants with roots split between SS had the lowest Ψ_π.

Turgor potential (Ψ_p). Significant differences in Ψ_p($\Psi_p = \Psi_w - \Psi_\pi$) were found for both cultivars averaged over all split-root treatments (Figure 5). Also, differences between all split-root treatments averaged over both cultivars were found to be highly significant. Cultivar by SS treatment interaction was not found to be significant, whereas, cultivar by SN and NN treatments interaction was found to be significant. Differences between split-root treatments for the drought resistant cultivar were all significant with NN grown plants having the highest Ψ_p, SS grown plants having the lowest Ψ_p, and SN grown plants having intermediate Ψ_p values. Conversely, the drought susceptible cultivar had Ψ_p values that were not significantly different from each other except for the SS treatment; SN grown plants had nearly the same Ψ_p as the NN grown plants, although they were slightly higher.

Ψ_p for both cultivars with roots split between SS were significantly different when averaged over both stress periods. In addition, a significant difference between stress periods of the SS treatment averaged over both cultivars was determined. Cultivar by stress period interaction for the SS treatment was not found to be significant. Turgor potential values are shown in Figure 5.

Stomatal resistance. Stomatal resistance averaged over all split-root treatments showed no significant difference between the two cultivars. However, cultivars grown with root split between SS were significantly greater in their stomatal resistance than cultivars grown with roots split between SN and NN. Moreover, significant differences between the two stress periods were exhibited by both cultivars. In this case, the stomatal resistance of the drought susceptible cultivar became elevated earlier than the stomatal resistance drought resistant cultivar. However, at the end of the experiment the drought resistant cultivar had a higher stomatal resistance than the drought susceptible cultivar although the difference was not significant. This suggests that after water was withheld from one side of the SS split-root treatments, little if any water was being transferred from the wet side of the soil to the dry side of the soil because of the high stomatal resistance values that were measured. In other experiments it has been observed that KanKing has a higher stomatal resistance under stress conditions than does Ponca (Kirkham, 1978; Kirkham and Ahring, 1978). In general, stomatal resistance was lowest, intermediate, and highest for both cultivars with roots split between NN, SN, and SS, respectively (Figure 6).

Labelled phosphorus (^{32}P). In all replicates of each treatment, no transfer of labelled phosphorus from the labelled side to the nonlabelled side of the split-root system was observed (Figure 7) as evidenced by the X-ray films of each replicate. It may be that 24 and 48 hours was not sufficient time lapse to allow for transfer from one side of the rooting system to the other in the SS and other two split-root treatments, respectively. The location of the labelled phosphorus input in the SS treatments may have been such that it was not in close proximity to the roots themselves, as phosphorus is immobile in the soil, hence, no uptake and no subsequent transfer could occur. However, no transfer was observed for any of the other treatments in which labelled phosphorus was in close proximity to the roots. In other experiments in which labelled phosphorus has been incorporated into the soil, the time between addition of the labelled phosphorus and analysis of labelled phosphorus in plant material has been longer than the 48 hours used in this experiment. The period ranged from 5 to 11 days for annuals such as corn (Zea mays L.), sorghum (Sorghum bicolor (L.)(Moench), and tomato (Lycopersicon esculentum Mill.) to as long as 3 weeks for apple trees (Lavy and Eastin, 1969; Thorup, 1969; Atkinson, 1974; Mohr and Sattler, 1979).

In comparing the treatments in which phosphorus was taken up and measured as optical density (3.5 being greatest), significant differences existed between the two cultivars, with the drought resistant cultivar having taken up nearly three times more labelled phosphorus than the drought susceptible cultivar (Table II). In addition, cultivars grown in SN took up significantly more labelled phosphorus (4.24 times more) than cultivars grown in NN. No significant cultivar by split-root treatment interaction for labelled phosphorus was observed.

Conclusions. The effect of Ψ_m on the growth of both cultivars was strong as evidenced by the significant differences in plant height, root and shoot dry-weights, and root length for each split-root treatment. In addition, when there was a nonhomogeneous distribution of water in the root zone (part of the root system in wet soil or nutrient solution and part in unwatered soil) the drought resistant cultivar of winter wheat grew better than did the drought susceptible cultivar. The response of the drought resistant cultivar to the SN treatment, after water was withheld, was striking. It increased in height 20.7 cm, whereas, the drought susceptible cultivar increased in height only 9.8 cm. The drought resistant cultivar also increased in height, more than did the drought susceptible cultivar, when one side of the SS treatment was allowed to dry, but the difference was small (15.2 cm vs. 13.9 cm). Plants grown under supposedly optimal conditions (NN) (aerated nutreint solution) did not increase in height. Consequently, the difference in matric potential of the rooting medium, created by not watering half of the root system, apparently caused the plant growth rate to increase more than if the rooting media was maintained at the same high potential. Moreover, this plant growth response was greatest when the potential difference of the rooting media was small, as in the SN treatment, in contrast with a large potential difference, as in the SS treatment when one side was allowed to dry.

Since the soil did not dry out in the SN treatment, it is reasonable to conclude that water was preferentially absorbed and translocated from the nutrient solution side. This suggests that the Ψ_m existed and plants did not increase in height or where the potential difference in Ψ_m was large and plant growth increase was small. The exact contribution of Ψ_m to increased plant growth under these conditions is not clear, but because the roots of each plant were spatially dissimilar, it may be that Ψ_m affects the flow of substance between the roots and the aerial organs when a small potential difference in rooting media exists.

Cultivar differences in ^{32}P uptake were evident. Although no ^{32}P uptake by either cultivar grown in SS was observed, it is clear that there was no transfer of ^{32}P from the labelled side to the unlabelled side by any of the other plants regardless of the split-root treatment in which they were grown. This is in agreement with hte findings of Lawlor (1973) in which no transfer of water was observed between wheat roots (cultivar 'Kolibir') split between a control solution (-0.03 mPa) and a solution with high Ψ_π (-1.0 mPa), obtained by adding ployethylene glycol (PEG) 4000. It was not determined, however, if PEG-4000 was transferred to roots in the control solution as PEG-4000 can be taken up by plants (Lawlor, 1970). Since no transfer of labelled phosphorus was observed, then any flow of substance that occurs between spatially dissimilar organs must be by other than reciprocal exchange or with a different carrier than phosphorus, such as a hormone.

In this experiment, the drought resistant cultivar had a lower Ψ_π and a higher Ψ_p than did the drought susceptible cultivar. Theoretically, it is possible for plants to remove water from the soil below the wilting percentage and this depends on the Ψ_π of the plant (Slayter, 1957). Anomolies in this regard, however, have been reported. Keim and Kronstad (1981) screened ten field grown winter wheat cultivars, two of which were classified as drought resistant. One drought resistant cultivar (cv. 'Yamhill') had a high Ψ_π, while the other drought resistant cultivar (cv. 'Wanser') had a low Ψ_π. They did not measure Ψ_p • Ψ_p of these two cultivars was probably higher than that of the other eight cultivars. Since Ψ_p is directly related to growth (Gardner, 1973), measurements of Ψ_p may be a better indicator of growth under conditions of water stress than measurements of

Ψ_w, Ψ_π, or stomatal resistance. Johnson and Brown (1977) have already suggested that Ψ_p be used to select plants with superior resistance to water stress. In this experiment where comparisons were made between split-root treatments, cultivars, and stress periods, Ψ_p was the physiological variable that showed significant differences in all cases.

TABLE I

SHOOT WEIGHT, ROOT WEIGHT, ROOT LENGTH, AND SHOOT:ROOT RATIO OF A DROUGHT RESISTANT AND A DROUGHT SUSCEPTIBLE CULTIVAR OF WINTER WHEAT WITH ROOTS SPLIT BETWEEN SS, SN, AND NN†††

Cultivar	Split-root Media					
	Soil (D) : Soil (ND) (SS)		Soil : Solution (SN)		Solution : Solution (NN)	
			Shoot Dry Weight, g			
KanKing	4.27a*		11.33b		7.23c	
Ponca	3.46a		4.50a		2.26a	
			Root Dry Weight, g			
KanKing	0.83a†	0.49a	5.03c	4.26c	1.36ab	1.79ab
Ponca	0.36a	0.42a	1.08a	0.55a	0.24a	0.30a
			Root Length, cm			
KanKing	1247d*†	928bc	3071h	2826g	1700e	1966f
Ponca	697ab	756ab	1284d	912bc	482a	572a
			Shoot:Root Ratio			
KanKing	3.21c††		1.24a		2.29b	
Ponca	4.69d		2.89bc		4.29d	

Means (within treatments) followed by the same letter do not differ at α = 0.05; L.S.D. values are as follows:
*L.S.D. = 2.40g; †L.S.D. = 0.93g; *†L.S.D. = 246 cm; ††L.S.D. = .77

††† Split-root treatments SS, SN, and NN are soil:soil, soil:nutrient solution, and nutrient solution:nutrient solution, respectively.

TABLE II

DENSITY OF ^{32}P IN ROOTS OF A DROUGHT RESISTANT AND A DROUGHT SUSCEPTIBLE WINTER WHEAT CULTIVAR SPLIT BETWEEN SN AND NN†

Cultivar	Split-Root Media	
	Soil:Solution (SN)	Solution:Solution (NN)
KanKing	0.758c*	0.261ab
Ponca	0.388b	0.009a

*Means (within treatments) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D. = 0.344.

†Split-root treatments SN and NN are soil:nutrient solution and nutrient solution:nutrient solution, respectively.

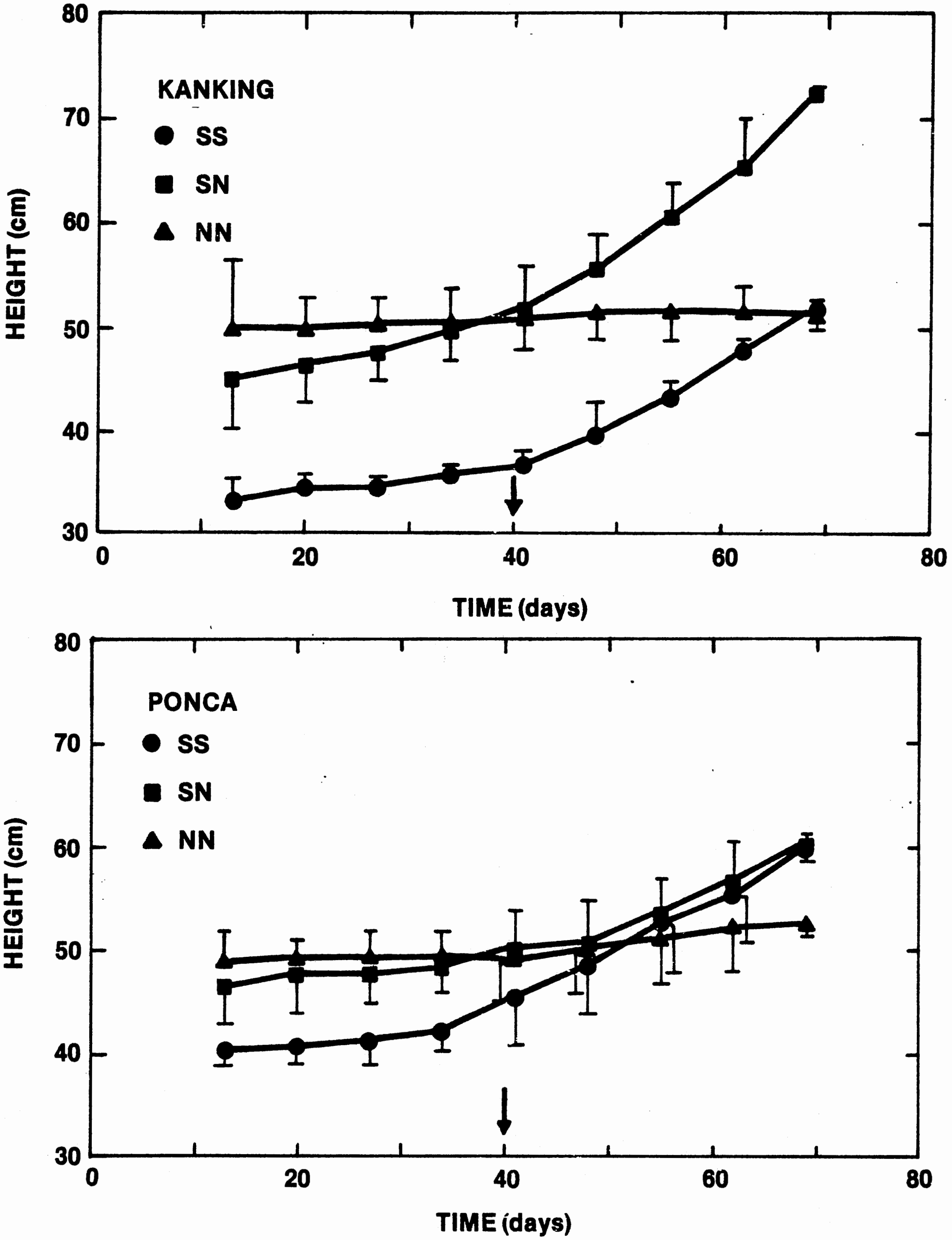


Figure 1. Height of a Drought Resistant (KanKing) and a Drought susceptible (Ponca) cultivar of winter wheat with roots split between SS, SN, and NN.

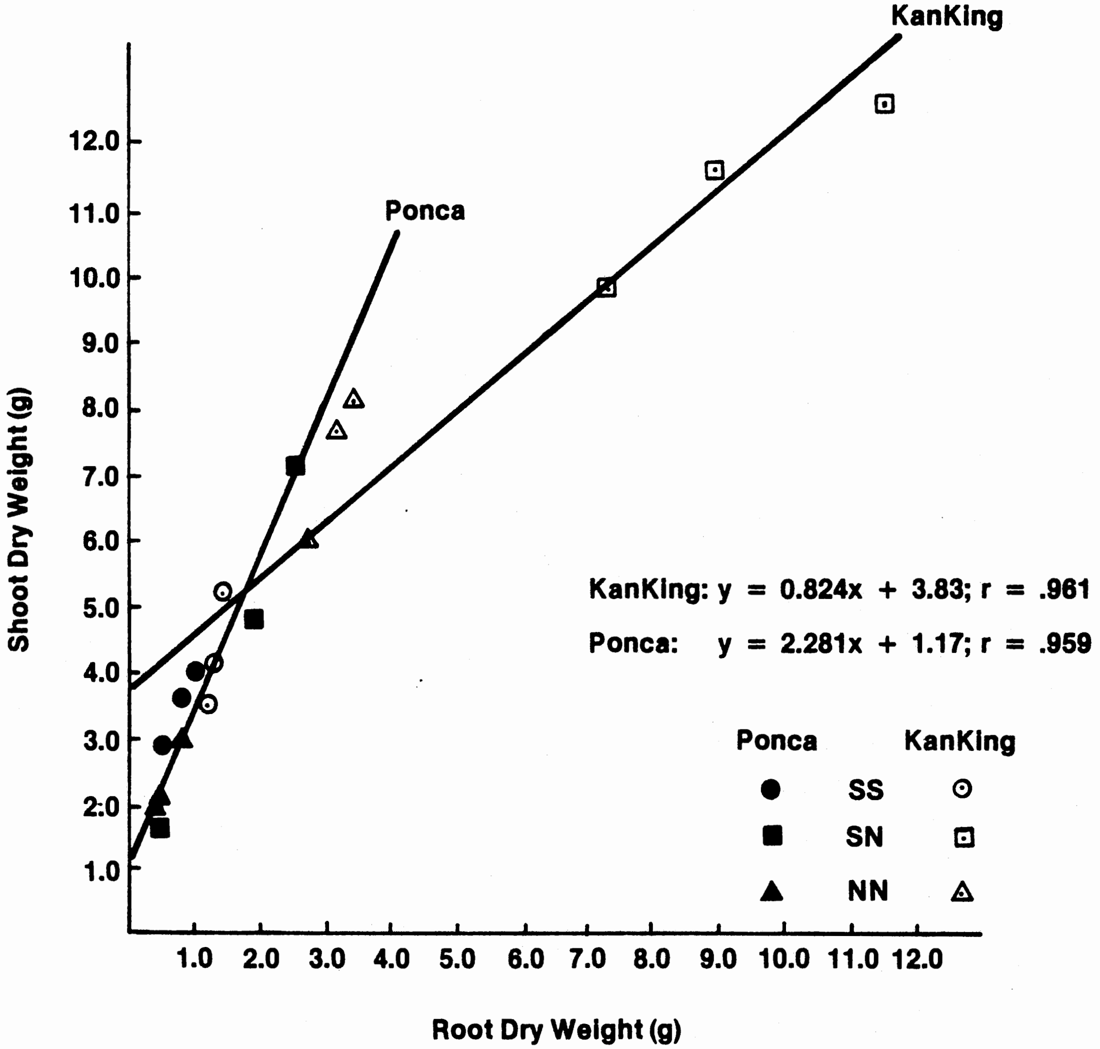


Figure 2. Shoot Dry Weight vs. Root Dry Weight of a Drought Resistant and a Drought Susceptible Cultivar of Winter Wheat With Roots Split Between SS, SN, and NN.

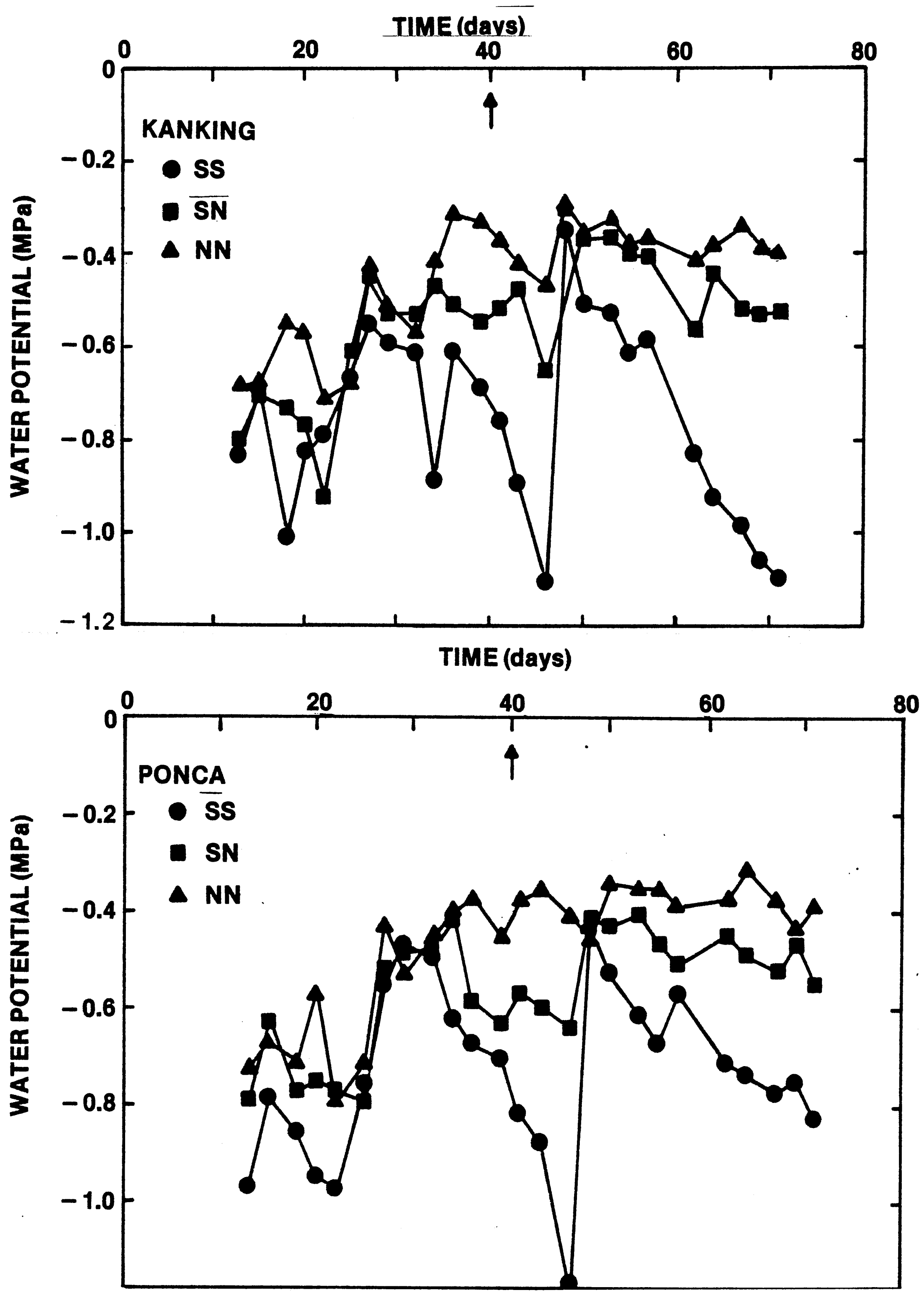


Figure 3. Leaf Water Potential of a Drought Resistant (KanKing) and a Drought Susceptible (Ponca) Cultivar of Winter Wheat With Roots Split Between SS, SN, and NN.

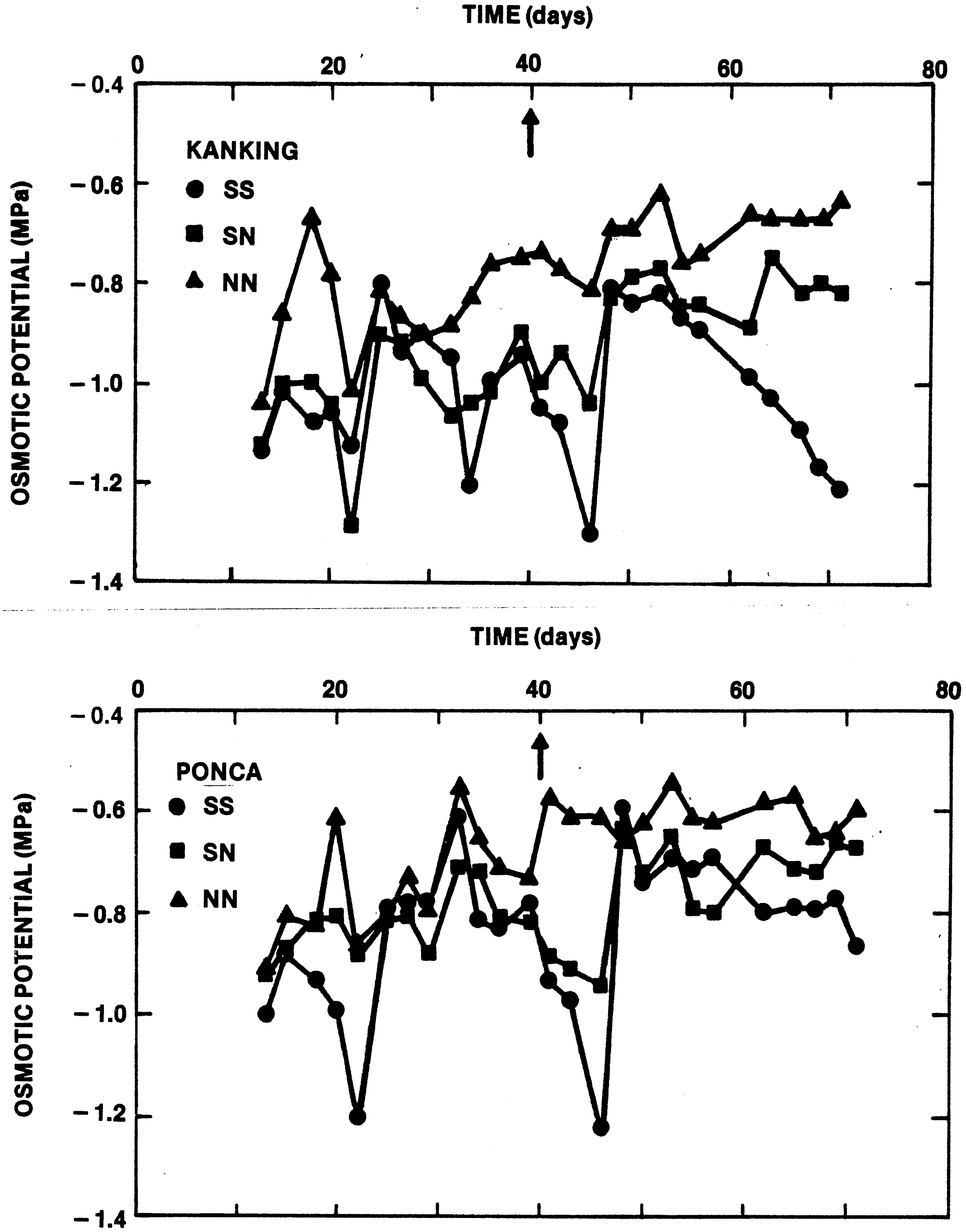


Figure 4. Osmotic Potential of a Drought Resistant (KanKing) and a Drought Susceptible (Ponca) Cultivar of Winter Wheat With Roots Split Between SS, SN, and NN.

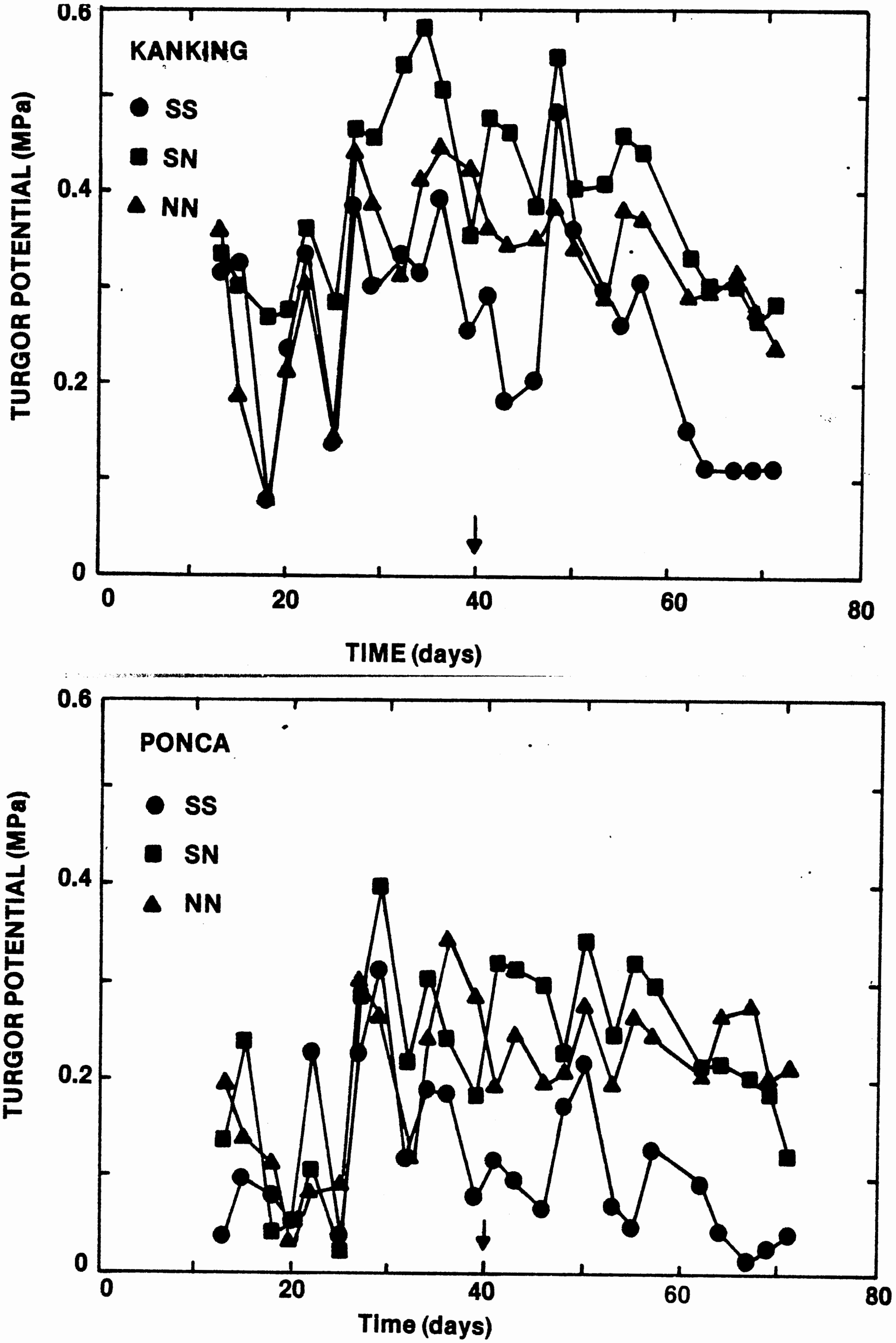


Figure 5. Turgor Potential of a Drought Resistant (KanKing) and a Drought Susceptible (Ponca) Cultivar of Winter Wheat With Roots Split Between SS, SN, and NN.

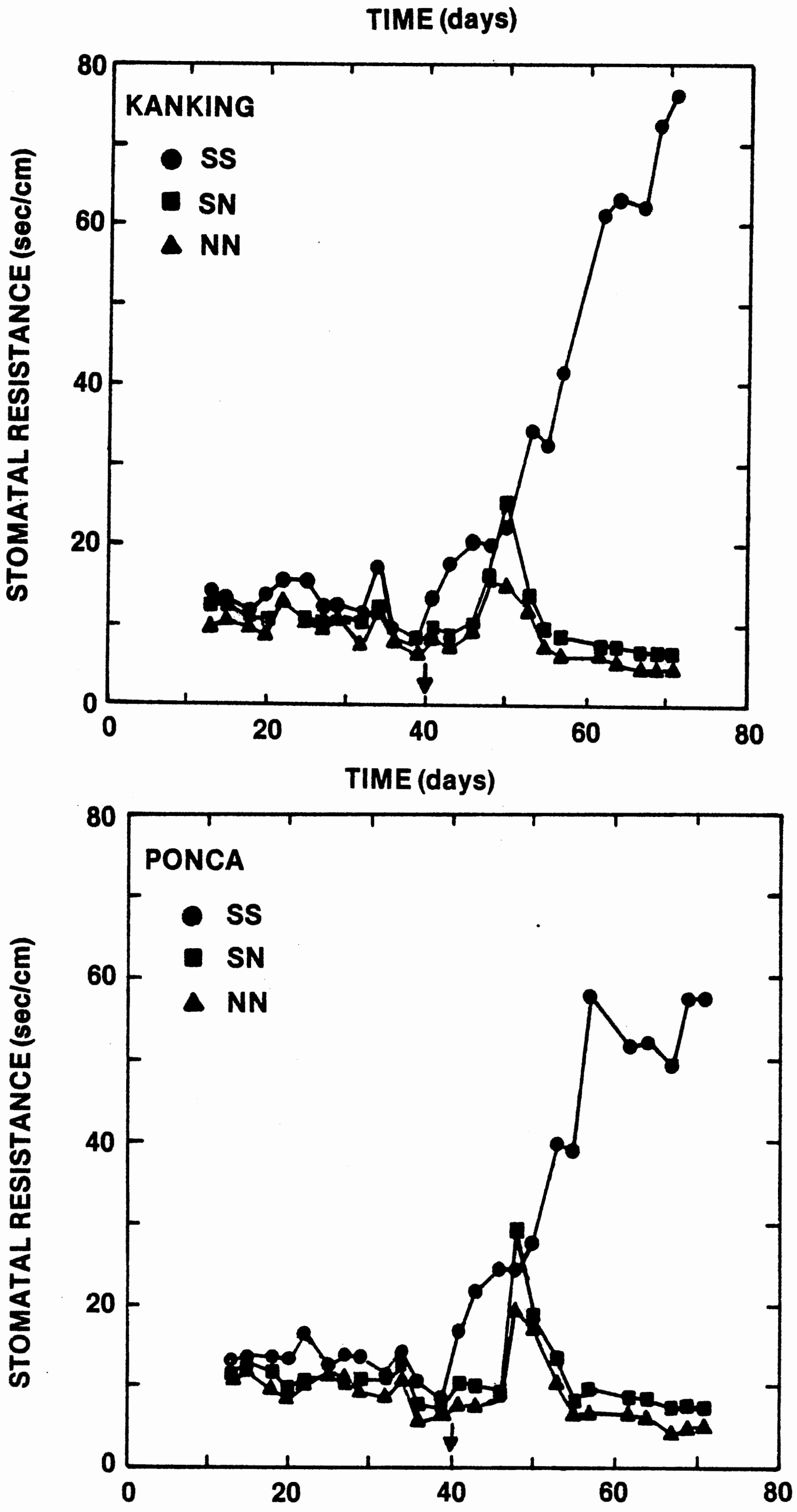
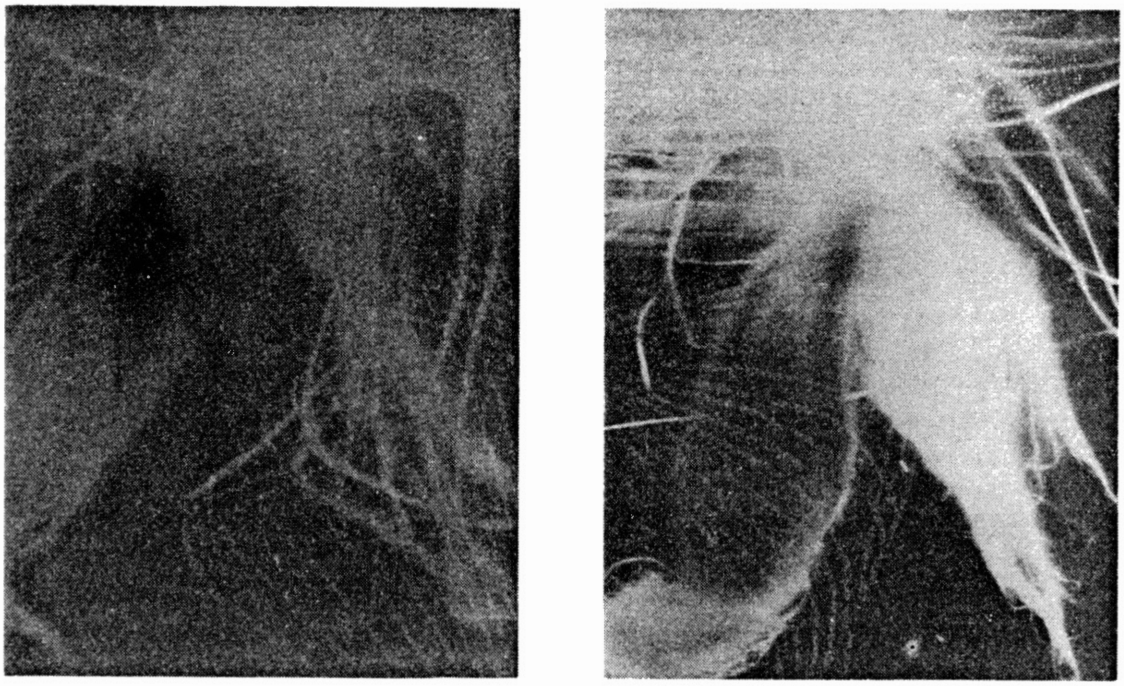
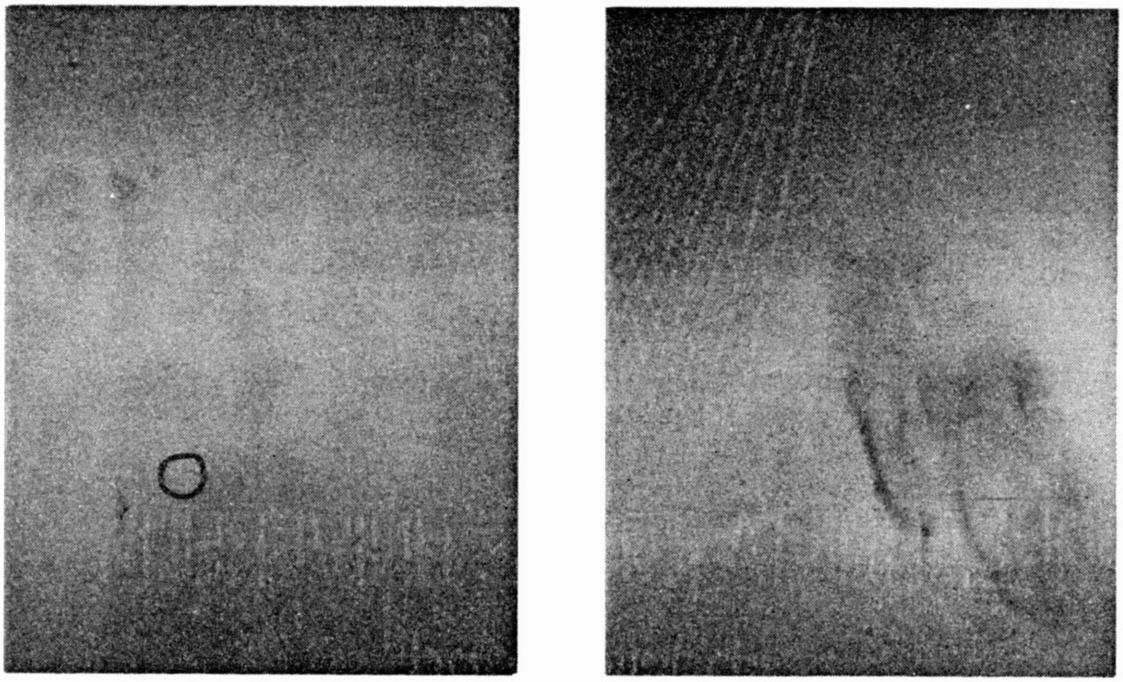


Figure 6. Stomatal Resistance of a Drought Resistant (KanKing) and Drought Susceptible (Ponca) Cultivar of Winter Wheat With Roots Split Between SS, SN, and NN.



Ponca SN

KanKing SN



Ponca NN

KanKing NN

Figure 7. Density of ^{32}P of a Drought Resistant and a Drought Susceptible Cultivar of Winter Wheat With Roots Split Between SN and NN.

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APPENDIX

VARIABLE MEANS

Water Potential (mPa)

	SS	SN	NN	Mean
Ponca	-0.761	-0.546	-0.452	-0.587
KanKing	-0.731	-0.562	-0.464	-0.586
Mean	-0.746	-0.554	-0.458	

L.S.D. (0.05) = 0.0842

Water Potential (mPa)

	SS_{ND}	SS_D	Mean
Ponca	-0.731	-0.732	-0.732
KanKing	-0.731	-0.788	-0.760
Mean	-0.731	-0.760	

L.S.D. (0.05) = -0.149

Osmotic Potential (mPa)

	SS	SN	NN	Mean
Ponca	-0.842	-0.737	-0.670	-0.766
KanKing	-1.015	-0.940	-0.771	-0.909
Mean	-0.928	-0.864	-0.720	

L.S.D. (0.05) = -0.066

Osmotic Potential (mPa)

	SS_{ND}	SS_D	Mean
Ponca	-0.867	-0.819	-0.843
KanKing	-1.016	-1.015	-1.016
Mean	-0.942	-0.917	

L.S.D. (0.05) = -0.113

Turgor Pressure (mPa)

	SS	SN	NN	Mean
Ponca	0.106	0.223	0.210	0.180
KanKing	0.254	0.397	0.674	0.442
Mean	0.180	0.310	0.261	

L.S.D. (0.05) = 0.050

Turgor Pressure (mPa)

	SS_{ND}	SS_D	Mean
Ponca	0.136	0.080	0.106
KanKing	0.285	0.227	0.254
Mean	0.210	0.154	

L.S.D. (0.05) = 0.023

Stomatal Resistance (sec-cm^{-1})

	SS	SN	NN	Mean
Ponca	28.49	10.52	8.83	7.97
KanKing	27.81	10.85	8.98	7.94
Mean	28.15	10.68	8.90	

L.S.D. (0.05) = 6.50

Stomatal Resistance (sec-cm^{-1})

	SS_D	SS_{ND}	Mean
Ponca	40.61	12.86	27.81
KanKing	42.05	12.67	28.49
Mean	41.33	12.76	

L.S.D. (0.05) = 10.99

CHAPTER III

Determination of *in situ* Root Growth of Winter Wheat Under Drought Stress: The Inverted Periscope Technique

Abstract

This research was conducted under field conditions during a severe drought (19.23 cm below average rainfall) to determine root growth behavior of three winter wheat cultivars of unknown drought resistance and to evaluate the differential drought resistance of each cultivar in terms of its physiological responses to drought stress. In addition to root growth, the physiological variables measured were plant height, leaf-water potential, stomatal resistance, and yield. Root growth observations were made using an inverted periscope, lowered into a clear acrylic column inserted into the soil. Sampling depths were between 0 and 70 cm at 10 cm intervals with observations made every three weeks for 182 days after planting. Growth and plant water relations measurements were conducted at the same times until harvest (224 days after planting) at which time yield and test weights were determined.

The inverted periscope technique for root observations worked well until the soil-column interface was disrupted due to drought 182 days after planting, after which root growth observations could not be performed. For those 182 days of observable growth, the results

showed significant differences in the root growth behavior of each cultivar at various depths. In addition, grain yield appeared to vary with total root length in an exponential manner.

Stomatal resistance was generally closely associated with leaf-water potential and the relationship appeared to have a common functional value (about 1 sec/cm @ -0.8 mPa) whereas below and above this value the linear functions for each cultivar were quite different.

It can be concluded from this study that: 1) the inverted periscope technique is not suitable for *in situ* root growth observations under severe drought conditions; and 2) wheat cultivars which have extensive rooting systems, and able to maintain low stomatal resistance at decreased leaf-water potentials, have a better capacity to tolerate drought stress, and will yield better under such conditions.

Introduction and Literature Review

There is great need to improve our understanding of root contribution to drought stress resistance in plants. Roots provide water and nutrients to the aerial portion of a wheat plant by exploring a large volume of soil under a wide range of conditions. Under conditions of water deficits, some cultivars are able to grow better and outyield others. A number of researchers have proffered that the survival and productivity of wheat (*Triticum aestivum* L, em Thell.), and other crops, is controlled by depth and density of their roots (Bohm et al., 1977; Levitt, 1972; Hurd, 1968; Weaver, 1926) while others (e.g. Ray et al., 1974) suggest that limited water may be more efficiently used by plants with small or limited root systems. This disagreement, as Hurd (1974) points out, illustrates the limitation of our knowledge of drought resistance in plants.

Since virtually all water that enters a plant must do so through the roots, their importance for the maintenance of plant water balance and role in drought resistance was observed by Weaver (1926), Khanna and Raheja (1947), and Misra (1956). Subsequent work has shown that plant water stress generally decreases as width, depth, and branching of root systems increase (Donald, 1963; Weatherly, 1965) and, therefore, root development and the capacity of plants to absorb water are closely related. This has been aptly demonstrated in controlled environment and greenhouse studies. However, verification of this relationship is lacking in field studies because satisfactory techniques and methodologies for quantitative evaluation of drought stress on root behavior are lacking. Moreover, indices typically used to assess the problem are limited in scope and applicability in defining cause-effect relationship of drought stress on plant roots and yield.

There are a number of ways that root behavior can be observed in the field, but most are destructive and require considerable time and expense. Until recently, there has not been a technique for non-destructive, simple, and precise evaluation of root characteristics for plants grown under a wide variety of environments in the field. A highly refined fiber optic duodenoscope was used by Sanders and Brown (1978) for observing and photographing root developmental patterns of soybeans in the field. This technique permitted viewing observations to a depth of 72 cm below the soil surface during the growing season. Gregory (1979) described the inverted periscope technique used to study in situ root growth of winter wheat and millet in comparison with that obtained from washed core samples. Like the fiber optic duodenoscope technique, the periscope technique gave similar results compared to washed soil samples and took only one eighth the time to obtain a complete profile of root distribution to 60 cm depth. The periscope technique, however, was much less expensive and easier to use than the fiber optic method. Both methods employed similar equations by Newman (1966) and Tennant (1975) to determine total root length.

This paper reports research conducted in situ on three cultivars of winter wheat using the periscope method to evaluate rooting behavior under drought stress conditions, and to characterize the resistance of each cultivar in addition to growth, yield, and water-relations data of the aerial plant portion. This information may be useful to plant breeders to improve the development and function of roots, and may offer considerable promise for increasing the yield potential of winter wheat grown under conditions of occasional or prolonged drought stress.

Materials and Methods

The study was conducted from October 17, 1980 to June 17, 1981 at the Agronomy Research Station, Oklahoma State University, Stillwater, Oklahoma, Plot #7200, S½ Sec. 16, T16N, R2E.

Three cultivars of winter wheat (Vona, Larned, and Osage, all of unknown drought resistance) were used as treatments. Each treatment was replicated four times in 9 x 3 m plots using a completely randomized design. A 6 m border of Osage was planted around the study area. Plots were planted on Octover 17, 1980 with a 17.5 cm row spacing in the north-south direction. Urea ammonium phosphate (28-28-0) was incorporated at a rate of 175 kg/ha on October 14, 1980.

The soil was a Bethany silt loam (Okla. Agric. Expt. Stn. Processed Series P-315, 1959) which is classified as a Paleustoll (Gray and Roozitalab, 1976). Clear acrylic columns measuring 70 x 15 (diam.) cm were inserted, using a geotome auger, in the middle of each plot on October 27 and 28, 1980. Each column was placed in the row with one plant growing on each north and south side. The two plant root systems were faced onto and separated by the column itself, which served as a viewing screen. The soil removed from the top 15 cm was used to fill small gaps between the column and the bulk soil. The soil was wetted and allowed to settle in order to achieve satisfactory seating of the column. Each column, which protuded 6.3 cm above the soil surface, was covered with black plastic secured with a rubber strap to prevent light penetration into the column and to the roots.

Root growth was monitored within the columns using a periscope. This instrument was fabricated in our laboratory using Crestline PVC-1 tubing measuring 81.3 x 7.6 (diam.) cm to which 10 x 14 cm double-backed silver plated mirror was fitted at a 45^{o} angle. The periscope was lowered (inverted) into the column through a modified NIBCO PVC-1 (Serial #4851-A) 10.2 x 7.6 (diam.) cm camode flange which served as a base plate and was used to align the periscope for observations. Into the collar of the baseplate were located two depth screws which were tightened when the periscope was lowered to the desired depth. Also, the collar rotated in the baseplate which permitted 360° viewing. This required five fields of view with a 100 cm^2 field size. A scale was marked on the side of the baseplate and the periscope so that azimuth and depth could be determined, respectively, per observation. Lighting was provided by a 12 V bulb fixed above the periscope mirror and attached to a 12 V (D.C.) power source.

Root length in each field of view was estimated by the Newman (1966) and Marsh (1971) method in which a 1.0 x 1.0 cm grid drawn on 75 x 48 cm clear plastic was inserted into the hole and pressed against the column walls. Through the periscope, the number of intersections or roots was observed and counted. The number of intersections was totaled for each depth of measurement and subsequently used to estimate total length of root in 10 cm increments down the profile. Values reported for root length are the mean of four measurements for each depth (one measurement per depth per plot x four replications).

Concurrent measurements of leaf-water potential and stomatal diffusive resistance were made on each sampling date at 1300 hr using a Wescor LI-51A *in situ* leaf hygrometer/psychrometer connected to a Wescor HR-33T Dew Point Microvoltmeter (Wescor, Inc., Logan, UT) (Campbell and Campbell, 1974) and a diffusion porometer (LI-65 Autoporometer and LI-20S Diffusion Resistance Sensor, Li-Cor Inc., Lincoln, NE) (Kanemasu et al., 1969), respectively. Leaf-water potential and stomatal resistance values reported are the mean of four measurements per sampling date (one measurement per plot x four replications).

Plant height was measured on each three week sampling date. Measurements of each plot were taken from the base of the plant to the top. The height values reported are the mean of four measurements (one measurement per plot x four replications).

Rod row samples were harvested on June 17, 1981 for yield and test weight. Two rod row samples per plot were harvested from the rows directly east and west of the row in which the column was located. Harvest values are the mean of eight measurements (to rod row samples per plot x four replications).

Meterological data were provided by the Oklahoma State University Agronomy Research Station Class AB Weather Station, Stillwater, Oklahoma.

Results

Root growth observations were made in the field on three winter wheat cultivars: Osage, Larned, and Vona. From these observations we were able to determine the length of root at 0 to 70 cm depth intervals using the line intercept method. Observations were made at three week intervals except during the last 6 weeks of the study since drought caused the separation of soil from the acrylic column. Meterological data (Table I) show two important points in regard to precipitation: 1) the nearly 20 cm deviation below average, and 2) 5 cm below average in April just prior to and during anthesis. At this time the soil-column interface separated and prevented further observations of root growth. This appeared to be the greatest limitation to the use of the periscope technique for studying the effects of drought on root growth and development. Data reported here are for 182 days after planting.

Total root length is shown for each cultivar as a function of time (Figure 1). The rate of growth is approximately linear for all three cultivars, which is in general agreement with the findings of Gregory (1979), that wheat root growth is essentially constant as determined by the periscope technique, and Hurd (1963), in which root growth was nearly linear with time as observed in growth boxes with glass faces.

Significant differences in root length at 10 cm depth intervals were found for all cultivars at each depth on nearly all sampling dates (Table II). A split-plot analysis was used with cultivars as main units and sampling dates as sub-units for each depth. These results showed significant cultivar by sampling date interaction, which indicates that root growth at each depth was not linear with time. This was particularly true for Larned, which had a tremendous increase in root growth at 10-20 cm, 20-30 cm, 40-50 cm, and 50-60 cm depths during the last two sampling dates. In general, though Osage had significantly greater root length at all depths during the entire study than either Larned or Vona. Osage was developed for the Southern Great Plains of the U.S. and therefore probably has some drought resistance which may be reflected in its comparatively more highly developed root system.

Total (cumulative) root length at each depth for each cultivar differed significantly among cultivars, and, as expected, between depths of penetration. Differences in root length at each depth were observed between respective depths for all three cultivars, except for the comparison between 40-50 cm and 50-60 cm depths for Osage (Table IV). Total root length at each depth is shown in Figure 2 for each cultivar. Vona had significantly less root length than either Osage or Larned at all depths except 60-70 cm deep, where root length was not greater than Larned. Larned and Osage did not differ in total root length at 10-50 cm depth; however, differences were observed at 0-10 cm and 50-70 cm depths. Total root length decreased linearly with depth for all three cultivars (Figure 2).

There appeared to be a distinct difference between cultivars in the time when the rate of change in root growth was greatest at a given depth (Figures 3,4, and 5). The rate of change for Osage was greatest between the first and fourth sampling dates (10/31 and 1/2, respectively) at 0-10 cm and 10-20 cm, whereas Larned showed the greatest rate of change between the seventh (3/6) and eighth (4/17) sampling dates for almost all depths. Vona followed a trend similar to that of Osage. Average rate of change in total root growth differed little among cultivars during the first nine weeks (Figure 6), after which differences became apparent with Larned having a striking increase between the seventh sampling date.

Shoot Growth. Significant differences in plant height were observed among cultivars on the second sampling date (11/21) and on all sampling dates after 3/6 (Table III). On 11/21, Vona was shorter than either Osage or Larned, which had nearly the same final height.

From 3/6 to harvest, the differences observed in plant heights showed Osage to have grown much taller than either Larned or Vona, except at harvest, when there was no difference between Osage and Vona.

All cultivars showed the same general trend in rate of change of shoot growth until the seventh sampling date (3/6), after which Osage increased strikingly in its rate of change of shoot growth and subsequently declined just prior to harvest (Figure 8). Larned and Vona increased in the rate of change shoot growth with Vona having increased slightly more in its rate of change than Larned. The steady decline in the rate of change of shoot growth from germination to stem extension for all three cultivars indicates that drought slowed shoot growth. This negative response was somewhat compensated for by an increased rate of change in root growth for Osage and Larned and to a lesser extent for Vona.

As a measure of the differential growth of the root and shoot organs, the root:shoot (R:S) ratio for each cultivar was determined for each sampling date on which observations were made (Figure 9). It is clear that drought stress caused much greater root growth over shoot growth for the first 119 days after planting when all cultivars were in the vegetative stage of development. Subsequently, Osage and Vona had a precipitous decline in R:S, whereas Larned showed a less steep decline. This may reflect the drougth resistant nature of each cultivar as previous research has shown R:S to be high in drought resistant cultivar (KanKing) and low in a cultivar that is not drought resistant (Ponca) (Erickson and Kirkham, 1982).

Stomatal resistance. Comparisons of stomatal resistance for each cultivar are shown in Table V. The data were not pooled due to large differences in the error mean square values for each sampling date; therefore, comparisons for each sampling date are shown separately. Differences were apparent just prior to anthesis. However, on the third and fourth sampling dates, (12/12 and 1/2, respectively), Osage had a higher stomatal resistance than either Larned or Vona. Prior to harvest, i.e., post-anthesis, Osage and Larned had lower stomatal resistances than Vona. This may be due to their generally more profuse root systems in general and the rate of change in root and shoot growth rates in particular.

Leaf-water potential. As was the case with stomatal resistance AOV, leaf-water potential error mean square values were not pooled and are, therefore, reported independently for each sampling date (Table VI). As a temporal function leaf-water potential showed a general increase for all three cultivars. Out of eleven sampling dates, only three showed significant differences in leaf-water potential: the fifth and sixth sampling dates (1/23 and 2/13, respectively) - Osage had a lower leaf-water potential than either Vona or Larned; the ninth sampling date (4/17) - Vona had a higher leaf-water potential than either Osage or Larned. Just prior to harvest, leaf-water potentials for all three cultivars was about the same (near -1.9 mPa).

Stomatal resistance vs. leaf-water potential (Figure 10) showed a generally linear function for all three cultivars. At high leaf-water potentials, Osage maintained a higher stomatal resistance than either Vona or Larned. This difference during drought stress may be the result of an extensive root system (total root length).

Yield. Osage had the highest yield (1882 kg/ha), Larned was intermediate (1648 kg/ha), and Vona had the lowest yield (1520 kg/ha) (Table VI). There is little doubt that drought stress depressed the yield of all three cultivars. When these data are compared to yearly averages for the same three cultivars, i.e., Osage = 2277 kg/ha, Larned - 2271 kg/ha, and Vona - 2047 kg/ha (1981 Performance tests with winter wheat varieties. Ag. Expt. Stn., Kansas State University, Progress Report 404, August.; 1981 Oklahoma State University Current Report CR-2067. Performance of wheat varieties, August.). Test weight values showed no differences among cultivars.

Linear correlation of yield to total root length was not as high as that of an exponential function (Figure 11). It would appear, therefore, that by increasing the total root length of a given cultivar a small amount, significant increases in yield potential would result. Under drought stress conditions, the contribution of a more profuse root system may be more than simply the capacity to explore a greater volume of soil for water and nutrients, that is, it may suppress the decrease in yield that a cultivar encounters under drought stress conditions.

Conclusions

It can be concluded that: 1) long term root growth observations cannot be effectively conducted under severe drought conditions using the inverted periscope technique. Coefficients of variation (Table VIII) for cultivars and sampling dates indicated the technique used was a success for 189 days during the 224 day growing season. 2) based on the available root growth data from nine sampling dates and shoot growth, water relations, and yield data, Osage appeared to be more drought resistant than either Larned or Vona. Larned appeared to be more drought resistant than Vona. 3) greater root length should be considered a drought resistant character in winter wheat and under drought stress conditions. This character was shown to contribute to higher yield.

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TABLE I

METEROLOGICAL DATA (JULY 1980 TO JUNE 1981)

Sampling Date	Temperature (°C) Maximum	Temperature (°C) Minimum	Month	Precip. (cm)	Deviation from Average (cm)
31 Oct 1980	21.11	0.56	July	0.13	-7.59
21 Nov 1980	14.44	-4.44	August	8.84	+1.19
12 Dec 1980	16.11	1.11	September	3.56	-5.89
02 Jan 1981	11.67	-7.22	October	4.27	-2.79
13 Feb 1981	5.00	-5.56	November	0.99	-3.71
06 Mar 1981	12.22	0.56	December	4.06	+0.66
17 Apr 1981	25.00	14.44	January	0.18	-2.77
08 May 1981	33.33	21.67	February	2.74	-0.68
29 May 1981	34.67	24.56	March	5.66	+1.45
			April	2.26	-5.00
			May	16.23	+4.50
			June	12.19	+1.42
			Total	61.11	-19.23

TABLE II

ROOT LENGTHS FOR THREE WHEAT CULTIVARS AT 10 CM DEPTH INTERVALS

Cultivar	Sampling Dates								
	10/31/80	11/21	12/12	1/2/81	1/23	2/13	/6	3/27	4/17
	Root Lengths, cm								
0-10 cm:									
Vona	15.8a*a†	37.0ab	67.8ac	83.0ad	94.0ae	110.2af	112.2	151.0ah	166.0ai
Larned	11.8aa	37.0ab	65.2ac	82.2ad	103.8be	113.8af	128.0ag	169.0bh	186.2bi
Osage	12.8aa	37.0ab	50.5ac	107.2bd	121.5ce	134.2bf	148.2bg	178.2ch	204.0ci
10-20 cm:									
Vona	0a*a†	18.5ab	36.5ac	49.5ad	61.5ae	75.5af	83.2ag	101.5ah	126.0ai
Larned	0aa	20.8ab	34.8ac	34.8ac	74.5be	90.2bf	101.0bg	133.5bh	158.2bi
Osage	5.0aa	22.5ab	39.5ac	70.5cd	92.5ce	101.5cf	117.2cg	143.8ch	162.2bi
20-30 cm:									
Vona	0a*a†	4.8ab	26.0ac	34.2ad	43.8ae	54.8af	64.0ag	81.0ah	101.8ai
Larned	0aa	2.2aa	18.5bb	27.5ac	36.8ad	47.5ae	64.8af	106.5bg	123.0bh
Osage	0aa	8.5ab	28.0ac	43.0bd	57.5be	72.2bf	85.0bg	109.0bh	115.0ci
30-40 cm:									
Vona	0a*a†	0.0aa	9.0ab	14.5ab	22.2ac	35.5ad	50.5ae	64.8af	79.0ag
Larned	0aa	0.0aa	2.0ba	10.8ab	21.2ac	32.0ad	44.2be	92.5bf	108.5bg
Osage	9aa	0.0aa	13.2cb	19.0bb	29.2bc	47.2bd	65.5ce	84.0cf	100.5cg
40-50 cm:									
Vona	0a*a†	0.0aa	2.2aa	6.8ab	12.2ac	19.8ad	31.0ae	44.0af	61.5ag
Larned	0aa	0.0aa	0.0aa	2.0ba	9.8ab	25.2bc	44.8bd	63.8bd	81.8bf
Osage	0aa	0.0aa	4.2bb	10.0ac	17.5bd	41.8ce	53.0cf	64.2bg	77.8ch

TABLE II (Cont.)

Cultivar	10/31/80	11/21	12/12	1/2/81	1/23	2/13	3/6	3/27	4/17
50-60 cm:									
Vona	0a*a†	0.0aa	0.0aa	0.0aa	1.8aa	11.5ab	17.5ac	29.2ad	38.0ae
Larned	0aa	0.0aa	0.0aa	0.0aa	1.5aa	18.2bb	29.8bc	47.5bd	58.8be
Osage	0aa	0.0aa	0.0aa	2.5aa	11.8bb	25.5cc	39.5cd	47.5be	71.0cf
60-70 cm:									
Vona	0a*a†	0.0aa	0.0aa	0.0aa	0.0aa	3.8ab	7.8ac	11.5ad	15.5ae
Larned	0aa	0.0aa	0.0aa	0.0aa	0.0aa	4.0ab	7.0ab	12.2ac	13.0ac
Osage	0aa	0.0aa	0.0aa	0.0aa	1.8aa	17.5bb	20.5bb	30.8bc	35.8bd

	Observation Depth Interval						
L.S.D.	0-10	10-20	20-30	30-40	40-50	50-60	60-70
*	6.6	7.9	7.5	4.2	3.3	3.8	3.4
†	5.3	5.4	4.3	6.6	3.0	3.2	3.6

*Means (within dates) followed by the same letter do not differ at α= 0.05. L.S.D listed.
†Means (within cultivars) followed by the same letter do not differ at α= 0.05, L.S.D listed above.

TABLE III

PLANT HEIGHT FOR THREE WHEAT CULTIVARS AT 3 WEEK SAMPLING DATES

Date	Vona	Larned	Osage	L.S.D. 0.05
	Plant Height, cm			
31 October 1980	4.0a*	3.1a	4.2a	1.6
21 November 1980	5.9a	6.8b	7.0b	0.9
12 December 1980	7.0a	8.0a	8.8a	1.7
02 January 1981	9.6a	9.7a	10.6a	1.9
23 January 1981	12.2a	12.4a	11.9a	2.5
13 February 1981	14.5a	13.0a	13.5a	2.0
06 March 1981	21.2a	17.0b	21.0a	2.7
27 March 1981	32.8a	26.8b	41.7c	5.5
17 April 1981	47.3a	39.1b	53.5c	5.4
08 May 1981	69.4a	51.4b	76.2c	6.0
29 May 1981	80.2a	64.3b	90.0c	4.0
17 June 1981	93.9a	69.7b	97.4a	4.3

*Means (within dates) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D. is shown for each respective sampling date.

TABLE IV

CUMULATIVE ROOT LENGTH FOR THREE WHEAT CULTIVARS AT 10 CM DEPTH INTERNODES

Sampling Depth (cm)	Cultivar Vona	 Larned	 Osage
	Cumulative Root Length, cm		
0 - 10	166.0a*†	185.2ba	204.0ca
10 - 20	126.0ab	158.2bb	162.2bb
20 - 30	101.8ac	123.0bc	115.0bc
30 - 40	79.0ad	108.5bd	100.5bd
40 - 50	61.5ae	81.8be	77.8be
50 - 60	38.0af	58.8bf	71.0ce
60 - 70	15.5ag	13.0bg	33.8cf

*Means (within depths) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D = 11.2 cm.

†Means (within cultivars) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D. - 11.5 cm.

TABLE V

LEAF WATER POTENTIALS FOR THREE WHEAT CULTIVARS AT THREE WEEK SAMPLING DATES

Date	Cultivar Vona	 Larned	 Osage	L.S.D. 0.05
	Leaf Water Potential, mPa			
31 October 1980	-0.69a*	-0.64a	-0.55a	0.13
21 November 1980	-0.63a	-0.67a	-0.60a	0.12
12 December 1980	-0.78a	-0.80a	-0.72a	0.11
01 January 1981	-0.79a	-0.90a	-0.81a	0.13
23 January 1981	-1.14a	-0.94b	-1.11a	0.13
13 February 1981	-1.09a	-0.96a	-1.16a	0.16
06 March 1981	-1.02a	-1.02a	-1.08a	0.22
27 March 1981	-1.08a	-1.18a	-1.24a	0.18
17 April 1981	-1.54a	-1.36b	-1.38b	0.15
08 May 1981	-1.59a	-1.59a	-1.57a	0.19
29 May 1981	-1.74a	-2.00a	-1.86a	0.32

*Means (within dates) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D is shown for each respective sampling date.

TABLE VI

STOMATAL RESISTANCE FOR THREE WHEAT CULTIVARS AT THREE WEEK SAMPLING DATES

Date	Cultivar			L.S.D.
	Vona	Larned	Osage	
	Seconds$^{\cdot 1}$cm$^{\cdot 1}$			
31 October 1980	0.76a*	0.64a	0.84a	0.16
21 November 1980	0.95a	0.90a	0.98a	0.39
12 December 1980	0.94a	1.02a	1.12b	0.10
02 January 1981	1.00a	1.02a	1.15b	0.10
23 January 1981	2.40a	1.74a	2.41a	0.81
13 February 1981	2.23a	1.86a	2.38a	0.66
06 March 1981	1.08a	1.30a	1.07a	0.23
27 March 1981	0.96a	1.26b	0.90a	0.21
17 April 1981	3.83a	1.86b	1.82b	0.93
08 May 1981	3.57a	2.16b	1.98b	0.62
29 May 1981	4.98a	5.39a	3.82a	1.80

*Means (within dates) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D. is shown for each respective sampling date.

TABLE VII

GRAIN YIELD (KG/HA) AND TEST WEIGHT FOR THREE WHEAT CULTIVARS

Analysis	Vona	Cultivar Larned	Osage
	-------	$Kg^{-1}ha^{-1}$	---------------
Yield	1520*	1648b	1882c
	-------	$Kg^{-1}hl^{-1}$	---------------
Test Weight	117.2a†	116.6a	118.2a

*Means (within yields) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D. = 32 kg/ha.

†Means (within test weights) followed by the same letter do not differ at $\alpha = 0.05$, L.S.D. = 2.7 kg/hl.

TABLE VIII

COEFFICIENTS OF VARIATION FOR CULTIVARS AND SAMPLING DATES AT 10 CM DEPTH INTERVALS

Depth	Cultivars	Dates
0-10	12.1 %	7.5 %
10-20	17.9	8.0
20-30	24.9	9.4
30-40	17.5	17.3
40-50	19.4	11.3
50-60	24.0	13.1
60-70	42.5	29.2

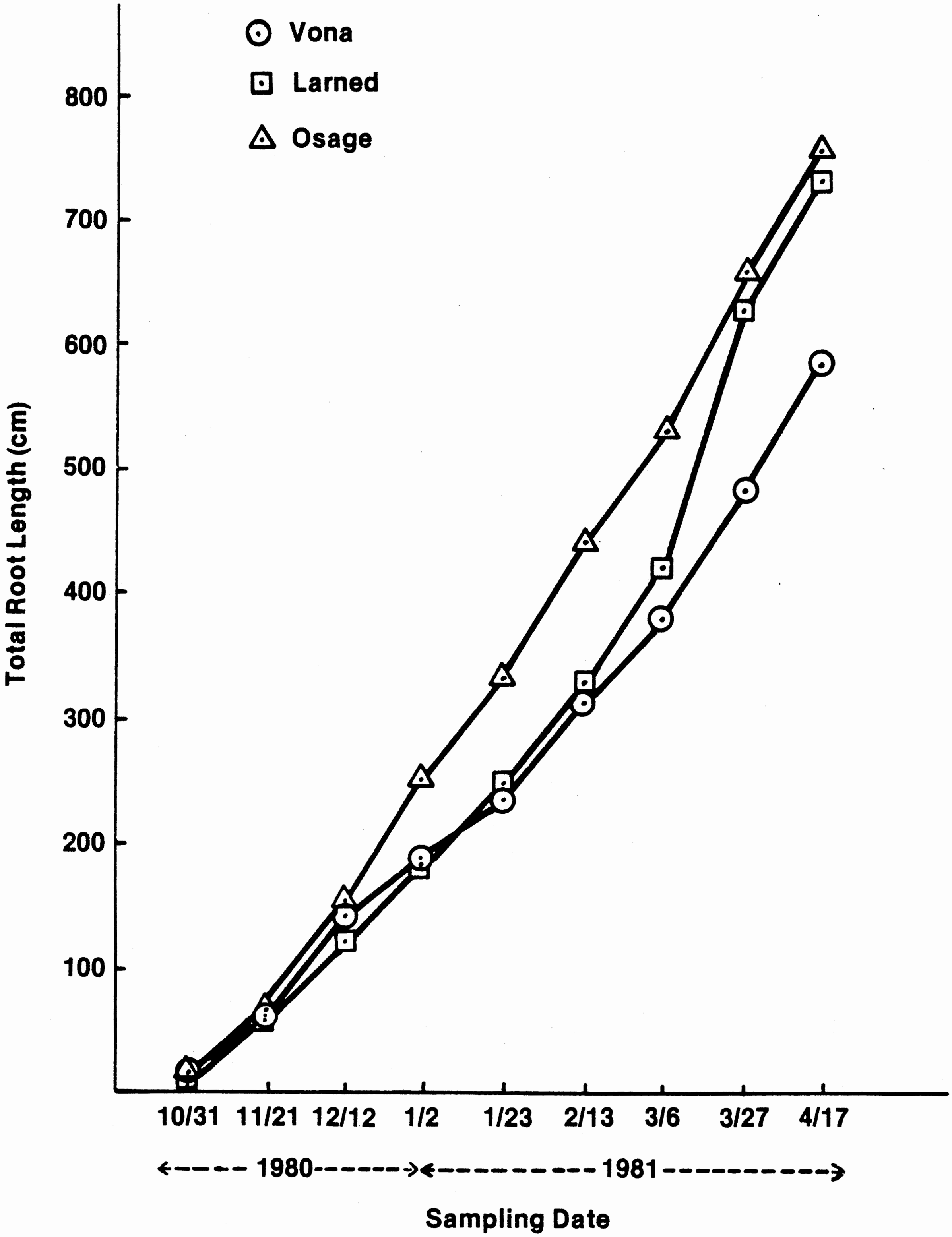

Figure 1. Total Root Length at Each Sampling Date.

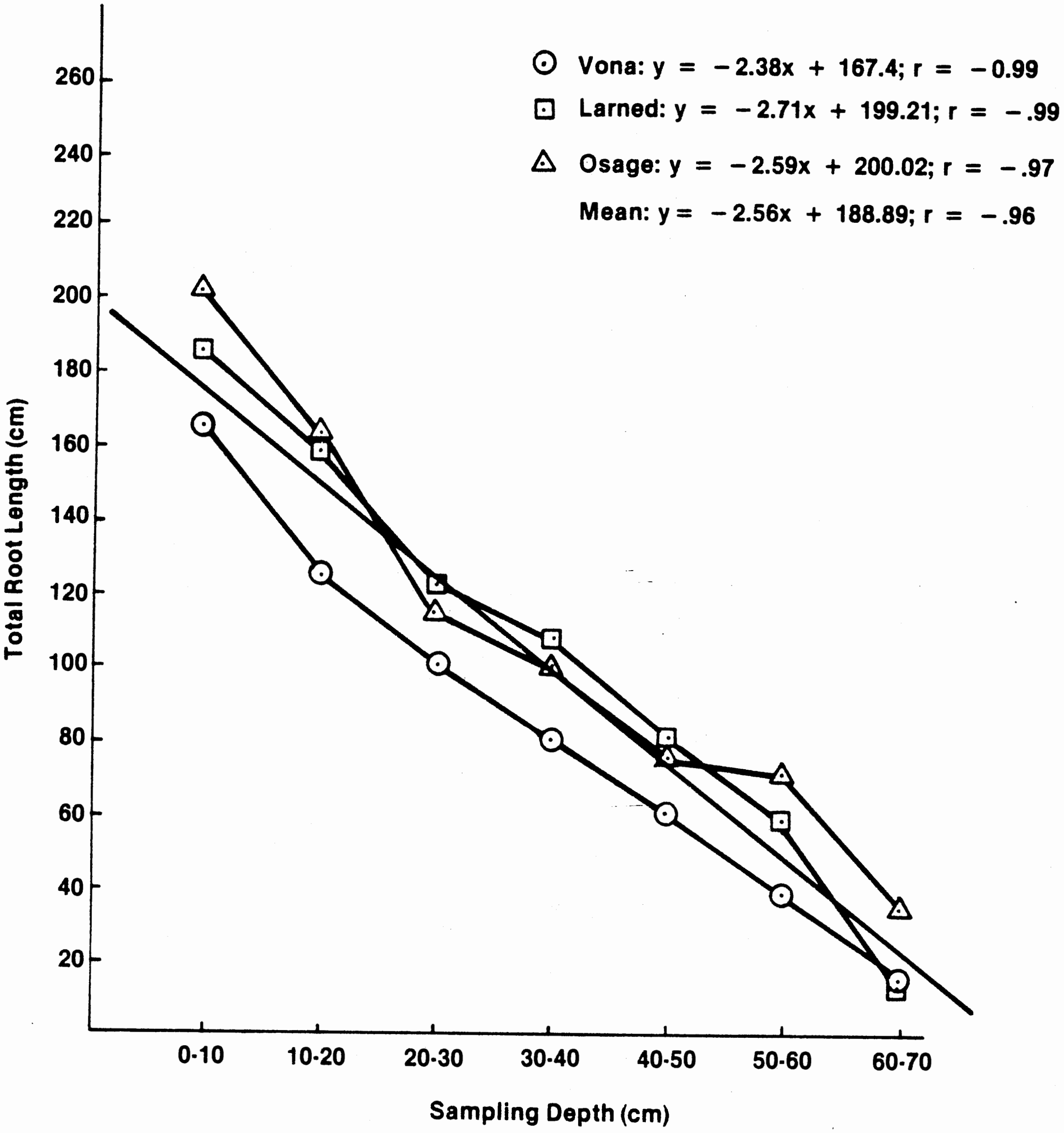

Figure 2. Total Root Length at Each Soil Depth.

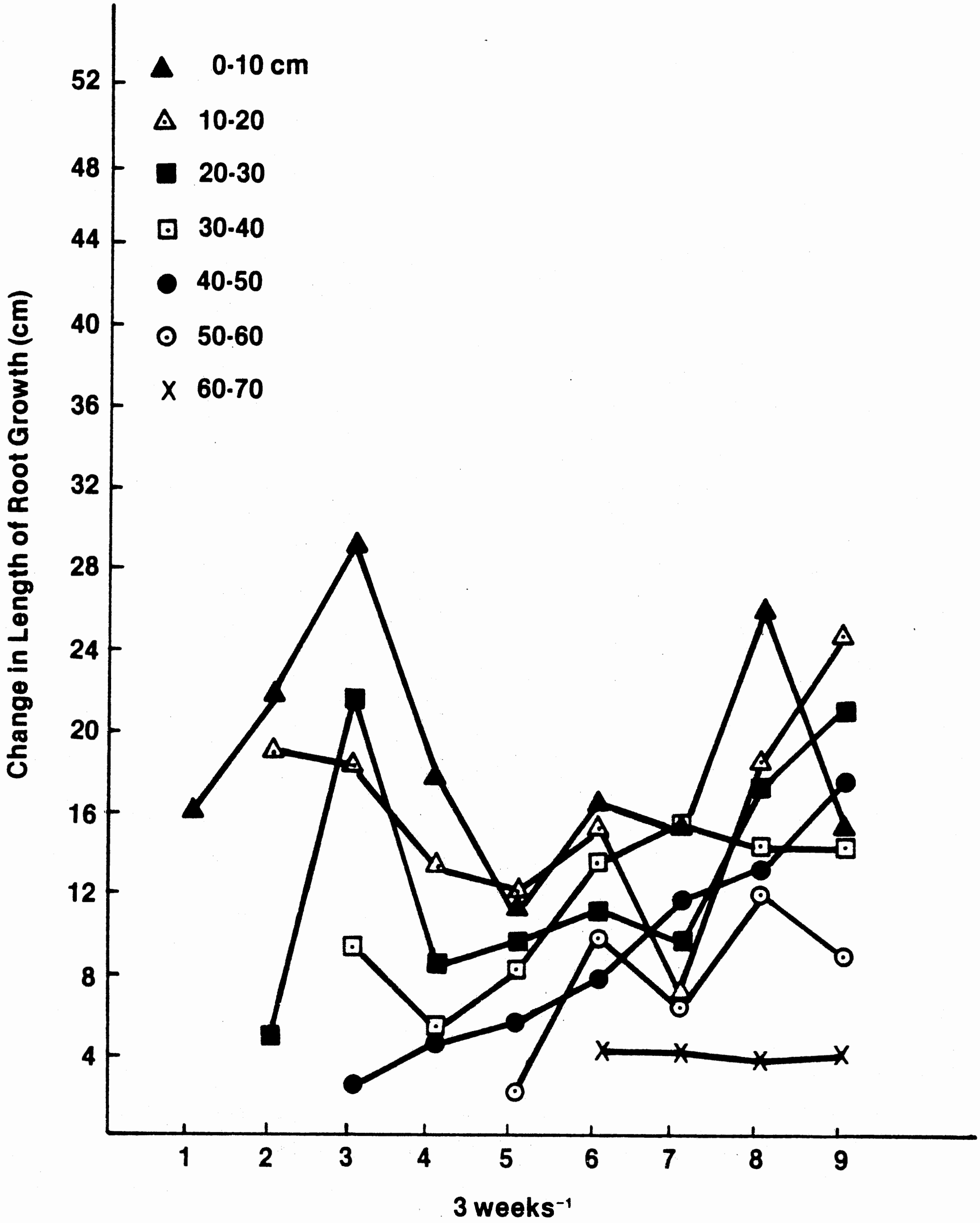

Figure 3. Change in Root Growth for Vona at 3 Week Sampling Dates for Various Depths.

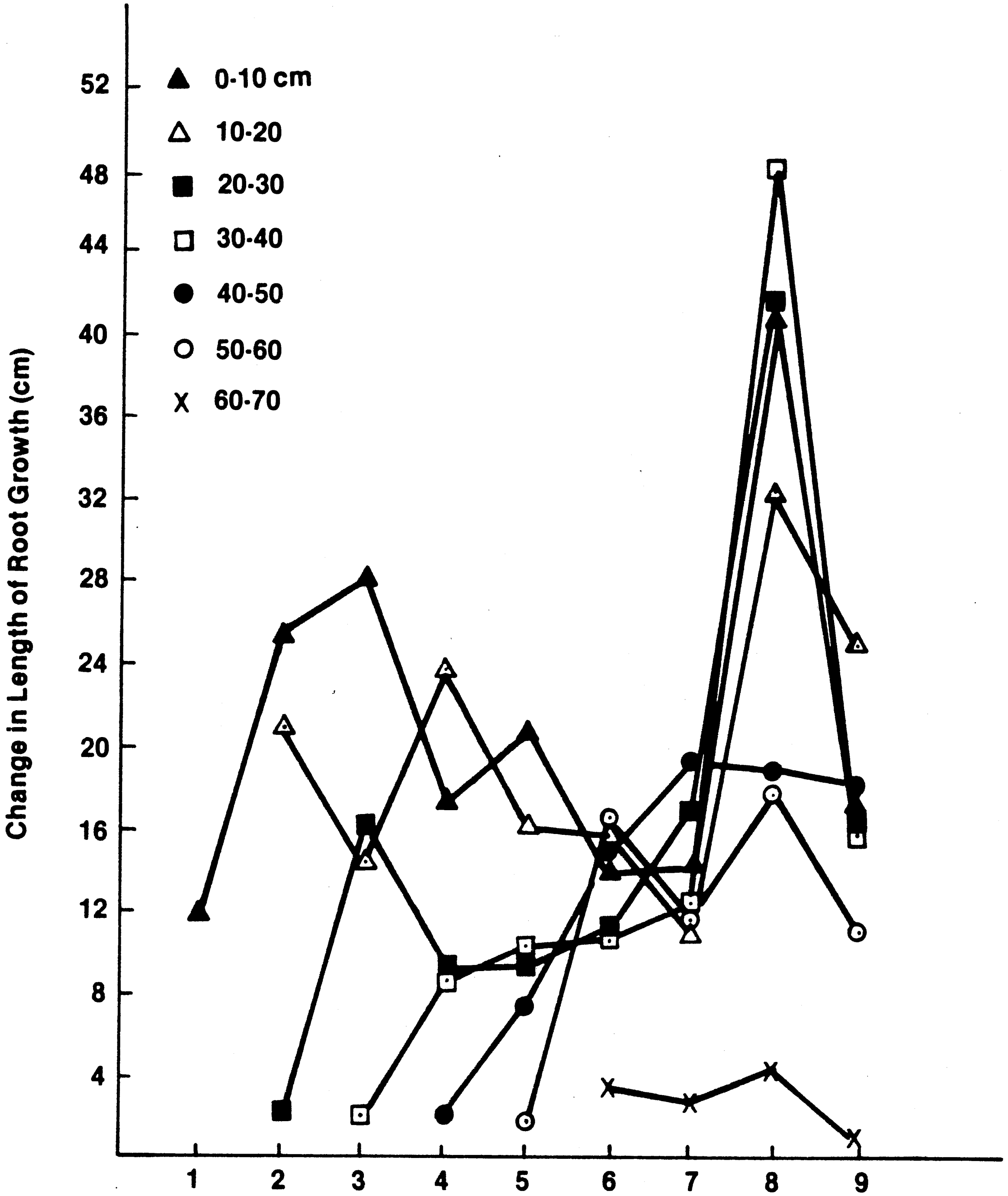

Figure 4. Change in Root Growth for Larned at 3 Week Sampling Dates for Various Depths.

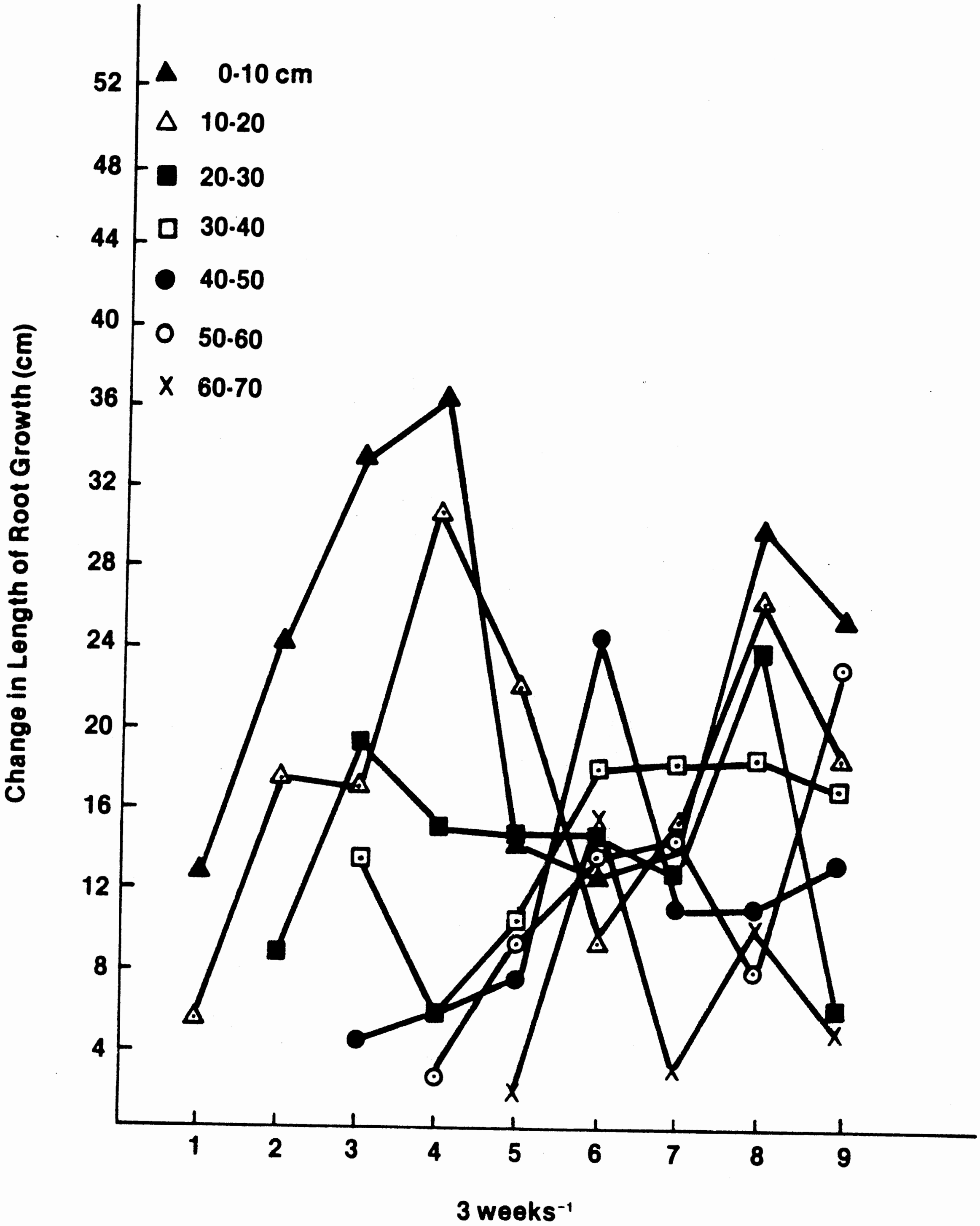

Figure 5. Change in Root Growth for Osage at 3 Week Sampling Dates for Various Depths.

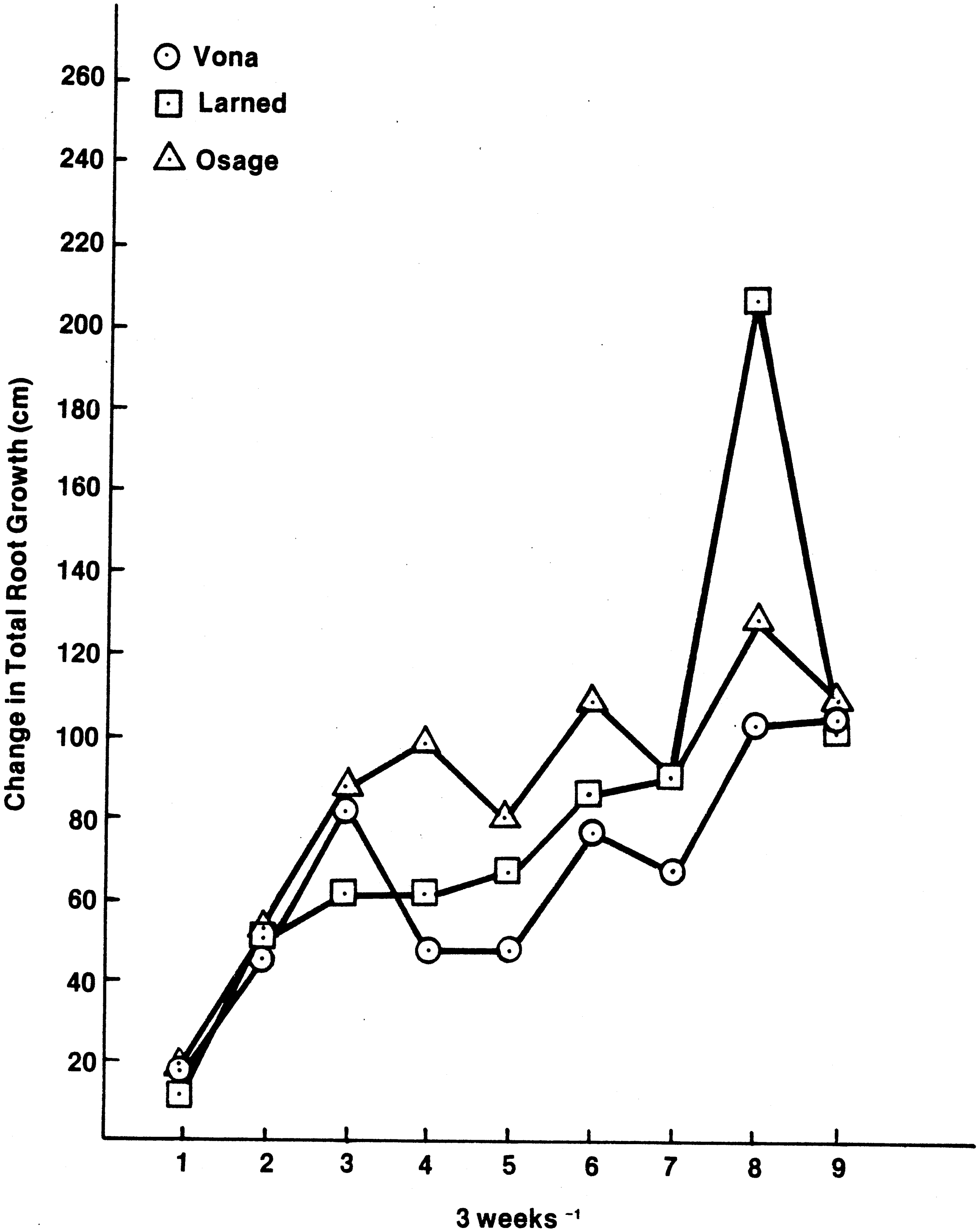

Figure 6. Change in Total Root Growth for Three Cultivars of Winter Wheat at 3 Week Sampling Dates.

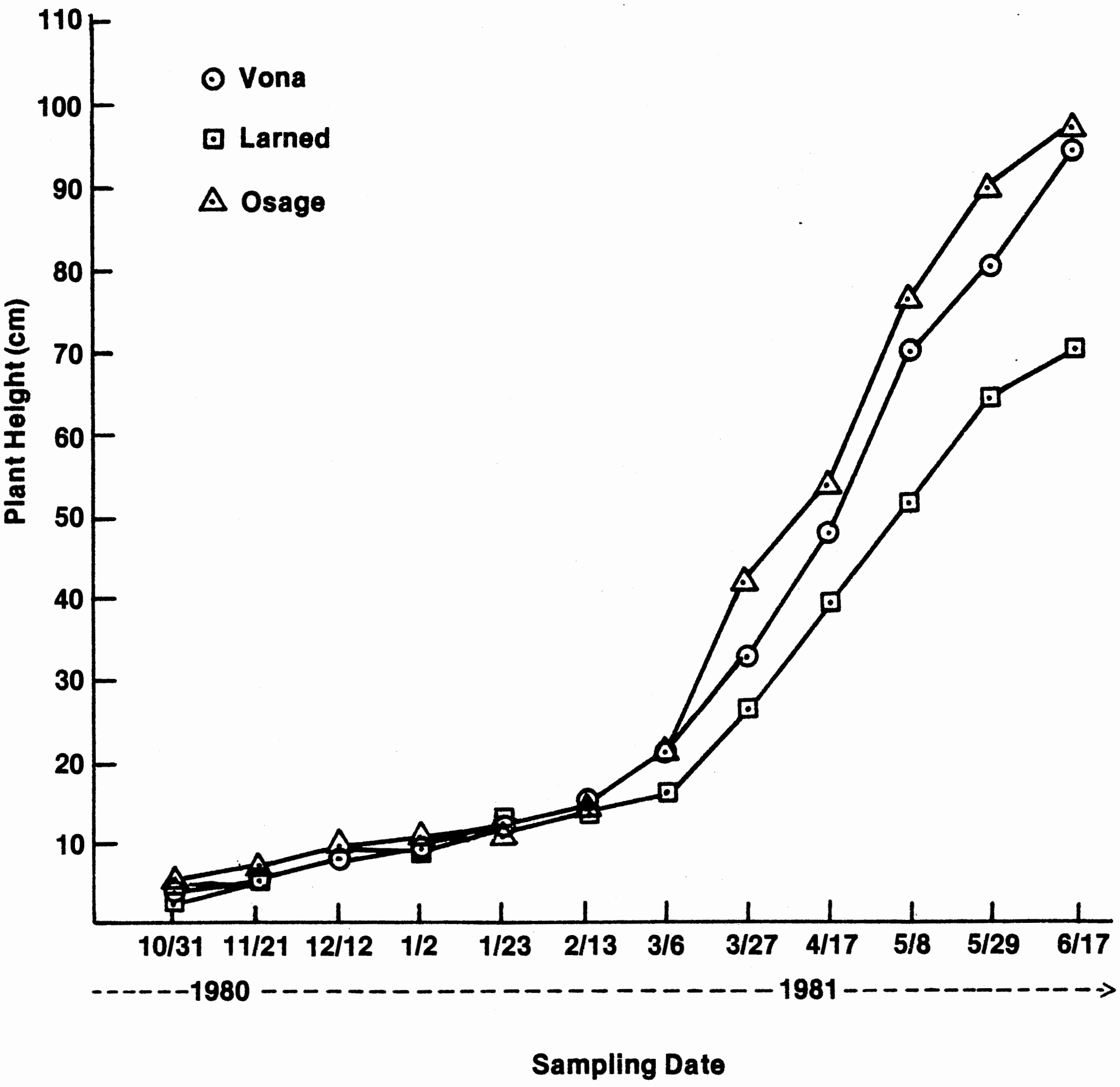

Figure 7. Plant Height

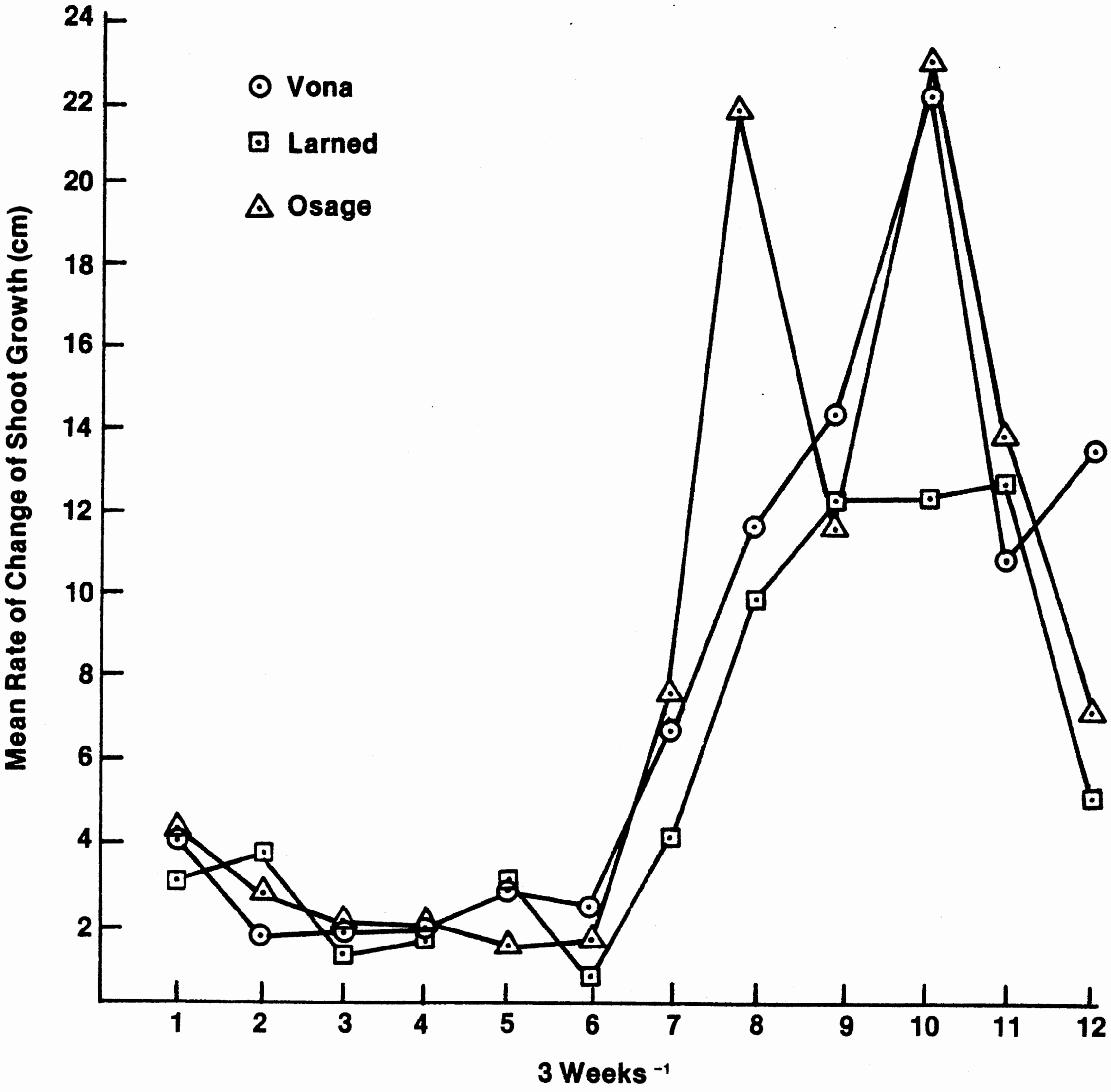

Figure 8. Rate of Change of Shoot Growth.

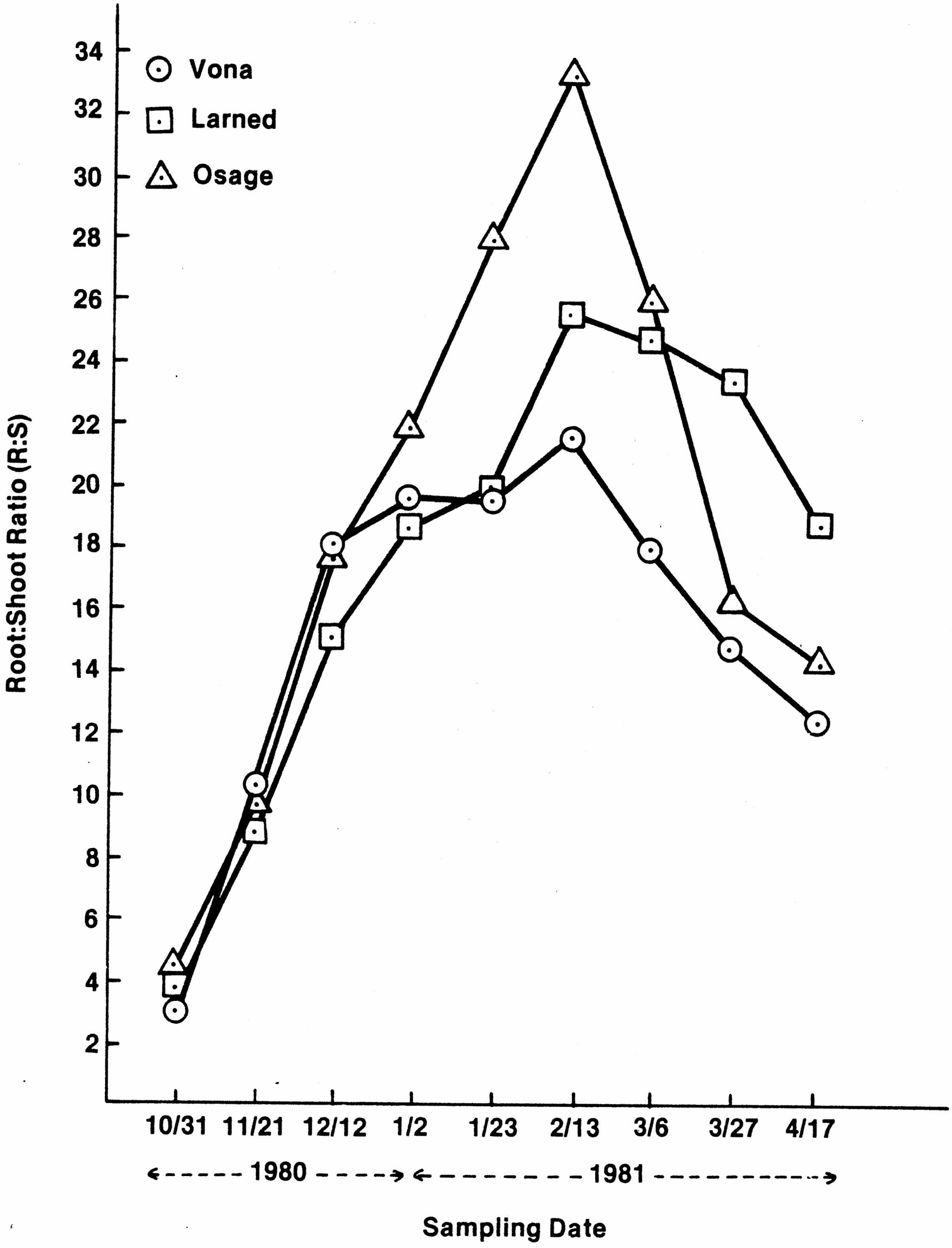

Figure 9. Root:Shoot Ratio at Each Sampling Date.

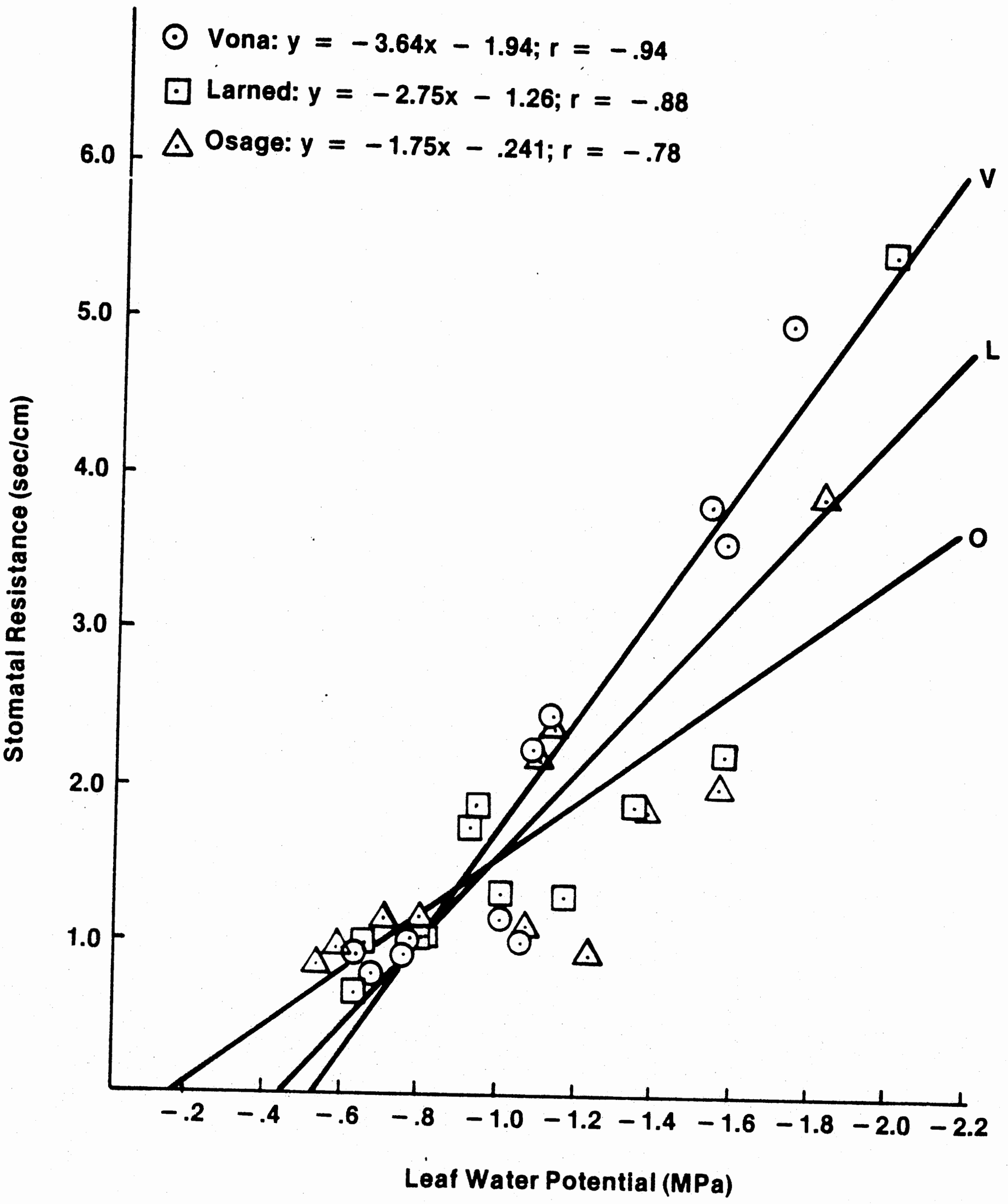

Figure 10. Stomatal Resistance vs. Leaf Water Potential For Three Wheat Cultivars.

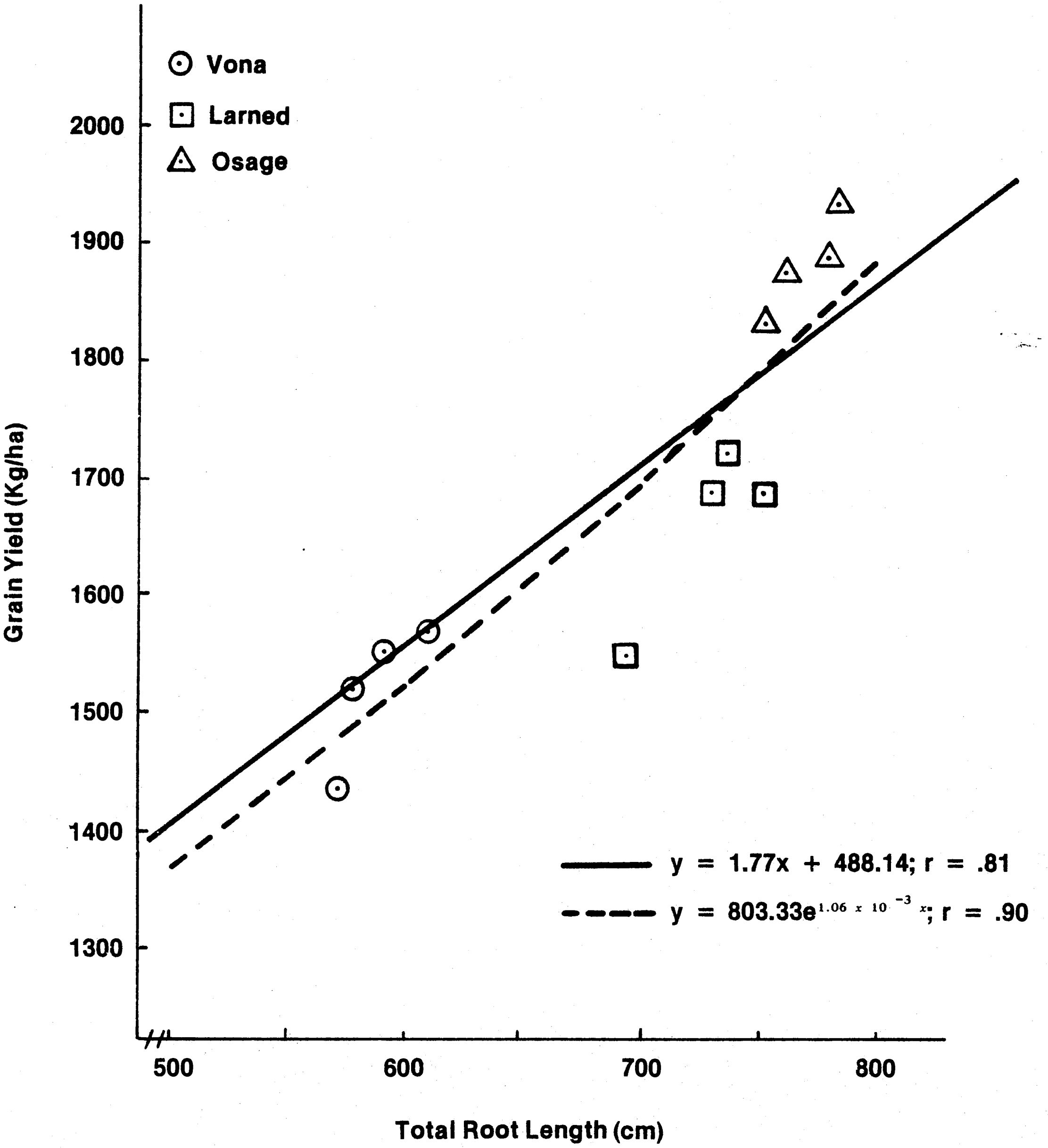

Figure 11. Grain Yield vs. Total Root Length for Three Cultivars of Winter Wheat.

CHAPTER IV

Summary and Conclusions

The major purpose of this research was to identify the relationship between drought resistance and some physiological responses of winter wheat and the relationship of such responses to growth, productivity, and survival under conditions of decreasing soil water potential. Two experiments were conducted under different environmental conditions: one in a growth room at the Controlled Environmental Research Laboratory, Oklahoma State University, Stillwater, Oklahoma, and other in the field at the Oklahoma State University Agronomy Research Station, Stillwater, Oklahoma. The research in both experiments was focused on the rooting characteristics of five winter wheat cultivars with known and unknown levels of drought resistance. Other physiological responses investigated were shoot growth, internal water relations, and stomatal resistance. In addition, the uptake of phosphorus was measured in the growth room experiment and yield was determined in the field experiment.

Root growth in this research was observed using split root containers in growth room experiment in which media consisting of soil and nutrient combinations were placed. In the field experiment, root growth was observed with an inverted periscope which was lowered into a clear column imbedded in the soil to 70 cm. Total root length was determined in both experiments using the line intercepts.

Results from the growth room experiment emphasized the presence of characteristic root growth differences between the two cultivars investigated and their response to varying levels of soil matric potential. Roots of the drought resistant cultivar (KanKing) were found to be extensive and highly branched under split root treatments, whereas the drought susceptible cultivar (Ponca) had a less branched and comparatively more reduced root system in terms of total root length and root dry weight. In addition the drought resistant cultivar had a much greater proportion of root hairs and new root growth than did the drought susceptible cultivar. The magnitude of the assessed characteristics were indeed different which indicated that each cultivar had a different kind of root system.

The drought resistant cultivar had a highly exploratory or 'dynamic' kind of root system, whereas the drought susceptible cultivar had a static or 'maintenance' kind of root system. The latter differed from the former by its minimized root mass to maintain maximum shoot growth at high soil water potentials, but at decreasing or low soil water potentials little increase in root growth above the minimum occurred. Therefore, the drought susceptible cultivar placed greater reliance on its established root system to provide support, nutrients, and water to the aerial portion of the plant without increasing its overall root mass at decreasing or low soil water potentials. Without appreciable new root growth, existing roots would tend to become suberized and consequent water and nutrient uptake would be more restricted. The dynamic kind of root system appeared to behave in a contrary fashion in which the root mass was not minimized at high soil water potentials and large increases in root growth occurred at decreasing or low water.

The inverted periscope technique used to observe in situ root growth of three winter wheat cultivars grown under drought stress conditions was found to be suitable for 189 days after planting as indicated by the coefficients of variation for each sampling date. Significant differences in root growth were observed among the cultivars during this period of time. In addition, differences in the rate of change of root growth at each sampling depth was observed among cultivars in which largest increases occurred during tillering and prior to anthesis. Root observations were not measured after 189 days after planting due to separation of the soil-column interface caused by severe drought. It can be concluded from these results that the inverted periscope technique is unsuitable for long term in situ root growth observations during severe drought conditions.

The advantage of a drought resistant plant to transfer water from soil with high water potential to roots where the soil water potential is low was tested for in the growth room experiment using labelled phosphorus (^{32}P) as a tracer. The results showed that ^{32}P was not transferred from one rooting side to the other rooting side for either the drought resistant or the drought susceptible cultivar in any split root treatment. Moreover, it was found that ^{32}P was taken up differentially by both cultivars and the amount varied depending on the split-root media combination. The drought resistant cultivar took up nearly three times more ^{32}P than the drought susceptible cultivar averaged over all split root treatments and under optimum conditions (aerated nutrient solution @ $\Psi_m = 0$) the drought resistant cultivar took up nearly 29 times more ^{32}P than the drought susceptible cultivar. These results indicated that the exploratory capacity of the dynamic kind of root system may be related to phosphorus uptake capacity. Thus, screening for phosphorus capacitance in plant tissue may be a viable selection criterion for drought resistance in winter wheat since drought stress is known to cause a number of deleterious effects on plant biochemical and physiological processes in which phosphorus is vitally involved.

Results from the internal water relations measurements in the growth room showed significant differences between the drought resistant and the drought susceptible cultivar. In general, the drought resistant cultivar maintained a higher leaf turgor potential and lower osmotic potential than the drought susceptible cultivar averaged over all split root treatments. Leaf water potential did not differ between cultivars when averaged over all split root treatments. Internal water relations comparisons between split root treatments, cultivars, and stress periods showed leaf turgor potential to be the only physiological variable that differed significantly in all cases. The drought resistant cultivar had consistently higher turgor potentials than the drought susceptible cultivar in all split-root treatments throughout the experiment.

Although high stomatal resistance is usually associated with drought resistance, no significant differences in this respect were found in the growth room experiment. The drought susceptible cultivar, however, tended to close its stomates earlier than the drought resistant cultivar in response to imposed drought stress.

Results from the field experiment showed little difference in leaf water potential values among the three cultivars investigated. However, each cultivar appeared to have a different relationship between leaf water potential and stomatal resistance, in which a common convergence point occurred at about 0.8 mPa and 1.0 sec/cm respectively. At lower leaf water potentials, Osage had a less elevated stomatal resistance than either Vona or Larned, which had less extensive root systems than Osage. It may be that a more extensive root system is associated with a different leaf water potential/ stomatal resistance relationship that contributes to drought resistance than a less extensive root system, which appears to contribute little to drought resistance.

Grain yield was compared among cultivars in the field experiment. Results showed the cultivar with the highest yield had the greatest total root length. The relationship between grain yield and total root length (for 189 days after planting) was found to fit an exponential function better than a linear function. These results indicated that significant increases in yield potential would result from a small increase in the total root length of a given cultivar when grown under drought stress conditions.

The data obtained from this research support the hypothesis that superior rooting characteristics contribute to drought resistance in winter wheat under conditions of decreasing soil water potential and that a rapidly penetrating and extensive rooting system should be considered as primary physiological characters in programs to develop drought resistant cultivars for semi-arid and arid regions of the world. This research has shown that an extensive root system of a drought resistant cultivar contributed to greater phosphorus uptake and shoot growth. Also, *in situ* growth observations were well correlated with grain yield.

VITA

Paul Irvin Erickson

Candidate for the Degree of

Doctor of Philosophy

Thesis: PHYSIOLOGICAL RESPONSES OF TRITICUM AESTIVUM L. TO DECREASING SOIL WATER POTENTIAL

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