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
Montana State University
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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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A thesis submitted in partial fulfillment
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Agronomy

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June, 1981

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ABSTRACT

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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 numbers of 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^{o} 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 ($105^{o}C$), 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.

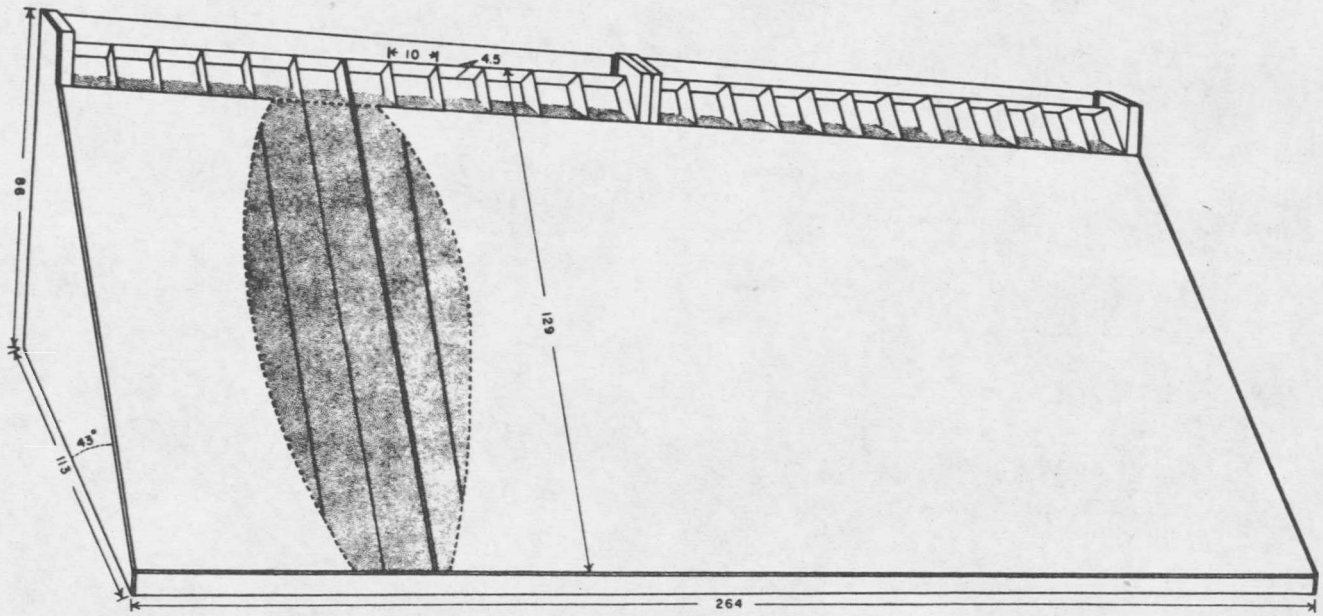

Figure 1. The slant-box used for measuring root elongation rates (dimensions are in cm).

H Hannchen

HE Hannchen-early

B Betzes

BE Betzes-early

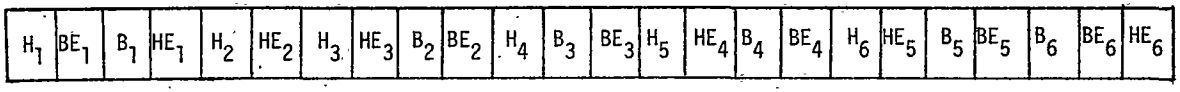

Figure 2. Arrangement of barley maturity isotypes in slant-boxes for Experiment I (subscripts represent replications).

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 $60^{o}C$ 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°C for 24 hr and ashed (593°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^{o}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		Mean Seminal Root No. (germ. boxes)
	Seed Size (sieve openings 64th in)	Seed Weight (g)	
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

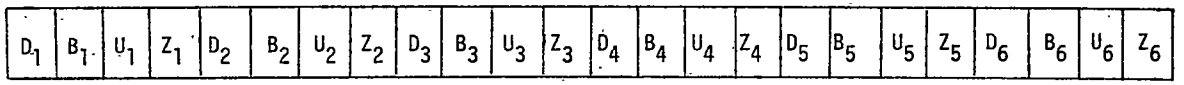

Figure 3. Arrangement of barley varieties in slant-boxes for Experiment V (subscripts represent replications).

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 (p = .002)	25.5	14.5 (p = .004)	11.5	6.5 (p = .001)	14.3	5.7 (p = .001)
Root dry weights (g)	1.37	.89 (p = .039)	2.18	1.29 (p = .001)	2.62	1.60 (p = .004)	2.85	1.37 (p = .001)
Shoot dry weights (g)	5.26	5.46 NS	4.76	5.99 (p = .010)	8.80	9.34 (p = .402)	9.14	8.09 (p = .010)
Root:shoot ratios	.26	.16 (p = .001)	.46	.22 (p = .003)	.30	.17 (p = .001)	.31	.17 (p = .001)
Number of root axes	52	36 (p = .018)	53	39 (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