Root morphological characteristics of barley (Hordeum vulgare L.) varieties grown in slant-boxes and pots
by Daniel Mark Roddy

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Agronomy
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Abstract:

Early maturing isotypes of 'Betzes' and 'Hannchen' barley (Hordeum vulgare L.) grown in slant-boxes produced smaller root volumes, root weights, and root:shoot ratios than 'normals' due to a reduction in the elongation rate and number of adventitious root axes. A similar decrease in root volumes, weights, and root:shoot ratios characterized early isotypes grown in pots.

Twenty-five two-row and 25 six-row barley varieties were grown in germination boxes to determine differences in mean seminal root numbers. Significant varietal differences in mean seminal root numbers were observed. Two-row barley varieties generally developed a greater number of seminal roots than six-row varieties.

Four barley varieties representing a wide range in mean seminal root numbers were evaluated in slant-boxes and pots to determine if increased branching compensates for low root number. Mean varietal root numbers were correlated with mean root volumes ($r = .96$; 2 degrees of freedom) in slant-boxes. The fresh root volume of 'DeKap' was significantly greater than 'Unitan' ($p = .007$), 'Briggs' and 'Zephyr' ($p = .05$) at 25 days from transplanting. Varieties differed in mean elongation rate of seminal axes in six of eight measurement periods.

Seminal root numbers were more important than elongation rates in determining the total length of seminal axes at day 12 when grown in pots.

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DANIEL MARK RODDY

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Approved:

Jarvis H. Brown
Chairperson, Graduate Committee

Dwane G Miller
Head, Major Department

Michael Malone
Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

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ABSTRACT

Early maturing isotypes of 'Betzes' and 'Hannchen' barley (Hordeum vulgare L.) grown in slant-boxes produced smaller root volumes, root weights, and root:shoot ratios than 'normals' due to a reduction in the elongation rate and number of adventitious root axes. A similar decrease in root volumes, weights, and root:shoot ratios characterized early isotypes grown in pots.

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INTRODUCTION

The association between root characteristics and cereal grain yield in arid and semi-arid climates has been studied extensively (Troughton, 1962; Hurd, 1976; Jordan, 1980). These authors generally agree that the value of any specific root characteristic depends on the environment in which the crop is produced.

Significant amounts of plant available water may remain in the lower soil zones (below 60 cm) at harvest time in many prairie soils. Plant breeders have sought to increase the extensivity of the root systems in spring wheat lines to use this moisture (Hurd, 1976).

In many drier areas it may be desirable for wheat grown solely on stored soil moisture to conserve water during early growth stages. Australian researchers were able to limit soil water use by wheat during early growth stages by decreasing seminal root numbers (Passioura, 1972).

Measurements by Brown (1980) in Montana indicate that current barley varieties leave a considerable quantity of plant available water in the lower root zone. A three year study in the Gallatin Valley determined that 'Betzes' barley rooted to 150 cm each year on a fallowed loess soil. Soil water use (initial plant available H_2O-harvest plant available H_2O) ranged from 13.2 - 14.2 cm. Seasonal rainfall ranged from 5.6 - 16.5 cm. Plant available water to 182 cm (6 feet) ranged from 14.2 - 20.1 cm. All available water from the upper 60 cm was used by the crop each year. In a later study on glacial till in Chouteau County, Montana, Brown found that 'Shabet' barley rooted to 150 - 180 cm. Most of the available water was used in the upper 122.0 cm, but 5.8 cm of plant available water remained in the 150 - 180 cm depth. Brown et al. (1981) also reported that barley yields increased approximately 148 kg/ha-cm of H_2O (7 bushels/acre-inch). Barley yields could be increased by approximately 1600 kg/ha (30 bu/acre) if the root systems of barley varieties were modified to use this water.

The objective of this research was to examine the root morphological characteristics of barley which control soil water extraction patterns. We postulate that the root system of barley varieties grown in Montana may be modified to utilize the residual soil moisture described by Brown (1980).

REVIEW OF LITERATURE

Barley, like other temperate cereals, develops two root systems: the seminal, which develops from primordia within the seed, and the adventitious, which initiates in the basal nodes of the stem (Troughton, 1962). The seminal roots are important for seedling establishment since they develop first (Fritsch, 1977). Adventitious roots develop anytime after the 3-4 leaf stage (Briggs, 1978).

Researchers have amputated the adventitious roots of wheat and barley to assess the relative importance of the seminal roots beyond the seedling stage (Simmonds and Sallans, 1933; Sallans, 1942; Gliemeroth, 1957). The results of these amputation studies were generally inconclusive. Hackett (1971) demonstrated that the removal of one part of the barley root system is generally compensated for by increased growth of the remainder.

The adventitious roots may dominate the seminal roots due to greater numbers. Pavlychenko and Harrington (1935) demonstrated that widely spaced barley is capable of producing 83 adventitious roots/plant. Eight barley cultivars grown in Montana averaged 14.5 adventitious roots/plant (Hockett, 1980). Briggs (1978) reported that barley seminal roots generally ranged from 5-7, over a range of seeding rates.

Troughton (1962) noted that wheat crops may reach maturity with only seminal roots when drought prevents the formation of adventitious roots. Ferguson and Boatwright (1968) demonstrated that the adventitious roots of spring wheat will not elongate more than a few millimeters when the soil adjacent to the crown is below a minimum water content. Failure of adventitious root development does not occur frequently in Montana. Most barley production areas have at least a 70% chance of receiving 13 cm or more of precipitation during the growing season (Caprio et al., 1980).

Weaver (1926) and Gliemeroth (1957) observed that barley seminal roots penetrate deeper than adventitious roots. When plants were widely spaced, however, both the adventitious and the seminal roots of 'Hannchen' barley penetrated to 160 cm (Pavlychenko and Harrington, 1935). Barley may be almost entirely dependent on the seminal roots to use moisture stored deep in the soil profile when surface moisture is depleted (Troughton, 1962). Although the soil water extraction patterns of barley have been studied extensively in Montana, the relative depth of penetration of the seminal and adventitious roots has not been determined.

MacKey (1980) described barley seminal roots as thinner and more branched than adventitious roots. Goedewaagen (1942) and Krassovsky (1926) reported that seminal roots were able to absorb more H_2O/unit dry weight than adventitious roots.

The number of adventitious roots/ha is highly variable within and between varieties, and between years. In field studies, 'Betzes' barley produced half as many adventitious roots/ha in 1971 as in 1972 (Hockett, 1980). Seeding rate was 80.7 kg/ha (72 lbs/acre) both years. July precipitation was 2.43 cm greater in 1972 than in 1971. This may account for the large differences in adventitious roots/ha between years.

A positive relationship often exists between the number of adventitious roots and tillers per plant (Brouwer, 1965). Adventitious roots are capable of developing at each lower node of the main culm. In addition, each axillary bud or tiller is capable of developing an independent system of adventitious roots (Troughton, 1962).

The ratio of adventitious roots to tillers is not consistent (Brouer, 1965). Hockett (1980) reported an average of 4.3 adventitious roots/tiller in 1972, but only 1.7 adventitious roots/tiller in 1971 for 'Betzes'. The average numbersof tillers/plant were similar for the two years.

MacKey (1980) described the adventitious root system of cereals as "highly flexible" and responsive to daily environmental variation. Conversely, he described the seminal root system as "pre-adapted" or "fixed" because the eventual size is largely determined by number. Seminal root number is expressed during germination. As a result, breeders have an opportunity to control the size and distribution of the seminal root system.

The value of seminal root number as a selection criterion has been considered by several researchers. Fritsch (1977) stressed the importance of a high number of seminal roots for seedling establishment. Pavlychenko and Harrington (1935) and Pavlychenko (1937) suggested that cereals with a large number of seminal roots were more capable of development under adverse conditions. Sallans (1942) found that wheat plants which produced the greatest number of seminal roots also produced the greatest yield due to an increase in the number of kernels/spike. Hurd (1975) reported that total seminal root length at 5-6 days ranked cultivars in a previously determined order of total root length at maturity and yield under moisture stress. Total root length at 5-6 days is largely a function of seminal root number.

Histological examinations of wheat embryos indicate a theoretical maximum of 10 seminal roots: the primary axis and 3 whorls with 3 primordia each (MacKey, 1980). Merry (1941 and 1942) found 9 primordia in 'Alpha' barley, each capable of producing a seminal root.

Significant varietal differences in barley seminal root numbers were reported by Pope (1945). It was not determined whether these differences were due to the number of primordia differentiated in the embryo or to the number of primordia actually expressed (i.e., visibly elongated).

The variation in seminal root numbers commonly observed within barley lines tends to obscure inherent varietal differences. Larger, broader kernels of cereals have been observed to produce a greater number of seminal roots within a variety (Taylor and McCall, 1936; MacKey, 1980).

Pope (1945) was unable to relate varietal differences in seed weight to seminal root numbers of barley. MacKey (1980), however, described a good correlation ($r = .71$) between seed size and seminal root number when comparing wild and cultivated wheat. The primitive Aegilops mutica has one seminal root per seed while numbers up to five or six were recorded for some modern varieties.

The primitive barley, Hordeum spontaneum L., had the smallest seminal root number (4.7 roots/seed) of the Hordeum species tested by Pope (1945). The apparent evolutionary trend toward increasing seminal root number may, in part, result from selection for kernel plumpness (MacKey, 1980).

Environmental variables during germination, such as soil temperature, depth of planting and soil moisture, influence the expression of seminal root number. The relative maturity of the embryo is also an important variable (Troughton, 1962). Varietal comparisons are valid only under controlled conditions.

The degree of branching of the seminal axes will determine the ability of the root system to either explore a limited soil volume exhaustively or a larger volume more extensively. The degree of dominance of the seminal axes over the branch roots would become an important selection criterion if the objective is to increase the depth of penetration of the seminal axes (MacKey, 1980).

The seminal root axes show the strongest positive geotropic response, extending vertically downward. The primary laterals extend horizontally and then progressively develop positive geotropic curvature (Russell, 1976). The strong geotropic tendancy of the seminal axes allow them to extend deeper in the soil than the branch roots (MacKey, 1980).

The degree of vertical orientation of the seminal axes could also be considered as a selection criterion, if genotypic differences are found to exist.

The seminal root axes will penetrate deeper than the branch roots because of their higher growth rate. The growth rate of the axes, primary, and secondary laterals are typically in the ratio of 4:1:½ (Milthorpe and Moorby, 1974). The rate of extension is often related to root diameter with the larger meristems elongating more rapidly (MacKey, 1980; Russell, 1976; Barley, 1970).

Detailed measurements of the seminal root system of barley indicate that the branching pattern is under strict genetic control throughout the development of the plant. For each genotype, as branch roots progress from lower to higher orders of magnitude, the characteristic distance between points of branching decreases and the characteristic orientation becomes more horizontal (Hackett, 1971).

The number of seminal axes, orientation, degree of branching, growth rate, and duration of the growth period, appear to control the root distribution pattern and thus the ability of the seminal root system to extract available moisture throughout the soil profile. These morphological characteristics are identifiable at very early growth stages, thus enhancing their potential value as selection criteria (Hurd, 1975; MacKey, 1980).

Montana State University researchers studied the relationship between heading date and the root growth pattern of barley varieties (Smail, 1980; Brown, 1980).

Smail (1980) reported a significant correlation ($p = .05$) between heading date and soil water use when comparing 25 maturity isotypes of barley. The early maturing isotypes generally used less soil moisture than the 'normals'.

Brown (1980) reported that differences in total soil water use between 'Betzes' and 'Erbet' isogenic lines (differing in heading date by 8 days) decrease with increasing rates of nitrogen fertilizer. In 1971, 'Betzes' used 2.3 cm more soil water than 'Erbet' at 0 kg N/ha, 1.5 cm more at 67.4 kg N/ha, but only 0.2 cm more at 134.7 kg N/ha. A similar trend was exhibited in 1972. 'Betzes' rooted deeper than 'Erbet' and generally used more H_2O at each soil depth at both 0 and 67.4 kg N/ha. There was little effect of heading date on rooting depth and total soil water use at the 134.7 kg N/ha rate.

In 1971, a very dry growing season, 'Erbet' produced a greater number of adventitious roots/ha than 'Betzes' at all nitrogen levels. 'Betzes' used more H_2O at 0 and 67.4 kg N/ha despite having fewer adventitious roots. In 1972, a relatively wet year, 'Betzes' produced a greater number of adventitious roots/ha than Erbet at all nitrogen levels.

MATERIALS AND METHODS

Experiment I: The Relationship Between Heading Date and Barley Seminal and Adventitious Root Growth (Slant-Boxes)

Four slant-boxes constructed of .25 inch plexiglass were used to measure root growth. Each box (64.5 cm x 4.5 cm x 122 cm) was partitioned into 6 cubicles (10 cm x 4.5 cm x 122 cm) giving a total of 24 experimental units. The boxes were situated at a 43^0 angle in a cabinet in the greenhouse (Fig. 1). Opening sliding doors in the cabinet back allowed observation of the roots growing along the lower plexiglass face. The boxes were easily removed from the cabinet for washing roots.

The soil used in the slant-boxes was from the A_p horizon of a typic calciboroll, coarse loamy mixed (Manhattan series). The soil was oven dried (105^oC), ground, and sieved to a maximum particle size of 850 microns. Dry soil was packed into the boxes (bulk density = 1.3 g/cm^3) and wetted to field capacity (18% H_2O by weight). The boxes were covered with polyethylene sheeting to prevent vapor loss and allowed to equilibrate for one week.

Isogenic pairs of 'Betzes' and 'Hannchen', each pair differing in heading date by eight days, were evaluated in the slant-boxes (Fig. 2).

In the Hannchen study, three seeds of uniform size and weight were planted in each cubicle. The early and the normal isotype were replicated 6 times. Germination was 100% and emergence relatively uniform.

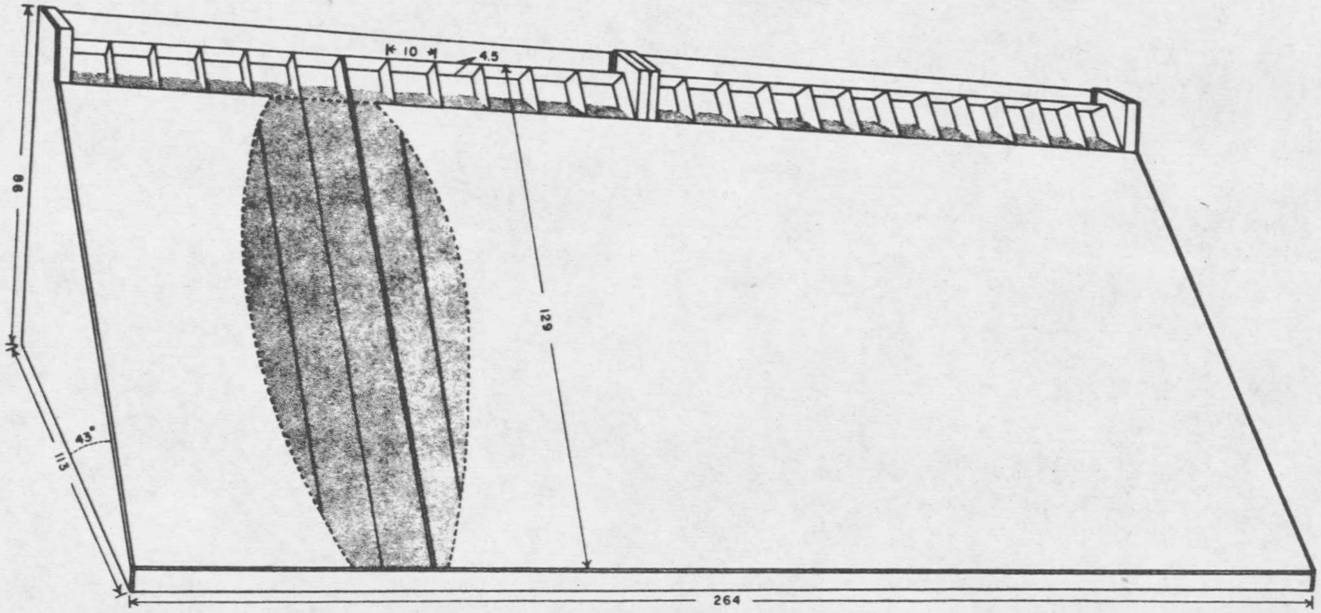

Figure 1. The slant-box used for measuring root elongation rates (dimensions are in cm).

H	Hannchen
HE	Hannchen-early
B	Betzes
BE	Betzes-early

H_1	BE_1	B_1	HE_1	H_2	HE_2	H_3	HE_3	B_2	BE_2	H_4	B_3	BE_3	H_5	HE_4	B_4	BE_4	H_6	HE_5	B_5	BE_5	B_6	BE_6	HE_6

Figure 2. Arrangement of barley maturity isotypes in slant-boxes for Experiment I (subscripts represent replications).

The 'Betzes' isotypes were replanted due to poor germination. Therefore, the 'Betzes' and 'Hannchen' experiments were not run concurrently. To circumvent the poor germination, seeds of 'Betzes' (uniform size and weight) were pre-germinated for 48 hr. One viable seedling was transplanted into each cubicle. This was a convenient and reliable method of starting plants in the slant-boxes.

Seminal roots were visible through the plexi-glass within 5 days of imbibition, and reached the bottom of the box in approximately 21-23 days.

Because of visible wilting, the plants of the Hannchen and Betzes isolines were irrigated beginning on the 15th and 17th day, respectively. Adventitious roots appeared shortly after irrigation. Approximately 100 ml H_2O/cubicle was applied every 5-6 days to facilitate normal plant development.

Average elongation rates of the seminal and adventitious axes were calculated by the following method: the location of each axial root tip was marked on the plexiglass at the end of each measurement period (typically 48 hr). The distance between successive marks was measured. Average axial elongation rates were expressed as cm/root hr.

Plants were harvested after 50 days and the numbers of tillers and heads recorded. The stems and leaves were dried for approximately 48 hr at 60°C and weighed.

The cubicles were saturated for several hours to facilitate removal of most of the soil from the roots. After soaking, the soil was washed away using a high pressure nozzle, leaving the root system virtually intact. The root mass from each cubicle was immersed in a Calgon solution and gently agitated by hand to disperse the remaining clays. Root samples were then placed in distilled water to equilibrate for several hours.

The samples were blotted dry with paper towel and submerged in a graduated cylinder for approximately 2 minutes. The amount of water displaced by the sample was regarded as the fresh root volume.

Total number of root axes per plant was counted. The seminal roots were not distinguishable from the adventitious roots after washing.

The root samples were dried at $60^{o}C$ for 24 hr and ashed ($593^{o}C$ for two hours) to estimate the amount of inorganic soil material left on the roots after washing. The corrected root weights (g dry weight - g ash) were used to calculate the root:shoot weight ratios.

Experiment II: The Relationship of Heading Date to Barley Fresh Root Volume, Root Dry Weight, and Root:Shoot Weight Ratios (Pots)

The two isogenic barley pairs, 'Betzes' and 'Hannchen', were evaluated in 21 cm diameter pots in the greenhouse. Seeds of uniform size and weight were pregerminated. Three seedlings of the same genotype were transplanted into each pot after 48 hr. The four treatments were replicated seven times (1 replication/pot). The plants were grown in a gravel and sand medium and watered on alternate days with 1/2 strength Hoagland's solution. Pots were arranged on the greenhouse bench in a randomized block design. At 48 hr intervals, the pots were rotated both within and between blocks.

Plants were harvested after 60 days and the number of tillers and heads, and plant dry weights determined. Root volumes and root dry weight were determined using the method described in Experiment I.

Experiment III: The Relationship of Seed Size to Seminal Root Number of Barley (Germination Boxes)

Two seed lots each of 'Betzes' and 'Compana' were separated into six size ranges using pairs of sieves with openings 3/4 in long and widths in 64ths of an inch of: 4.5 and 5.0, 5.0 and 5.5, 5.5 and 6.0, 6.0 and 6.5, 6.5 and 7.0, 7.0 and 8.0. For each size range, seed passed through the second (larger) openings and was retained by the first (smaller) sized openings. Fifty seeds from each size range were germinated on moist blotter paper in the dark at 15°C. The number of seminal roots per seedling was counted after eight days.

Experiment IV: The Effect of Genotype on Seminal Root Number of Barley (Germination Boxes)

A diverse collection of 50 barley varieties consisting of 25 two-row and 25 six-row types was evaluated for differences in seminal root number. Seed lots produced in one location at Bozeman, Montana in 1979 were separated into five size ranges using pairs of sieves whose openings had the following widths in 64ths of an inch: 5.0 and 5.5, 5.5 and 6.0, 6.0 and 6.5, 6.5 and 7.0, 7.0 and 8.0 (see Experiment III above).

Only the seed size range most characteristic of the variety was evaluated. One hundred seeds/variety were germinated on moist blotter paper at 15°C and the number of seminal roots per seedling counted after eight days.

Experiment V: The Relationship of Seminal Root Number to Fresh Root Volume, Root Dry Weight, and Average Axial Elongation Rate (Slant-Boxes)

The barley varieties 'DeKap', 'Briggs', 'Unitan' and 'Zephyr' were selected from the 50 varieties tested in the previous experiment, for their uniform seed size and weight, and range in mean seminal root number (Table 1).

Seeds were treated with Orthocide-Trivax (Vitavax and Captam at .007 g/50 seeds) fungicide and pre-germinated on moist blotter paper for 48 hr. One viable seedling was transplanted into each cubicle. The plot diagram is given in Fig. 3. The soil in the cubicles was wet to field capacity prior to planting. No additional moisture was added during the course of the experiment.

Plants emerged uniformly within 48 hr of transplanting. Seminal roots were visible on the plexiglass face at the time of emergence. Plants were harvested on the 25th day (six leaf stage). All other

Table 1. Characteristic seed size range, associated seed weight, and mean seminal root number of Dekap, Briggs, Unitan, and Zephyr barley.

Cultivar	Characteristic Seed Size (sieve openings 64th in)	 Seed Weight (g)	Mean Seminal Root No. (germ. boxes)
Dekap (2-row)	6.5-7.0	.049	6.9
Briggs (6-row)	6.5-7.0	.047	5.9
Unitan (6-row)	6.5-7.0	.048	5.0
Zephyr (2-row)	6.5-7.0	.047	5.9

D	Dekap
B	Briggs
U	Unitan
Z	Zephyr

D_1	B_1	U_1	Z_1	D_2	B_2	U_2	Z_2	D_3	B_3	U_3	Z_3	D_4	B_4	U_4	Z_4	D_5	B_5	U_5	Z_5	D_6	B_6	U_6	Z_6

Figure 3. Arrangement of barley varieties in slant-boxes for Experiment V (subscripts represent replications).

materials and methods were similar to those described for Experiment I.

Experiment VI: Seminal Root Number and Mean Seminal Root Axial Elongation Rate (Pots)

The varieties evaluated in Experiment V were grown in 21 cm diameter pots as described for Experiment II. Plants were harvested 12 days after transplanting, seminal root axes were counted, and the length of each seminal root axis measured.

RESULTS AND DISCUSSION

Experiments I and II

Fresh root volume

Fresh root volumes of the early maturing barley isotypes were significantly lower than for the normal isotypes grown in the slant-boxes and pots (Table 2). The mean root volumes of the 'Betzes-early' isotype were 59% and 56% of the 'normal' in the slant-boxes and pot experiment, respectively. 'Hannchen-early' exhibited a similar tendency, having a root volume 57% of the normal in the slant-box and 40% of the normal in the pot experiment.

Root dry weight

Mean root dry weights (Table 2), which were highly correlated (r = .94 over both experiments) to root volumes, were greater in 'normal' isolines. Root weights of 'Betzes-early' were 65% and 61% of the normal maturing 'Betzes' in the slant-boxes and pots, respectively. 'Hannchen-early' responded similarly, giving root dry weights of 59% and 48% of the 'normal' in the slant-boxes and pots, respectively.

Approximately 50% of the dry sample weight was removed during the ashing procedure which reduced the within-line variability of the 'Hannchen' isotypes. It appears that in the 'Hannchen' isotypes the ash correction procedure removed some of the random error associated with the inorganic soil material still left on the roots after washing.

Table 2. Mean fresh root volume (ml), root dry weight (g), shoot dry weight (g), root: shoot ratios, and total number of root axes of barley maturity isotypes (slant-boxes and pots)

	Slant-boxes (t test) Exp. I				Pots (ANOV) Exp. II			
	Betzes	Betzes-early	Hannchen	Hannchen-early	Betzes	Betzes-early	Hannchen	Hannchen-early
Root volumes (ml)	23.4	13.8	25.5	14.5	11.5	6.5	14.3	5.7
	(p = .002)		(p = .004)		(p = .001)		(p = .001)	
Root dry weights (g)	1.37	.89	2.18	1.29	2.62	1.60	2.85	1.37
	(p = .039)		(p = .001)		(p = .004)		(p = .001)	
Shoot dry weights (g)	5.26	5.46	4.76	5.99	8.80	9.34	9.14	8.09
	NS		(p = .010)		(p = .402)		(p = .010)	
Root:shoot ratios	.26	.16	.46	.22	.30	.17	.31	.17
	(p = .001)		(p = .003)		(p = .001)		(p = .001)	
Number of root axes	52	36	53	39	-	-	-	-
	(p = .018)		(p = .050)					

Probability values were decreased for the 'Hannchen' isotypes from .0339 to .0001. However, probability estimates of 'Betzes' and 'Betzes-early' were increased from .0147 to .0394.

The pot experiment allowed comparisons between the 'Betzes' and 'Hannchen' lines. Differences in mean root weights and volumes between 'Betzes-early' and 'Hannchen' were significant (.01) as were differences between 'Hannchen-early' and 'Betzes' (.01). 'Betzes' and 'Hannchen' were not different from each other nor was 'Hannchen-early' different from 'Betzes-early'.

Root:shoot ratios

Since mean shoot dry weights were similar, differences among root:shoot ratios generally reflected the respective differences in root weights (Table 2).

Total number of root axes

Differences among the average number of root axes roughly paralleled differences in root weight and volume in the slant-box. The early isotypes of 'Betzes' and 'Hannchen' had 69% (p = .018) and 74% (p = .049) as many root axes as the 'normal', respectively. The root weights of 'Betzes' and 'Betzes-early' were highly correlated (r = .94) to the total number of root axes (seminal + adventitious).

Seminal axes elongation rates

The axial elongation rates of 'Hannchen' and 'Hannchen-early' barley generally increased during the first 15-17 days (Fig. 4). Sharp declines of axial elongation rates from the 17-19th days were observed. The cause of these declines is unclear. Low soil moisture and/or high temperature may have limited root growth during that measurement period. Additionally, a portion of the photosynthate previously available for seminal root growth may have been partitioned to the adventitious roots which appeared on the 17th day. Apparent differences between the 'early' and the 'normal' maturing 'Hannchen' on the 21st and 23rd days may have been an artifact of the system. Measurements during these periods are inconclusive because a significant number of seminal axes had reached the bottom of the box.

The elongation rates of the seminal axes of 'Betzes' and 'Betzes-early' generally increased until the 11th day (Fig. 5). The rates stabilized during the next four measurement periods and markedly increased in the final measurement period (18-22). Seminal roots may have responded to surface irrigation on the 18th day. No significant differences between the 'early' and the 'normal' maturing Betzes were observed during the first 22 days.

After the adventitious roots began to develop, the seminal root axes of both isogenic pairs continued to extent vertically at least 7-10 days (or until they reached the bottom of the box). This suggests

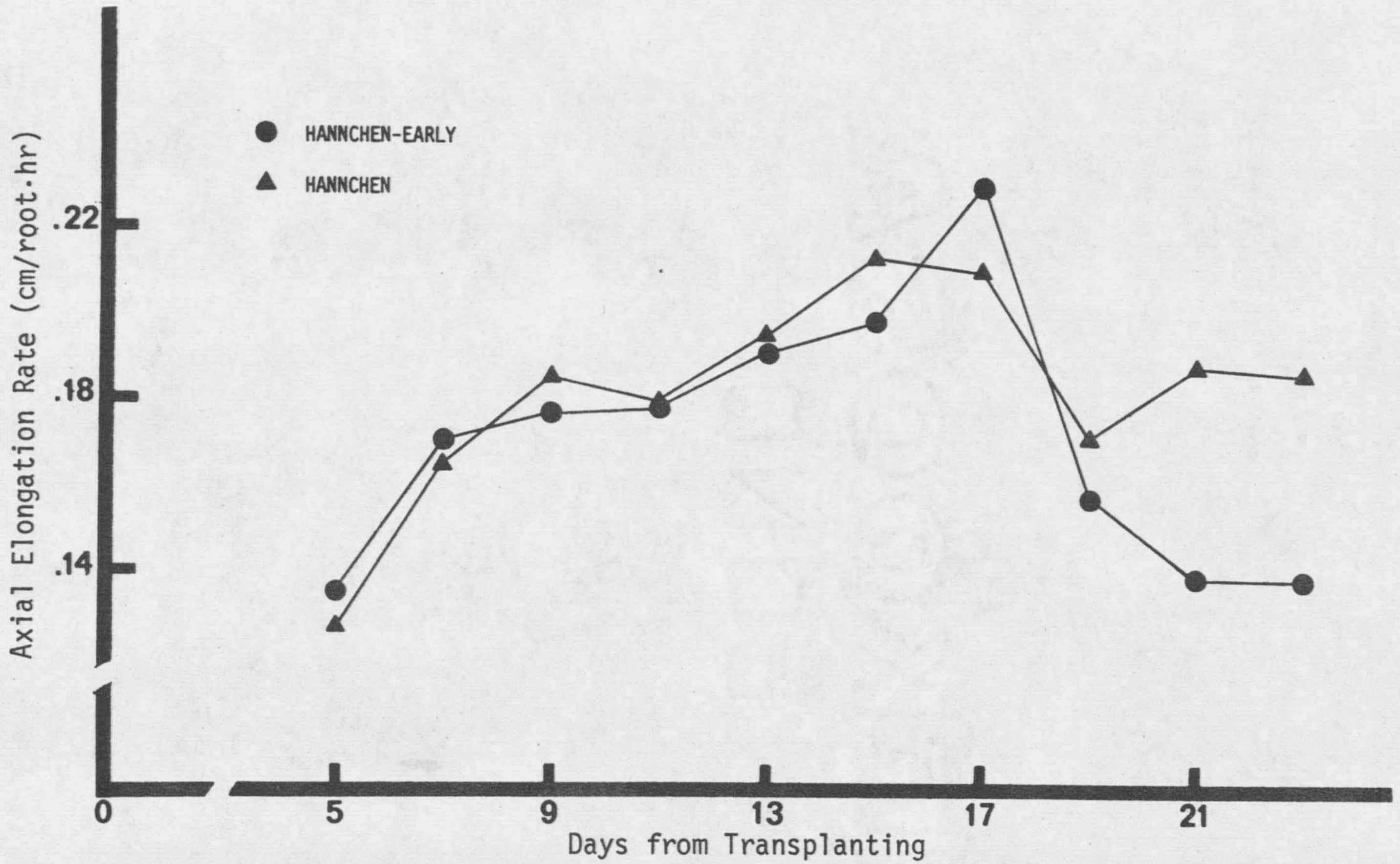

Figure 4. Elongation rates of barley seminal root axes:Hannchen and Hannchen-early.

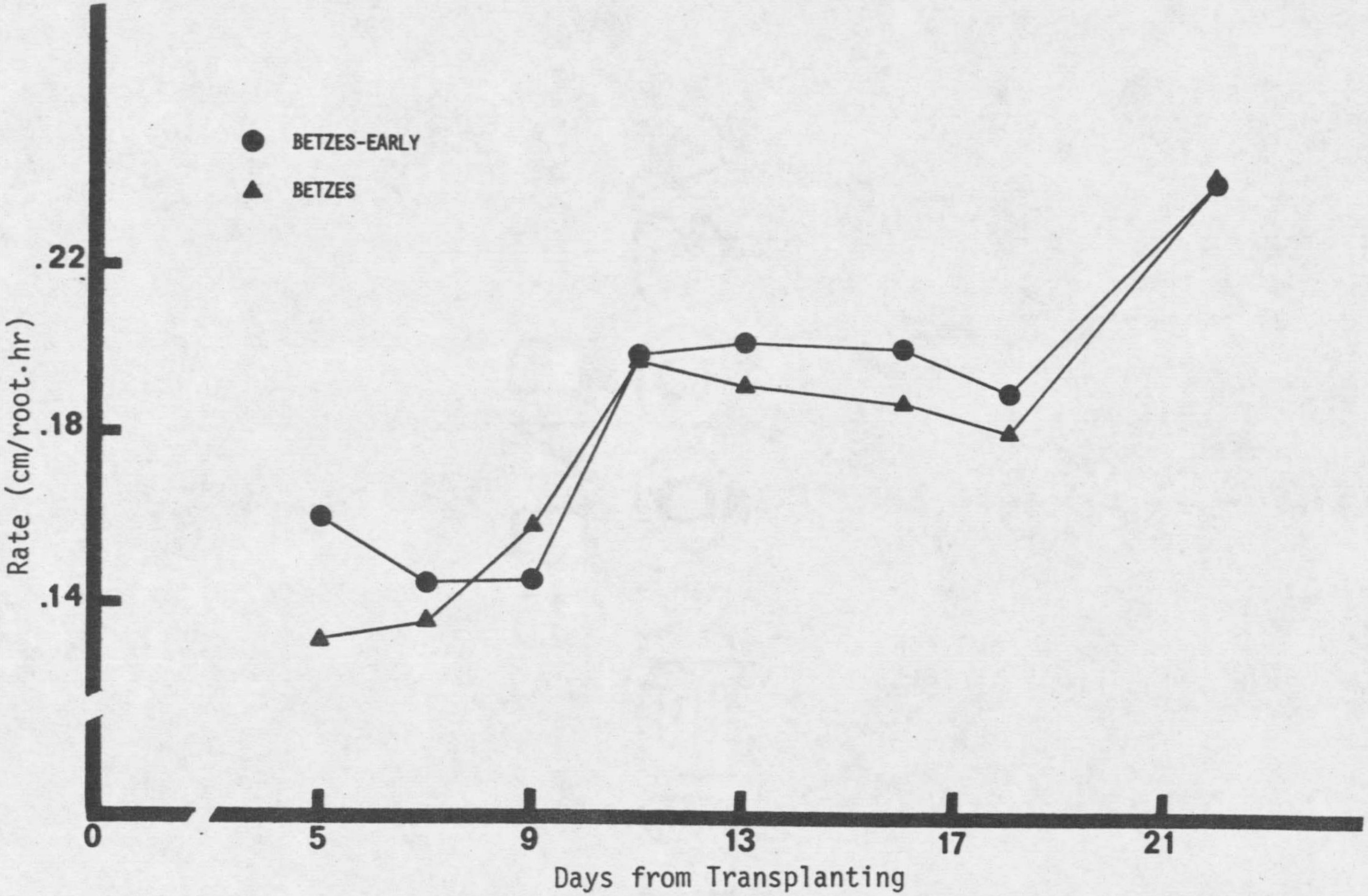

Figure 5. Elongation rates of barley seminal root axes:Betzes and Betzes-early.

that the seminal axes may not cease to elongate during the early stages of adventitious root development. The seminal axes may be able to penetrate deeper in the soil profile than the adventitious axes because the seminal roots typically have a 2 week head start. The axial elongation pattern of seminal roots was not observed during stem extension, anthesis, and heading because of the limited depth of the slant-boxes. Thus, we were not able to study the effect of heading date on seminal root elongation rates.

Elongation rates of the adventitious axes

Quantification of adventitious root development was very difficult largely because of the rapid increase in the number of axes. Elongation rates were very erratic (Fig. 6). Axes often elongated 10-15 cm, ceased elongation and were replaced by new axes initiating at the crown region.

No significant differences in adventitious root axial elongation rate were detected between 'Hannchen' and 'Hannchen-early'. Three plants per cubicle produced too many roots on the small viewing surface to allow accurate measurement of elongation rates. Uniform soil moisture was also difficult to maintain. The large differences in root volume and weight between 'Hannchen' and 'Hannchen-early' may have been due to the number of adventitious axes rather than elongation rates.

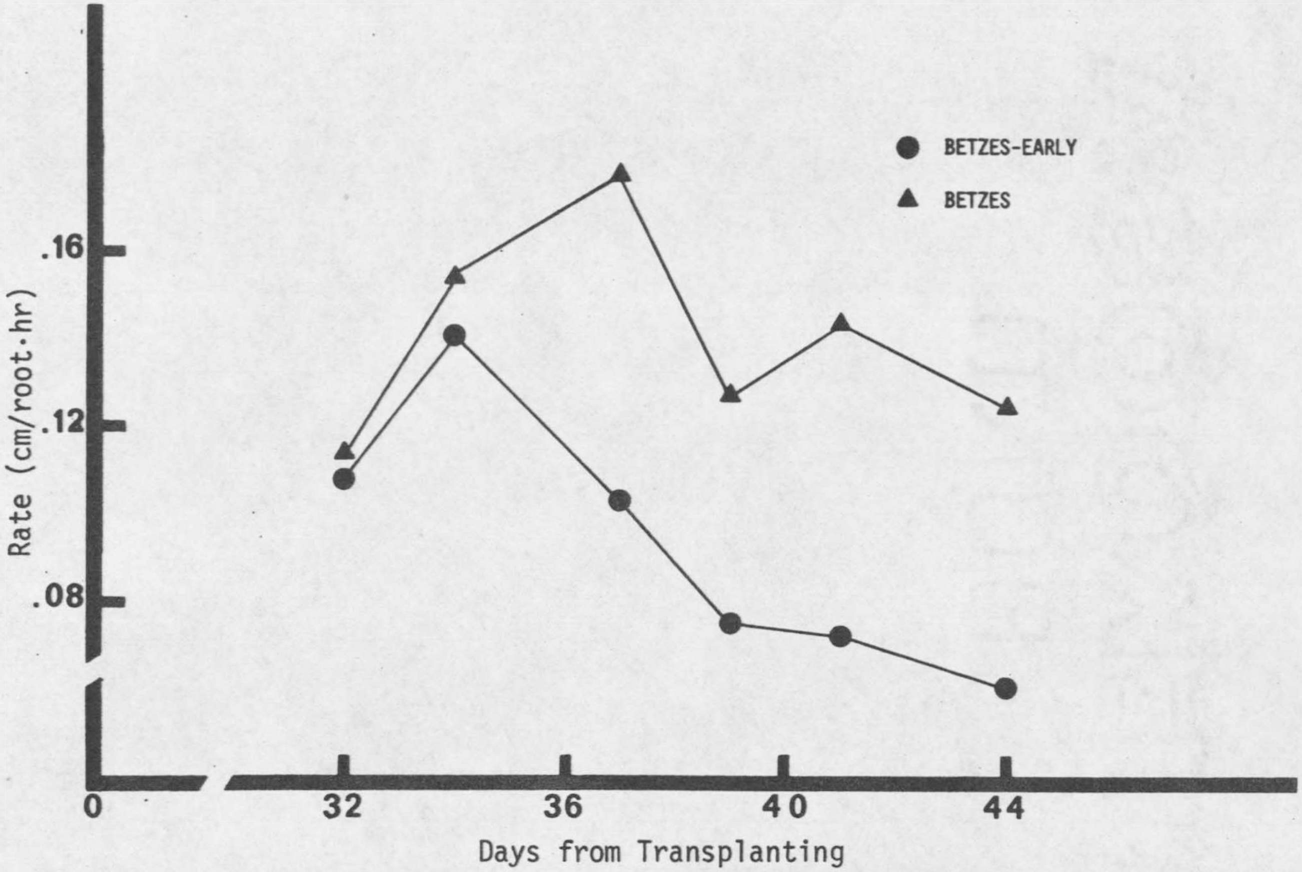

Figure 6. Elongation rates of barley adventitious root axes: Betzes and Betzes-early.

The average adventitious axial elongation rates of 'Betzes' and 'Betzes-early' roots are plotted in Fig. 6. 'Betzes' root axes elongated more rapidly than 'Betzes-early' after the 34th day. The heads of 'Betzes-early' were beginning to appear on the 35th day, while the plants of the normal maturing 'Betzes' were still in the tillering stage. 'Betzes-early' adventitious root axes elongation rates decreased at the onset of heading.

It is postulated that the adventitious roots of early types might fail to reach the lower soil zones if the lower elongation rates of adventitious axes exhibited by 'Betzes-early' are characteristic of early maturing isolines. Consequently, the early types might depend almost exclusively on their seminal roots to extract H_2O from the lower soil zones.

Experiment III

Mean seminal root numbers of six different seed size ranges and two different seed lots of 'Betzes' and 'Compana' barley are compared in Table 3. Significant correlations between seed size and seminal root number were observed for all four treatments. The high correlation ($r = .90$, all four seed sources combined) provides additional evidence of the within line variability in root number due to seed size.

Table 3. The effect of seed size on the seminal root number of Betzes and Compana barley.

Seed Size Range (sieve openings, 64ths in)	Mean Seminal Root Number			
	Compana I	Compana II	Betzes I	Betzes II
4.5 - 5.0	5.8	5.7	5.7	5.4
5.0 - 5.5	5.7	6.0	5.9	5.9
5.5 - 6.0	6.4	6.4	6.0	6.2
6.0 - 6.5	6.5	6.6	6.2	6.3
6.5 - 7.0	6.5	7.0	6.5	6.5
7.0 - 8.0	6.8	7.0	6.8	6.5

Based on this information, we concluded that within line variability in seminal root numbers may be minimized by selecting the seed size range most characteristic of the seed lot when testing varietal differences.

Experiment IV

The average seminal root numbers of the 50 barley varieties are reported in Tables 4 and 5. Most (21) of the 25 two-row varieties had average seminal root numbers that were greater than any of the 25 six-row varieties. The average seminal root number of the 25 two-row varieties (6.3) was significantly greater (p = .01) than that of the six-row varieties (5.2). Mean root numbers ranged from 5.5 - 6.9 (L.S.D. = .4) for two-row varieties and from 4.3 - 5.9 (L.S.D. = .2) for six-row varieties.

Experiments V and VI

Seminal root numbers

Mean seminal root numbers obtained in the various experiments are compared in Table 6. Ranges in mean seminal root numbers varied between experiments. However, the varietal rankings were the same in all three experiments.

Table 4. Mean seminal root numbers, seed sizes, and seed weights of 25 two-row barley varieties

Variety	Mean Seminal Root Number	Seed Size Range (sieve openings 64ths in)	Mean Seed Weight (g)
Dekap	6.9	6.5 - 7.0	.049
Erbet	6.8	6.5 - 7.0	.048
Herta	7.8	6.5 - 7.0	.042
Compana	6.7	7.0 - 8.0	.063
Piroline	6.6	6.5 - 7.0	.045
Haisa II	6.6	6.5 - 7.0	.043
Horn	6.5	6.5 - 7.0	.046
Marie	6.5	6.5 - 7.0	.048
Vanguard	6.5	6.5 - 7.0	.046
Georgie	6.4	6.5 - 7.0	.048
Heines Hanna	6.4	6.5 - 7.0	.046
Freja	6.4	6.5 - 7.0	.045
Otis	6.3	7.0 - 8.0	.056
New Moravian	6.3	6.0 - 6.5	.040
Hannchen	6.2	6.0 - 6.5	.040
Munsing	6.1	7.0 - 8.0	.060
Klages	6.1	5.5 - 6.0	.035
Firlbeck III	6.1	7.0 - 8.0	.049
Spartan	6.0	7.0 - 8.0	.053
Ingrid	6.0	6.5 - 7.0	.044
Betzes	6.0	6.5 - 7.0	.046
Maris Mink	5.9	6.0 - 6.5	.038
Zephyr	5.9	6.5 - 7.0	.047
Hector	5.9	6.0 - 6.5	.041
Vireo	5.5	6.5 - 7.0	.036

Table 5. Mean seminal root numbers, seed sizes, and seed weights of 25 six-row barley varieties

Variety	Mean Seminal Root Number	Seed Size Range (sieve openings 64ths in)	Mean Seed Weight (g)
Briggs	5.9	6.5 - 7.0	.047
Beecher	5.8	7.0 - 8.0	.056
Atlas 46	5.7	6.5 - 7.0	.051
Glacier	5.6	6.5 - 7.0	.059
Primus II	5.6	6.5 - 7.0	.039
Larker	5.6	6.5 - 7.0	.038
Galt	5.5	5.5 - 6.0	.032
Dickson	5.4	6.0 - 6.5	.037
Trophy	5.4	6.0 - 6.5	.034
Harlan	5.4	6.5 - 7.0	.049
Gem	5.4	7.0 - 8.0	.061
Hiland	5.3	6.5 - 7.0	.042
Nordic	5.2	5.5 - 6.0	.029
Bonneville	5.2	6.5 - 7.0	.047
Steptoe	5.2	6.5 - 7.0	.043
Vantage	5.2	5.5 - 7.0	.030
Montcalm	5.1	5.5 - 6.0	.029
Steveland	5.1	6.0 - 6.5	.038
Ca Mariot 67	5.1	6.5 - 7.0	.049
Traill	5.0	5.5 - 6.0	.032
Titan	5.0	6.0 - 6.5	.036
Unitan	5.0	6.5 - 7.0	.048
Liberty	4.8	6.0 - 6.5	.035
Trebi	4.7	5.5 - 6.0	.037
Frontier	4.4	6.5 - 7.0	.031

Table 6. Mean barley seminal root numbers obtained in germination trays, slant-boxes, and pots.

	Mean Seminal Root Numbers		
Variety	Germination Trays	Slant-Boxes	Pots
Dekap	6.9	7.2	7.5
Briggs	5.9	5.8	5.8
Unitan	5.0	5.6	5.2
Zephyr	5.9	5.8	5.8
No. of Replications	100	6	18

Root volumes

The fresh root volume of 'Dekap' was significantly greater than 'Unitan' ($p = .007$), 'Briggs' and 'Zephyr' ($p = .05$) in the slant-box experiment (Table 7). The root volumes of 'Unitan', 'Briggs' and 'Zephyr' did not differ significantly.

The correlation between root number and volume was not significant within lines. This was probably because a discrete variable (root number) was compared to a continuous variable (root volume) and because the range in root numbers and root volumes within lines was small. Mean varietal root numbers, however, are correlated with mean root volumes ($r = .96$; 2 degrees of freedom). Using varieties with a wider range in mean seminal root numbers may have yielded more conclusive information. No inverse relationship between seminal root number and volume was apparent when varietal means were compared. Dekap had the greatest number of seminal roots and the largest root volume after 25 days.

Root dry weight

Varieties had similar rankings for root dry weights, seminal root numbers and root volumes. Differences among mean root dry weights, however, were not significant. Root dry weights were significantly correlated to root volumes ($r = .73$) when individual values were used (Table 7). For comparison of varietal means, $r = .86$ with two degrees of freedom.

Table 7. Mean root volumes and root dry weights of barley grown in slant-boxes.

Variety	Root Volumes (ml)	Root Dry Weight (g)
Dekap	3.48	.2212
Briggs	2.85	.2168
Unitan	2.50	.2039
Zephyr	2.82	.2164
(ANOV)	(p = .007)	(p = .848)

Root growth pattern

The seminal axes elongation rates (cm/root·hr) of all barley varieties decreased between the 5th and the 8th day (Fig. 7). This decrease may have been due to the exhaustion of nutrient reserves in the seed. Williams (1960) attributed a decrease in root growth rates of wheat between the 8th and 11th day from seeding to the depletion of seed nutrient reserves. Leaf area and net photosynthesis may not have been sufficient to sustain root growth rates attained prior to the 8th day. On the 7th day of our study, mean leaf blade lengths of 'Dekap', 'Briggs', 'Unitan', and 'Zephyr' were 9.6, 7.8, 8.2, and 8.1 cm, respectively. The second leaf tip was visible on the varieties 'Dekap' and 'Zephyr'.

Root elongation rates of all varieties increased from day 8 through day 17. Root elongation rates decreased for the two-row types ('Dekap' and 'Zephyr') and increased for the six-row types ('Briggs' and 'Unitan') between days 17 and 20. Decreased root growth rates coincided with a period of high afternoon temperatures and associated high evapo-transpiration. All plants showed moisture stress (i.e., wilting) during the day but regained turgidity at night. Temperatures moderated after the 20th day and the axial elongation rates of all four varieties increased dramatically during the final measurement period. Normal shoot growth resumed when daytime temperatures remained below 21°C, indicating use of moisture in the soil held at higher tensions.

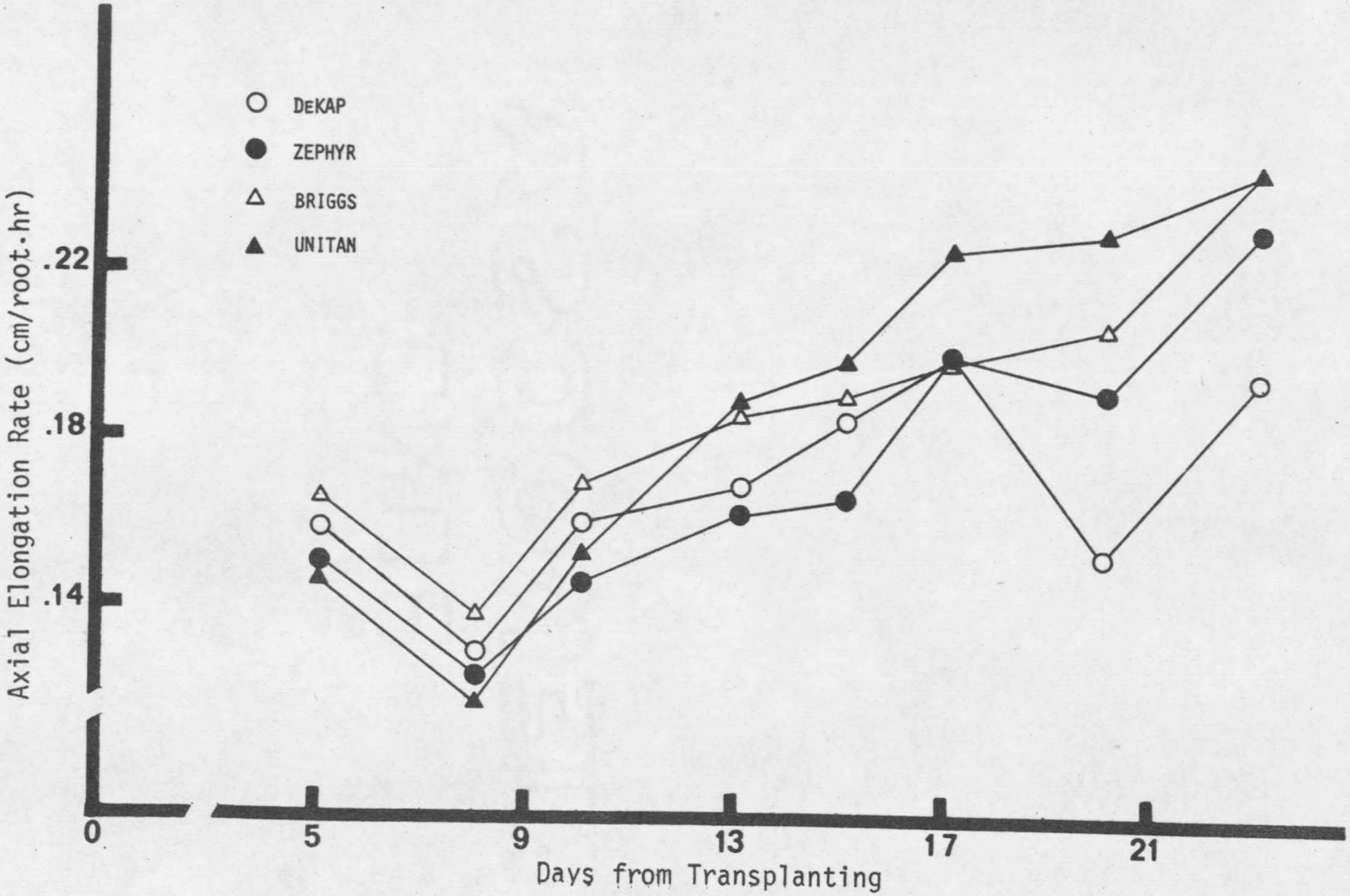

Figure 7. Elongation rates of barley seminal root axes: Dekap, Zephyr, Briggs and Unitan.

Varieties differed in response to moisture stress. Axial elongation rates were reduced the most for 'Dekap'. Since 'Dekap' had a greater root volume, it may have conserved less moisture at earlier growth stages. Additionally, the elongation of the branch roots was not reflected in the rate determination. 'Dekap' may have partitioned a greater proportion of photosynthate into lateral roots at the expense of axial elongation.

Significant varietal differences among mean axial elongation rates were calculated for six of the eight measurement periods (Fig. 7).

Axial elongation rates, averaged over the 23 day growth period in slant-boxes, indicate the penetrating capacity of the seminal root system (Table 8). The final depth of penetration can only be determined by observing the actual location of the axial root tips at plant maturity. The slant-boxes did not have sufficient depth to allow maximum penetration; the majority of the seminal root axes reached the bottom of the box within 25 days.

The average axial elongation rates of 'Dekap' (.166 cm/root·hr) and 'Zephyr' (.172 cm/root·hr) were not significantly different. 'Dekap' (7.2 axes/plant) may be capable of producing a greater root length at a given depth (assuming a similar degree of branching) than 'Zephyr' (5.8 axes/plant) because of the greater number of extended seminal axes.

Table 8. Mean elongation rates of seminal root axes of Dekap, Briggs, Unitan, and Zephyr (average rate during the 23 day growth period in slant-boxes)

Variety	Mean cm/root·hr
Dekap	.166
Briggs	.190
Unitan	.192
Zephyr	.172
(ANOV)	(p = .05)

The six-row types, 'Briggs' (.190 cm/root·hr) and 'Unitan' (.192 cm/root·hr), exhibited higher average axial elongation rates than 'Zephyr' and 'Dekap' ($p = .05$). Higher elongation rates suggest a corresponding increase in the depth of penetration of the seminal root system (at 23 days).

Daily observations of axial elongation rates facilitate the identification of important genotype-environment interactions (e.g., the apparent interaction between evaporative demand and the axial elongation rates of the varieties). Interactions occurring during later growth stages may preclude early determination of root growth patterns of barley.

Figure 7 shows that the root axes of all four varieties were elongating very rapidly near the end of the slant-box experiment. This suggests that the major limitation of the slant-boxes is the inability to monitor axial elongation rates beyond the six leaf stage of barley. Differences in seminal axial root elongation rates were greatest during the final two measurement periods.

Further investigation of the pattern of axial elongation during the reproductive phase of development is warranted. It would also be desirable to observe the rate of penetration of the seminal axes in a situation where the adventitious roots were allowed to develop normally.

Because of the limited surface moisture, adventitious roots did not elongate more than a few millimeters in the slant-boxes.

Significant varietal differences (p = .01) in the elongation rates of the seminal root axes were also measured in the pots (Table 9). 'Unitan' had the smallest seminal root number but the highest axial elongation rate. Thus, there may be some tendancy for root axial elongation rates to compensate for root numbers at early growth stages. Root number is more important than elongation rate in determining the total length of axes at 12 days. This is illustrated by comparing the cumulative root length indexes (mean seminal root number x cm/root·hr) of 'Dekap' (.557) and 'Unitan' (.438).

Table 9. Mean elongation rates of seminal axes and cumulative root length indexes of Dekap, Briggs, Unitan, and Zephyr (average rate during the 12 day growth period in pots)

Variety	Mean cm/root·hr	Cumulative Root Length Index*
Dekap	.074	.557
Briggs	.076	.440
Unitan	.085	.438
Zephyr	.077	.447
(ANOV)	(p = .01)	(p = .01)

*Cumulative root length index = mean seminal root number x (cm/root·hr).

SUMMARY AND CONCLUSIONS

Seminal and adventitious root morphological characteristics of barley maturity isotypes were compared. Early maturing isotypes of 'Betzes' and 'Hannchen' grown in slant-boxes produced smaller root volumes, root weights, and root:shoot ratios than 'normals' due to a reduction in the elongation rate and number of adventitious root axes. A similar decrease in root volumes, weights, and root:shoot ratios characterized 'early' isotypes grown in pots.

Twenty-five two-row and 25 six-row barley varieties were grown in germination boxes to determine differences in mean seminal root numbers. Significant varietal differences in mean seminal root number were observed. Two-row barley varieties generally developed a greater number of seminal roots than six-row varieties. Within line variability in seminal root number was reduced by testing the seed size range most characteristic of the variety. Four varieties representing a wide range in mean seminal root number were evaluated in slant-boxes to determine if increased branching compensates for low root number. No inverse relationship between mean seminal root number and root volume 25 days from transplanting was apparent when varieties were compared. Varieties differed in mean elongation rate of seminal axes in six of eight measurement periods. Seminal axial elongation rates of 'Dekap' and 'Zephyr' decreased during periods of high evapotranspiration. The elongation rates of 'Unitan' and 'Briggs' continued to increase during those periods. Because of these genotype-environment interactions neither the pattern of seminal axial elongation nor the final rooting depth is predictable at early growth stages.

Seminal axial elongation rates of varieties appeared to compensate for smaller root numbers when grown in pots. Seminal root numbers, however, were more important than elongation rates in determining the total length of seminal axes at 12 days.

The slant-boxes were better adapted to the study of seminal than adventitious roots. Adventitious root development was easily inhibited by maintaining a low soil water content adjacent to the plant crown. Seminal root elongation was observed daily until the 6 leaf stage of barley, when seminal root growth was restricted by the bottom of the slant-box.

Varietal differences in seminal root number should be demonstrated for other seed sources. The relationship between seed size and seminal root number for commercial varieties other than 'Betzes' and 'Compana' should also be determined.

Breeders may be able to increase the depth of penetration of the seminal root system of barley by combining high seminal root numbers with long root growth rate duration, vertical orientation, and decreased branching. All of these seminal root morphological characteristics must be incorporated to significantly increase utilization of residual soil moisture.

LITERATURE CITED

Barley, K. P. 1970. The configuration of the root system in relation to nutrient uptake. Adv. Agron. 22:159-201.

Briggs, D. E. 1978. Barley. Chapman and Hall, London.

Brouwer, R. 1965. Root growth of cereals and grasses. In The Growth of Cereals and Grasses. Milthorpe and Ivins, ed. Butterworths, London.

Brown, P. L., A. L. Black, C. M. Smith, J. W. Enz, and J. M. Caprio. 1981. Soil water guidelines and precipitation probabilities. Coop. Ext. Serv. Bull. 356, Montana State University, Bozeman.

Brown, P. L. 1980. Personal communication. Montana State University, Bozeman.

Caprio, J. M., R. D. Snyder, and G. K. Grunwald. 1980. Precipitation probabilities in Montana. Montana Agr. Exp. Sta. Bull. no. 712. Montana State University, Bozeman.

Ferguson, A. H. and G. O. Boatwright. 1968. Effects of environmental factors on the development of the crown node and adventitious roots of winter wheat. Agron. J. 60:258-260.

Fritsch, R. 1977. Uber morphologische Wurzelmerkmale bei Triticum L. und Aegilops L. Julturpflanze 25:45-70.

Gliemeroth, G. 1957. Investigations on the development and production of the radicle and crown roots of spring cereals. Z. Acker-u. Pflbau 103:1-21.

Goedewaggen, M. A. 1942. The root system of crops. Versl. landbouwk. Onderz. 173 pp.

Hackett, C. 1971. Relations between the dimensions of the barley root system:Effects of mutilating the root axes. Aust. J. Biol. Sci. 24:1057-1064.

Hockett, E. A. 1980. Personal communication. Montana State University, Bozeman.

Hurd, E. A. 1975. Phenotype and drought tolerance in wheat. In Plant modification for more efficient water use. Stone, J. ed. Elsevier Sci. Publ. Co., Amsterdam, 39-55.

Hurd, E. A. 1976. Plant breeding for drought resistance. In Water deficits and plant growth. Kozolowski, T. ed. 4:317-345.

Jordan, W. 1980. Sorghum root growth and morphology and field-rooting systems. In Plant roots. MacKey, J. ed. Iowa State Univ. Sym. on Plant Roots.

Krassovsky, I. 1926. Physiological activity of the seminal and nodal roots of crop plants. Soil Sci. 21:307-325.

MacKey, J. 1980. Crop improvement and root:water relations. In Plant roots. MacKey, J. ed. Iowa State Univ. Sym. on Plant Roots.

Merry, J. 1941. Studies on the embryo of Hordeum sativum. The development of the embryo. Bull. Torrey bot. Cl. 68:585-98.

Merry, J. 1942. Studies on the embryo of Hordeum sativum. 2. The growth of the embryo in culture. Bull. Torrey bot. Cl. 69:360-72.

Milthorpe, F. L. and J. Moorby. 1974. An introduction to crop physiology. Cambridge Univ. Press, Cambridge. 202 pp.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Pavlychenko, T. K. 1937. Quantitative study of the entire root system of weed and crop plants under field conditions. Ecology 18:62-79.

Pavlychenko, T. K. and J. B. Harrington. 1935. Root development of weeds and crops in competition under dry farming. Sci. Agric. 16:151-60.

Pope, M. N. 1945. Seminal root number in cultivated barley. J. Amer. Soc. Agron. 37:771-778.

Russell, R. S. 1977. Plant root systems: their function and interaction with the soil. McGraw-Hill, London.

Sallans, B. J. 1942. The importance of various roots to the what plant. Sci. Agric. 23:17-26.

Simmonds, P. M. and B. J. Sallans. 1933. Further studies on amputations of wheat roots in relation to diseases of the root system. Sci. Agric. 13:439-488.

Smail, V. W. 1980. Personal communication. Montana State University, Bozeman.

Taylor, J. W. and M. A. McCall. 1936. Influence of temperature and other factors on the morphology of the wheat seedling. J. Agric. Res. 52:557-568.

Troughton, A. 1962. The roots of temperate cereals. Mimeo. Publ. No. 2 Commonw. Bur. Past. Fld. Crops, Hurley, Berkshire.

Weaver, J. E. 1926. Root development of field crops. McGraw-Hill, New York.

Williams, R. F. 1960. The physiology of growth in the wheat plant. Aust. J. Biol. Sci. 13:401-28.

[redacted]

Roddy, Daniel M
Root morphological characteristics of barley ...

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