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Experiments were conducted to compare differences in P uptake characteristics between two winter wheat cultivars Stephens and Yamhill (Triticum aestivum L) as related to root morphologies. Root length, root surface area and mean root radius were compared. Plant roots and shoots were separately analyzed for P content. The cultivars were grown in a growth chamber with a 16 hour light period at 22° C and an 8 hour darkness at 16° C for approximately three weeks. A growth medium deficient only in P and with a pH high enough (6.4 to 6.6) to prevent Al toxicity was prepared by mixing a silt loam and a sand. Soil P variables were established by adding phosphoric acid (H_3PO_4) to the soil at rates of 0, 25 and 100 ug P g^{-1} soil.

The root growth rates of the cultivars were exponential with time. Stephens had more rapid root growth rate, greater root length and root surface area than Yamhill. There were no significant cultivar differences in root radius. Stephens had higher root to shoot ratio than Yamhill at all phosphorus levels. Stephens grown in soil without applied phosphorus showed the highest root to shoot ratio.

Phosphorus concentrations in shoot and root increased with increasing phosphorus treatment levels. Stephens tended to have higher P concentration when P was applied. Yamhill recovered more phosphorus than Stephens when phosphorus was applied. Cultivar differences in P uptake became apparent as plants grew beyond 14 days. P uptake by shoots was exponential with time at all phosphorus levels. Without applied phosphorus, however, the P uptake rates of both cultivars showed little increase with time. Root P uptake of both cultivars was linear with time at applied P.

Yamhill's greater ability to recover phosphorus from soil was not explained by differences in root size or morphology because Stephens had more extensive root systems than Yamhill. Differences in mycorrhizal association, root hair length and/or density, or P uptake kinetics may contribute to Yamhill's greater ability to take up phosphorus from soil.

Phosphorus Uptake by Winter Wheat Cultivars as Related to Root Characteristics

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INTRODUCTION

The phosphorus content in soil is low compared to other nutrients such as nitrogen, potassium and calcium. Phosphorus moves to plant roots primarily by diffusion and the diffusion coefficient of phosphorus is one hundred to ten thousand times smaller than that of potassium or nitrogen. Consequently, the distance that phosphorus can move in the soil is limited (Barber, 1984). Low concentration and immobility of P in soil sometimes become limiting factors for plant growth.

Phosphorus uptake by plants is determined by root characteristics, plant requirement and soil P supply mechanism. Generally, plants with extensive root systems and high root density have a greater ability to take up nutrients from the soil solution (Mengel and Kirkby, 1981). Plants with rapid root growth rates have an advantage in taking up P from the soil solution because of increased root surface area which is exposed to P. In other words, varietal differences in P uptake may be related to differences in root growth and morphology. Knowledge of why some varieties are more efficient than others in taking up P might allow for the selection of varieties which are better able to tolerate low soil P.

Winter wheat cultivars grown in western Oregon have shown different responses to phosphorus applications. The differences

in P responses may be due to differences in root properties. However, root growth is influenced by other factors such as aluminum toxicity in acid soils or root disease such as take-all root rot of wheat caused by Gaeumannomyces graminis var. tritici. Thus, to unambiguously evaluate wheat cultivar response to P applications, plants must be grown in an environment without growth limiting factors other than phosphorus.

Yamhill and Stephens soft white winter wheats exhibit contrasting responses to applied P when grown in the field on P deficient soils. Yamhill showed a better response to applied P than did Stephens. In this study, these two cultivars were grown in the growth chamber and growth, phosphorus uptake and root characteristics were compared at three levels of applied P. The objectives of this research were as follows:

1. To compare Yamhill and Stephens response to applied P when other limiting factors such as soil acidity, aluminum toxicity and root disease were absent.
2. To compare Yamhill and Stephens with respect to root morphology, root growth rate and P uptake.

LITERATURE REVIEW

Wheat variety Response to Phosphorus

Winter wheat (Triticum aestium L) is one of the major crops grown in western Oregon. There is some evidence that wheat varieties differ in their P responses. Bolger (1980) examined the root length and grain yield of two winter wheats (Yamhill and McDermid) which were grown in acid soil at different levels of phosphorus and lime application. The yield of Yamhill was 94 % higher than that of McDermid when grown without phosphorus or lime. Furthermore, Yamhill had a longer root length in the upper 20 cm of the soil. The soil had a pH of 5.2 which is borderline for Al-toxicity. The effect of Al-toxicity on root growth was not clear.

Sullivan (1981) took a more extensive look at the differences in P responses. He grew ten different winter wheat cultivars at the site which Bolger used. The wheat cultivars Yamhill and Stephens represented extreme differences in response to phosphorus application. The grain yield of Stephens was only 51% of that of Yamhill when they were grown without phosphorus and lime. Yamhill showed a greater response to a phosphorus application while Stephens responded more to a lime application. Without lime application, Hyslop and Hyslop Al-tolerant cultivars did not show any difference in grain yield, suggesting that Al-toxicity was not a major factor limiting yield. Sullivan observed similar responses at a site with low phosphorus and a higher pH soil.

Taylor et al. (1983) reported a similar trend when they investigated the effects of fertilizer application on take-all root rot of wheat caused by Gaeumannomyces graminis var tritici. They found that the numbered line Ymh/Hys 2M6 (subsequently released as Hill 81) was superior to Stephens on phosphorus deficient soil.

The Australian wheat varities Bencubbin and Charter have also shown different P uptake efficiencies (Lipsett, 1964). The total phosphorus uptake in straw and grain were not different, but the grain yield of Bencubbin was higher. Bencubbin had a lower P concentration and produced more grain per unit of phosphorus uptake.

Root Growth and Phosphorus Uptake

Root studies have attracted little attention in comparison with shoot studies because of difficulties in sampling roots (Gregory et al., 1978). Information about the root growth pattern of wheat in soils is limited.

Gregory et al. (1978) conducted field investigations on the growth of winter wheat root systems throughout the growing season. Most of the root growth was confined to the 0 to 150 cm depth of soil. Rate of root growth was rapid in the 0 to 10 cm depth of the soil. The root growth rate and the shoot growth stage were closely related. The ratio of root weight and total plant weight was influenced by the distribution of photosynthate.

As mentioned earlier, Yamhill had a longer root length than

McDermid. Since root growth is related to the growth stage of plant development, the root sampling time is important in comparing root growth rates. Bolger (1980) found that the most significant root length differences between Yamhill and McDermid on the acid, low phosphorus soil occurred at the late tillering stage of plant development.

Two tall and three semi-dwarf winter wheat cultivars were compared by Cholick et al. (1977). They applied radioactive phosphorus (^{32}P) to the foliage and observed soil moisture content at 30 cm intervals down to a 300 cm depth of soil. Rooting patterns of the varieties of wheat were measured and it was found that there was no significant difference between the tall and semi-dwarf wheats. They tended to have the same rooting patterns except that the semi-dwarf wheat Nugaines had the greatest amount of roots at the 180 cm depth.

Palmer and Jessop (1977) investigated the difference of phosphorus content and root growth between a semi-dwarf wheat (Israel M68) and a standard height cultivar (Olympic) grown in soil at different superphosphate applications (equivalent to 0, 4, 8, 16, 32 and 64 kg P ha^{-1}). Olympic had a higher dry weight of root, higher root to shoot ratio and lower P concentration in root and shoot. Israel M68 was more efficient in taking up phosphorus per gram of root. In a second experiment, root growth patterns were compared by using solution cultures. Israel M68 had a higher number of roots, lateral surface area, and lateral root volume per fresh weight root. The root system of Israel M68 was more extensive than that of Olympic.

Ningping and Barber (1985) and Anghinoni et al. (1981) examined root growth rate, root length, P uptake, and P influx kinetics of wheat grown in solution culture. Root length increased exponentially for 35 days after transfer of pre-germinated seeds to the solution culture. The P uptake rate decreased with plant age. The maximal net influx of P (Imax, nmol m^{-2} s^{-1}) was relatively constant until 38 days while the Michaelis-Menten constant (Km, solution concentration where influx equals 1/2 Imax) showed a slight decrease with plant age.

Effect of Root Hairs on Phosphorus Uptake

Root hairs are considered extensions of the epidermal cells. They grow into the pore space of soil and grow vigorously in humid air (Barber, 1984). According to Dittmer (1937), root hairs increase the surface area of a root system between 5 and 18 times. Therefore, many investigators consider that root hairs increase phosphorus uptake efficiency of a plant (Mengel and Kirkby, 1981).

Itoh and Barber (1983) developed a mathematical model involving P uptake kinetics, root morphology and soil P supply characteristics to predict P uptake by plants. When the model was tested on six plant species without considering root hairs it was found that the predicted P uptake by plants with long root hairs (Russian thistle and tomato) was less than half of the observed uptake. However, when root hairs were considered, the predicted uptake agreed closely with the observed uptake. The relationship of the predicted and observed uptake in wheat was not influenced

by ignoring root hairs. This suggests that the root hairs of wheat have a limited role in the uptake of phosphorus.

Barley and Rovira (1970) reported that root hairs increased P uptake by pea (Pisum sativum L.). By changing the voids ratio of clays, they controlled the development of root hairs. When the void ratio was 1.0, root hairs were absent. On the other hand, when the void ratio was 1.2 there was root hair growth. The plant with root hairs had 80% higher P uptake from the soil than the plant without root hairs. Barley and Rovira also found that root hairs did not make any difference for P uptake in solution culture experiments. The results of their experiment suggests that root hairs provide more root surface area which enhances P uptake from the soil.

Bole (1973) saw, however, no correlation between root hairs and P uptake when he grew wheat cultivars which were known to have different root hair densities. Densities of root hairs varied from 30 to 80 per mm of root, depending on the level of P in soil. As the root hair density increased, the P uptake rate increased until it reached a maximum. As root hair density increased beyond the optimum density P uptake rate tended to decrease. The relationship between the P uptake and the root density was not very consistent, however.

Effect of Al-toxicity on Roots

Aluminum toxicity and phosphorus deficiency appear in similar ways in plant tops. Plants injured by aluminum are stubby, small

and unusually dark green. Roots also become stubby and turn brown. The whole root system is affected and the root growth is inhibited by aluminum. In general, Al-toxicity is likely to occur in soils below pH 5.5 because of increased solubility of aluminum in the soil (Foy, 1974). Excess aluminum reduces phosphorus availability both in soils and in roots. In soils, the excess aluminum combines with phosphorus to form insoluble compounds, thus reducing the solubility of phosphorus. Aluminum accumulates in roots and inhibits the root growth. The limited root growth results in a decrease in P uptake (Mengel and Kirkby, 1981).

Neenan (1960) reported that wheat varieties responded differently to Al-toxicity. Aluminum content in plants was negatively correlated with the amount of lime applied .

Moore (1974) investigated the form of Al species which actually caused Al-toxicity to plant roots. He first grew wheat in an Al-free solution culture, then transferred the plants into solution cultures with pH from 4.0 to 4.7 containing different levels of Al but no P . The plants were again transferred into the Al-free solution culture. The root growth during the recovery period from Al-toxicity was used as the indication of Al-toxicity to plants. He also calculated the concentration of hydrolysis products of Al at different pH levels. He concluded that the Al specie toxic to wheat roots was $AlOH^{2+}$ rather than Al^{3+}.

The experiments with barley by Maclean et al. (1966) have shown the effect of Al on P uptake. As the concentration of aluminum increased in the plant, the yield of the tops and the root decreased. However, P concentration in the root increased

while the P concentration of the tops decreased. Foy et al. (1967) observed a similar result when two wheat varieties were grown together in the same container. The P content in the roots tended to increase as Al content increased. The rate of P accumulation in the roots was higher for the Al-sensitive wheat.

MATERIALS AND METHODS

Wheat Cultivars

Yamhill and Stephens soft white winter wheat (Triticum aestivum L.) demonstrate different tolerance to low soil P in the field. Therefore, they were chosen to evaluate their responses to different levels of P application. Stephens is a semi-dwarf cultivar released by Oregon State University in 1977. Stephens is a high-yielding wheat, and is grown on 70% of the wheat acreage in Oregon. Yamhill is a standard height, beardless soft wheat developed by Oregon State University in 1969 (Oregon State University Extension Service, 1986). Cereal Investigation/Plant Introduction numbers of both cultivars are listed in Special Report 749 (Agricultural Experiment Station, Oregon State University. 1985).

Soil Preparation

A growth medium (potting soil) was prepared by mixing a silt loam and a sand in the ratio of 2:1 using a large mixer. After thorough mixing, the potting mixture was air-dried and sieved through 2 mm wire mesh to discard the coarse fraction. The silt loam soil became cloddy when dry. Consequently, the potting mixture was pulverized in a soil grinder and mixed a second time.

The potting mixture (hereafter called soil) was divided into three equal portions for differential treatment with P.

Phosphorus was added as phosphoric acid (H_3PO_4) at rates of 0, 25 and 100 ug P g^{-1} soil, designated P1, P2 and P3, respectively. Phosphoric acid was diluted with deionized water and sprayed on the soil with an atomizer. The soil was air-dried again to equilibrate phosphorus with the soil. Each lot of air-dried P-treated soil was again thoroughly mixed in a soil blender to insure uniform phosphorus distribution. Chemical properties of soil (Table 1) were determined by Oregon State University Soil Testing Laboratory, following procedures described by Topper and Gardner (unpublished). Since the same soil was divided into three equal portions, cation exchange capacity and organic matter content were determined only on the soil which did not receive added P. Physical properties of the soil are given in Table 2.

According to the results of the soil test, the soil were relatively uniform with respect to all chemical properties except extractable P. Soil pH ranged from 6.4 to 6.6, indicating that Al-toxicity was not a limiting factor. Phosphorus was the only growth limiting factor.

Experimental Design

A randomized block, split-plot design was used with plant age as main plots and the factorial combination of two cultivars and three P treatments as sub plots. The number of replications and harvest dates are given in Table 3. In experiment 2, two different statistical analyses were made. One analysis was a randomized block, split-plot with plant age as main plots with two

Table 1. Chemical properties of the soil.

Treat.	P rate	pH	P*	K**	Ca	Mg	Na	CEC	O.M.
	ug g^{-1}		--ug g^{-1}--		-----cmol(p+) Kg^{-1}-----				g Kg^{-1}
P1	0	6.6	8	98	9.5	5.1	0.34	12.0	0.83
P2	25	6.4	21	98	9.3	5.1	0.35	——	——
P3	100	6.4	40	94	9.3	5.0	0.12	——	——

* Bray P1 acid-fluoride extractable P

** Ammonium acetate extractable K

Table 2. Physical properties of the soil.

Particle size			Soil water content		Bulk density
			kPa		
Sand	Silt	Clay	-10	-30	
--------- % --------			--------- % ----------		-- Mg m^{-3} --
61.3	27.1	11.6	23.0	16.0	1.00

Table 3. Design of experiments and harvest dates.

Experiment	Experimental design	Number of replications (pairs)	Harvest date (days from emergence)
1	Pared t-test	14	6, 12, 17.
2-a	Randomized Block Split-plot	2	6, 14, 22.
2-b	Randomized Complete Block	6	22
3	Randomized Block Split-plot	3	5, 11, 16, 21.

replications. In order to have the same number of replications, averages from replication 1 through 3 and 4 through 6 were taken at the last harvest. Another analysis was made for 22 day-old plants as a randomized block design with 6 replications.

Experiment 1 was designed as randomized block split-plot experiment. However, germination of seeds was low due to excess water and fungus infection. Therefore, root characteristics of pairs of Yamhill and Stephens plants which had received the same P rate and were the same age as well as similar height were compared using a paired t-test.

Potting and planting

Soil (500g) was added to a pot 6.2 cm in diameter and 25 cm deep through a powder funnel to obtain a uniform bulk density of 1.0 Mg m^{-3}. About two to three grams of polyester fibers were placed in the bottom of pots before addition of soil. Before seeding, soil in each pot was brought to field capacity by capillary action by placing the bottom of each pot in contact with deioninized water for several hours.

Seeds of similar size were chosen in order to reduce variability in germination and rate of development. The seeds were treated with fungicide (Thiram 75SD) before seeding in experiments 2 and 3. Seeds were directly planted at a depth of 1.5 cm into the moistened soil. In experiment 1, one seed per pot was sown. In experiment 2, each pot was sown with four wheat seeds. In experiment 3, two seeds were sown per pot but the stand

was thinned to one plant per pot shortly after germination. This was done because the germination rate of seeds was not 100%.

In experiment 1, the soil surface was covered with Whatman no. 50 filter papers to prevent disturbance of surface soil while applying water. Applying water during seed germination caused low germination rate. Therefore, no extra water was added in experiments 2 and 3 and the plants were kept in the dark until germination. The growth chamber was turned on as soon as the plants emerged. To make sure that other elements were not limiting during the experiment, 10 ml of mixed salt solution (0.2 mol/l KNO_3, 0.1 mol/l $(NH_4)_2SO_4$, 0.1 mol/l NH_4NO_3) was added to each pot as soon as the wheat plants germinated. 10 ml of nutrient solution per pot included 84 mg N, 78 mg K and 32 mg S. Small rocks were placed on the surface of the soil to reduce evaporation when the height of plants reached 4 to 5 centimeters. In a preliminary experiment, nutrient concentrations in 3-week-old plants were measured and it was found that there were no limiting factors other than phosphorus (Appendix Table 1).

Growth Chamber Conditions

The wheat plants were grown in the growth chamber with a 16 hour light period and an 8 hour darkness. The temperatures were set at 22° C during the light period and at 16° C during the dark period. The photosynthetic photon flux density at the top of the pots was 310 umol photon $m^{-2}s^{-1}$. Soil water content was checked daily. When irrigation was needed, pots were taken out of the

growth chamber and soil was rewetted by capillary action.

Plant Sampling and Analysis

In experiments 1 and 3, root morphology and root growth were compared. At harvest, plants were separated into shoots and roots. The roots were placed on a wire mesh of 2 mm openings. Soil was washed from the roots with running water using a hose with an adjustable nozzle. The roots were washed again in a 400 ml beaker to remove small soil particles which adhered to the roots. The roots were preserved in 400 ml beakers with water. The roots were wrapped in dry paper towels for two minutes and the root fresh weight was measured. The root length was measured using the line intercept procedures described by Tennant (1975). Root radius and root surface area were calculated from the root length and the root fresh weight as follows.

$$r = (Fw/3.14L)^{1/2}$$

where r is root radius in cm, Fw is root fresh weight in g and L is root length in cm.

$$RS = 2 \times 3.14rL$$

where RS is root surface area in cm^2, r is root radius in cm, and L is root length in cm (Ningping and Barber, 1985). It is assumed that root specific gravity is 1.0 and the root is cylindrical in shape (Classen and Barber, 1976). Shoots and roots were oven dried at 60^{o} C and dry matter yields were measured.

In experiment 2, phosphorus uptake by plants was determined. Shoots and roots were sampled as described in the previous

paragraph, oven dried at 60° C and digested in nitric acid (HNO_3) and perchloric acid ($HClO_4$). Since the dry weights of shoot and root were small, plant tissues were not ground. Whole samples per pot were digested in a flask. Phosphorus concentration in plants was measured colormetrically (Molybdate blue method) using a RFA-300 Rapid Flow Auto-Analyzer.

Statistical Analysis

Statistical Interactive Programming System (SIPS) at OSU computer center was used for statistical analysis of data. F tests were used to compare mean differences among main effects and treatment interactions. In experiment 1, a pair of Yamhill and Stephens plants of similar height from the same experimental treatment (Age and P treatment) were compared using a paired t-test. All results are expressed as mean per plant. Regression analyses were made by using software programs "Lotus 1-2-3".

RESULTS

The data and results of statistical analysis of experiment 1 are presented in Table 4. Summaries of analyses of variance of experiments 2 and 3 are given in Tables 5, 6 and 7.

Shoot Growth Characteristics

Shoot growth rates of the cultivars were exponential with time at all phosphorus levels (Fig. 1 and Fig. 2). The cultivars did not show any marked responses to P nor varietal differences until after day 14 in experiment 2. Yield responses to P became apparent at 14 days after emergence, with the greatest response occurring when P was increased from the P1 to the P2 level. When no phosphorus was applied, the dry weights of two cultivars were not significantly different up to the last harvest. Yamhill responded more to increasing P from the P2 to the P3 level than did Stephens. In experiment 2, there was a tendency for Yamhill to have higher shoot dry weights at 22 days than Stephens when P was applied. When several plants per pots were grown, size of shoots were reduced in comparison with when one plant per pot was grown.

Root Growth Characteristics

A. Root dry weight

The three-way treatment interaction for dry weight of root was significant at the 1% level in experiment 2 (Table 5). Plant age by cultivar interaction was significant at the 1% level in experiment 3 (Table 7). No significant varietal differences were found until 11 to 14 days after emergence (Table 8). As the plants grew more than two weeks, there was a strong tendency for Yamhill to have higher root dry weight than Stephens in experiment 2. At 22 days after emergence, Stephens showed little response to P when P was increased from 25 to 100 ug P g^{-1} soil. In contrast Stephens had significantly higher root dry weight than Yamhill at 21 days in experiment 3 (Table 9). Average root dry weight of Stephens was 168% of Yamhill at 21 days.

B. Root length and mean root radius.

Although excess water supply and the infection of fungi caused variability in plant growth in experiment 1, it was found that Stephens had significantly longer root length than Yamhill. Average root length of Stephens was 1.38 times as long as that of Yamhill (Table 4).

Root characteristics of Stephens and Yamhill in experiment 3 are given in Table 9. Two two-way treatment interactions, plant age by cultivar and plant age by P treatment, were significant at the 5% level for root length. These interactions are illustrated in Fig. 3. Cultivar differences became apparent as the wheat plants grew. At 21 days after emergence, the root lengths of Stephens were 5.39, 12.62 and 8.00 m greater than for Yamhill in

the P1, P2 and P3 treatment, respectively. Both cultivars showed a reduction in root growth from the P2 to the P3 treatment even though shoot dry weights did not change very much. Rapid root growth rate of Stephens was reflected in the higher root:shoot ratio of Stephens (Table 9 and Table 13).

No significant varietal differences in mean root radius were found in experiments 1 and 3 (Table 4 and 7). Root radius decreased with time from 0.27 to 0.16 mm (Table 10). Differences within cultivars and P treatment disappeared at the last harvest.

C. Root surface area.

Stephens had significantly greater root surface area than Yamhill in experiment 1 (Table 4). In experiment 3, plant age by cultivar interaction significantly ($P = 0.05$) influenced root surface area (Table 7). The exponential increase in root surface area with time is illustrated in Fig. 4. Stephens tended to have more root surface area than Yamhill as the cultivars grew. The cultivars showed a reduction in root surface area as P was increased from the P2 to the P3 level. At 21 days from emergence, Stephens grown on the P2 treatment had the highest root surface area with 390 cm^2 per plant.

Phosphorus uptake characteristics

A. P uptake by shoot.

The three-way treatment interaction was significant at the 1% level for shoot P uptake and concentration (Table 5). Effects of plant age, P treatment and cultivar on shoot P uptake are illustrated in Fig. 5 and P concentrations are given in Table 11. When P was not applied, P uptake by Stephens was almost linear over the time of the experiment. Yamhill showed slight exponential P uptake after 14 days without P (P1). When P was applied, the two cultivars demonstrated exponential P uptake with time. At six days after emergence, there were no significant responses to P nor were there significant differences between cultivars. Cultivar and P treatment differences became clear from day 14. At 14 and 22 days, P uptake from the P1 level to the P2 level increased dramatically, and Yamhill took up significantly more phosphorus than did Stephens at the highest P level (P3).

P concentration in shoots (Table 11) varied from 0.13 to 0.59% for Yamhill and from 0.11 to 0.62% for Stephens. P treatment increased the P concentration in shoots of both cultivars. There was a tendency for Stephens to have higher P concentration at the highest P level than Yamhill.

B. P uptake by root.

Three two-way interactions, plant age by cultivar and P treatment by cultivar at the 5% level and plant age by P treatment at the 1% level, were significant for P uptake (Table 5 and Fig. 6). Plant age by P treatment interaction was significant at the 5% level for P concentration (Table 5). Roots showed a little

different P uptake patterns than did shoots. As illustrated in Fig. 6, P uptake rate was almost linear with time when no P was applied (P1) and P uptake was linear increase with time at the highest level of applied P (P3) while P uptake by roots was exponential with time at the intermediate (P2) level. When P was applied, the cultivars showed different P uptake rate as the wheats grew. At 22 days from emergence, average root P uptake was 0.35 mg for Yamhill and 0.30 mg for Stephens. P treatment increased P concentration in roots (Table 12) as well as shoots (Table 11). Average P root concentration for Stephens at 22 days was significantly higher than that for Yamhill. P concentration was 0.17% for Yamhill and 0.19% for Stephens.

Root:shoot ratio

Root:shoot ratio is an indication of the distribution of photosynthates in plants and changes with the physiological age of plant (Mengel and Kirkby, 1981). Root:shoot ratio based on dry weight has little meaning in terms of nutrient uptake ability by plants because roots grow differently in different types and volumes of growth media (Barber, 1984). In this experiment, however, the wheat plants grew in a uniform growth medium under controlled climate. Therefore, the comparison of root:shoot ratio between cultivars is legitimate. Root:shoot ratios of the two cultivars were significantly different at the 5% level in experiment 2. The average root:shoot ratio was 0.62 for Stephens and 0.52 for Yamhill, suggesting that Stephens diverted more

photosynthate to root growth than did Yamhill. In experiment 3, effects of P treatment and cultivar on root:shoot ratio were more apparent (Table 13). When no phosphorus was applied, both cultivars showed higher root:shoot ratio than when phosphorus was applied. The root:shoot ratios of 5 day-old Stephens were larger than 1.0 at all P levels, suggesting the size of roots exceeded that of shoots at all P levels. The root:shoot ratios of Yamhill on the P2 and the P3 levels became comparable from day 11 while Stephens had similar root:shoot ratio on the P2 and the P3 levels from day 16. At 21 days from emergence, root:shoot ratios of Stephens were about 0.1 unit higher than those of Yamhill at the same P levels.

Table 4. Comparison of root characteristics and results of paired t-test (Experiment 1).

Cultivar	Plant height	Root length	Root fresh weight	Root mean radius	Root surface area
	cm	cm	mg	mm	cm^2
Yamhill	20.76	205.0	246.6	0.21	25.5
Stephens	22.26	282.2	358.2	0.20	35.4
Difference	NS	*	NS	NS	*

* significant at the 5% level

Table 5. Statistics summarizing plant dry weight, P concentration and P uptake responses to plant age, cultivar and P treatment variables (Experiment 2).

Source	df	Dry weight		P concentration		P uptake		Root: shoot ratio
		shoot	root	shoot	root	shoot	root	
Age (A)	2	**	**	**	NS	**	**	**
error a	2	9.04_{-4} x10	2.13_{-4} x10	1.90_{-5} x10	1.10_{-2} x10	1.07_{-2} x10	9.03_{-4} x10	1.24_{-2} x10
Cult.(C)	1	**	*	NS	NS	*	NS	*
Phos.(P)	2	**	**	**	**	**	**	NS
AxC	2	**	**	**	NS	NS	*	NS
AxP	4	**	**	*	*	**	**	NS
CxP	2	*	*	**	NS	NS	*	NS
AxCxP	4	*	**	**	NS	*	NS	NS
error b	15	2.22_{-4} x10	1.20_{-4} x10	6.85_{-4} x10	3.25_{-3} x10	2.91_{-3} x10	9.27_{-4} x10	1.76_{-2} x10

* significant at the 5% level

** significant at the 1% level

Table 6. Statistics summarizing plant dry weight, P concentration and P uptake responses of 22-day-old wheat (Experiment 2).

Source	df	Dry weight		P concentration		P uptake		Root: shoot ratio
		shoot	root	shoot	root	shoot	root	
Cult.(C)	1	**	**	*	*	*	**	NS
Phos.(P)	2	**	**	**	**	**	**	*
CxP	2	*	**	**	NS	NS	NS	NS
error	25	2.26_{-3} x10	6.91_{-4} x10	5.21_{-4} x10	7.00_{-4} x10	9.42_{-3} x10	2.47_{-3} x10	2.79_{-3} x10

* significant at the 5% level

** significant at the 1% level

Table 7. Statistics summarizing plant dry weight and root morphology responses to plant age, cultivar and P treatment variables (Experiment 3).

Source	df	Root morphology			Dry weight		Root: shoot ratio
		length	mean radius	surface area	shoot	root	
Age (A)	3	**	**	**	**	**	**
error a	6	$0.34_{x10^{6}}$	$0.31_{x10^{-3}}$	$0.35_{x10^{4}}$	$0.13_{x10^{-2}}$	$0.10_{x10^{-2}}$	0.04
Cult. (C)	1	*	NS	*	NS	**	**
Phos. (P)	2	*	NS	*	**	NS	NS
AxC	3	*	NS	*	NS	**	**
AxP	6	*	*	NS	**	NS	**
CxP	2	NS	NS	NS	NS	NS	NS
AxCxP	6	NS	NS	NS	NS	NS	*
error b	40	$0.21_{x10^{6}}$	$0.58_{x10^{-3}}$	$0.22_{x10^{4}}$	$0.33_{x10^{-2}}$	$0.85_{x10^{-3}}$	0.07

* significant at the 5% level

** significant at the 1% level

Table 8. Dry weight of roots as influenced by plant age, cultivar and P treatment (Experiment 2).

Cultivar	P treatment	Days from emergence		
		6	14	22
		mg plant^{-1}		
Yamhill	P1	24.3	66.2	107.8
	P2	25.7	59.9	214.5
	P3	29.0	69.8	260.1
Stephens	P1	33.3	59.6	110.1
	P2	35.5	89.3	170.1
	P3	28.7	64.2	183.1

Standard error of means = 7.8 (15 error df)

Table 9. Root characteristics of Stephens and Yamhill (Experiment 3).

Cultivar	Days from emergence			
	5	11	16	21
	Root length			
	m			
Yamhill	1.24	4.72	10.30	21.77
Stephens	1.44	5.35	10.29	30.45
	Root dry weight			
	mg			
Yamhill	15.7	31.2	71.3	116.6
Stephens	30.6	34.6	73.4	195.6
	Root surface area			
	cm^2			
Yamhill	18.10	50.79	123.16	216.34
Stephens	23.13	56.86	113.96	313.08
	Root:shoot ratio			
	d.w./d.w			
Yamhill	0.80	0.32	0.23	0.20
Stephens	1.77	0.37	0.31	0.30

Values obtained from averages of P1, P2 and P3 treatment.
Standard error of means for root length = 1.54 (40 error df)
Standard error of means for root dry weight = 9.7 (40 error df)
Standard error of means for root surface area = 15.6 (40 error df)
Standard error of means for root:shoot ratio = 0.0894 (40 error df)

Table 10. Effects of P treatment and plant age on root growth (Experiment 3).

P Treatment	Days from emergence			
	5	11	16	21
	Root length			
	m			
P1	1.48	4.85	7.91	19.18
P2	1.37	5.69	11.30	31.08
P3	1.17	4.58	11.67	28.07
	Root fresh weight			
	g			
P1	0.2532	0.4674	0.7319	1.5832
P2	0.2491	0.4759	1.1644	2.5882
P3	0.2682	0.4689	1.1841	2.3474
	Root radius			
	mm			
P1	0.23	0.18	0.17	0.16
P2	0.24	0.16	0.20	0.16
P3	0.27	0.18	0.18	0.16
	Root:shoot ratio			
	d.w./d.w.			
P1	1.08	0.42	0.35	0.32
P2	1.02	0.31	0.25	0.22
P3	1.76	0.27	0.22	0.22

Values include Stephens and Yamhill.
Standard error of means for root length = 1.88 (40 error df)
Standard error of means for root fresh weight = 0.156 (40 error df)
Standard error of means for root radius = 0.01 (40 error df)
Standard error of root:shoot ratio = 0.110 (40 error df)

Table 11. Phosphorus concentration in shoot (Experiment 2).

Cultivars	P Treat.	Days from emergence		
		6	14	22
		%		
Yamhill	P1	0.28	0.17	0.13
	P2	0.53	0.33	0.17
	P3	0.59	0.36	0.24
Stephens	P1	0.33	0.18	0.11
	P2	0.38	0.30	0.19
	P3	0.62	0.47	0.29

Standard error of means = 0.018 (15 error df)

Table 12. Effects of P treatment and plant age on root P concentrations (Experiment 2).

P treatment	Days from emergence		
	6	14	22
	%		
P1	0.34	0.20	0.13
P2	0.36	0.27	0.18
P3	0.37	0.43	0.24

Values include Yamhill and Stephens
Standard error of means = 0.029 (15 error df)

Table 13. Root:shoot ratio in experiment 3.

Cultivars	P Treat.	Days from emergence			
		5	11	16	21
Yamhill	P1	0.79	0.43	0.30	0.27
	P2	0.73	0.26	0.21	0.16
	P3	0.89	0.27	0.18	0.17
Stephens	P1	1.35	0.42	0.41	0.37
	P2	1.31	0.42	0.28	0.27
	P3	2.63	0.28	0.26	0.26

Standard error of means = 0.15 (40 error df)

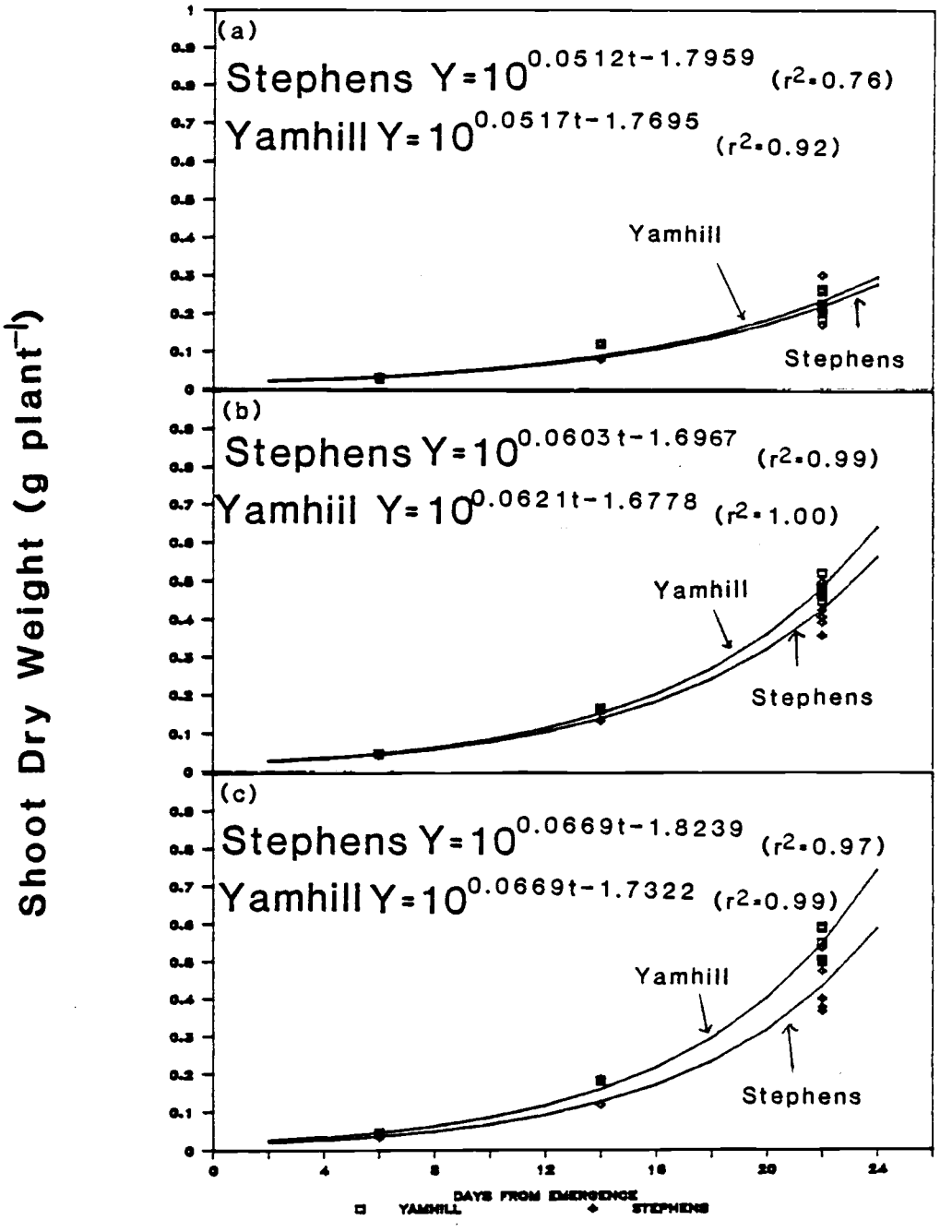

Figure 1. Shoot growth rate as function of time with several plants per pot (Experiment 2, data in Appendix Table 2). (a) 0 ug P g^{-1} soil, (b) 25 ug P g^{-1} soil and (c) 100 ug P g^{-1} soil.

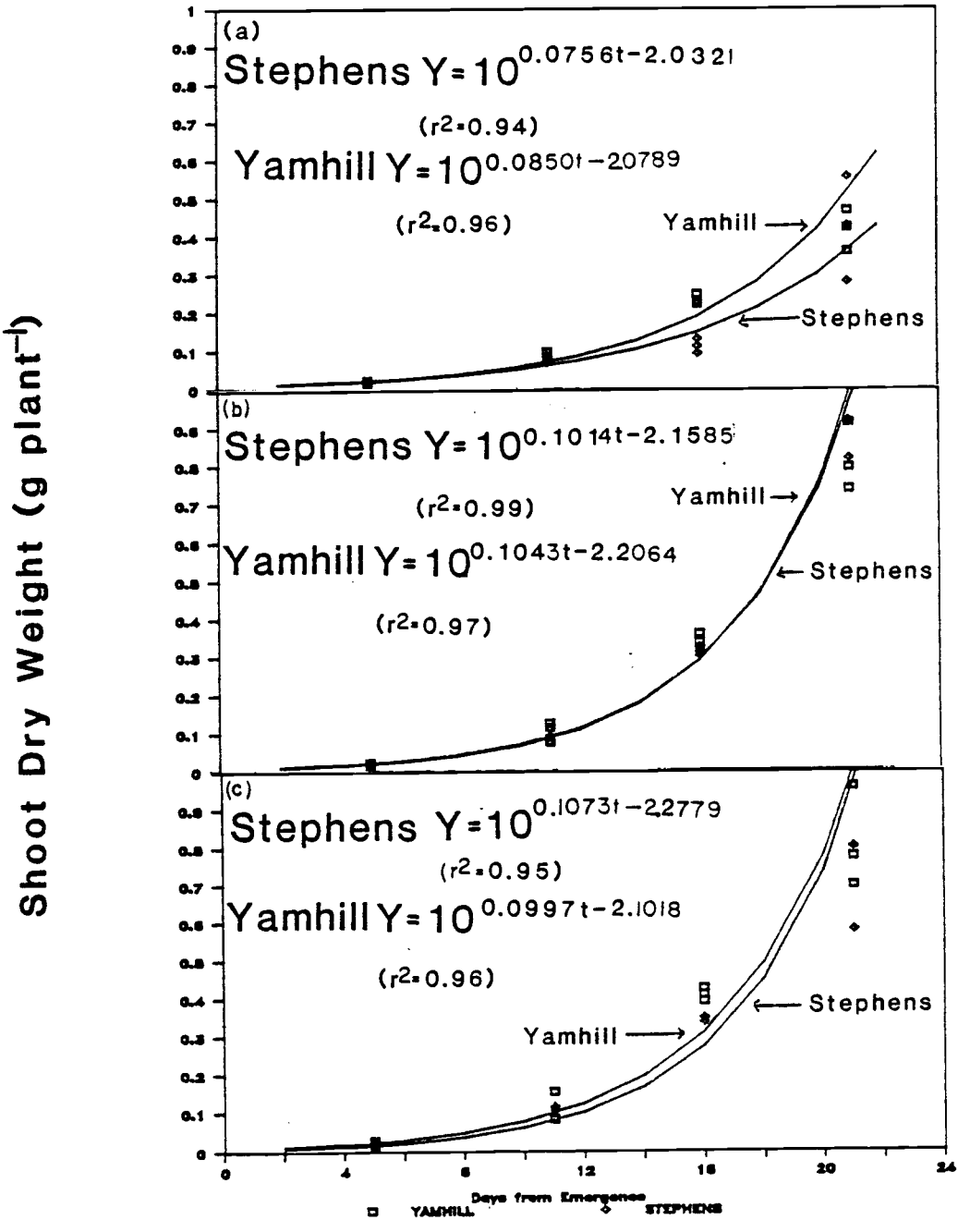

Figure 2. Shoot growth rate as function of time with one plant per pot (Experiment 3, data in Appendix Table 3). (a) 0 ug P g^{-1} soil, (b) 25 ug P g^{-1} soil and (c) 100 ug P g^{-1} soil.

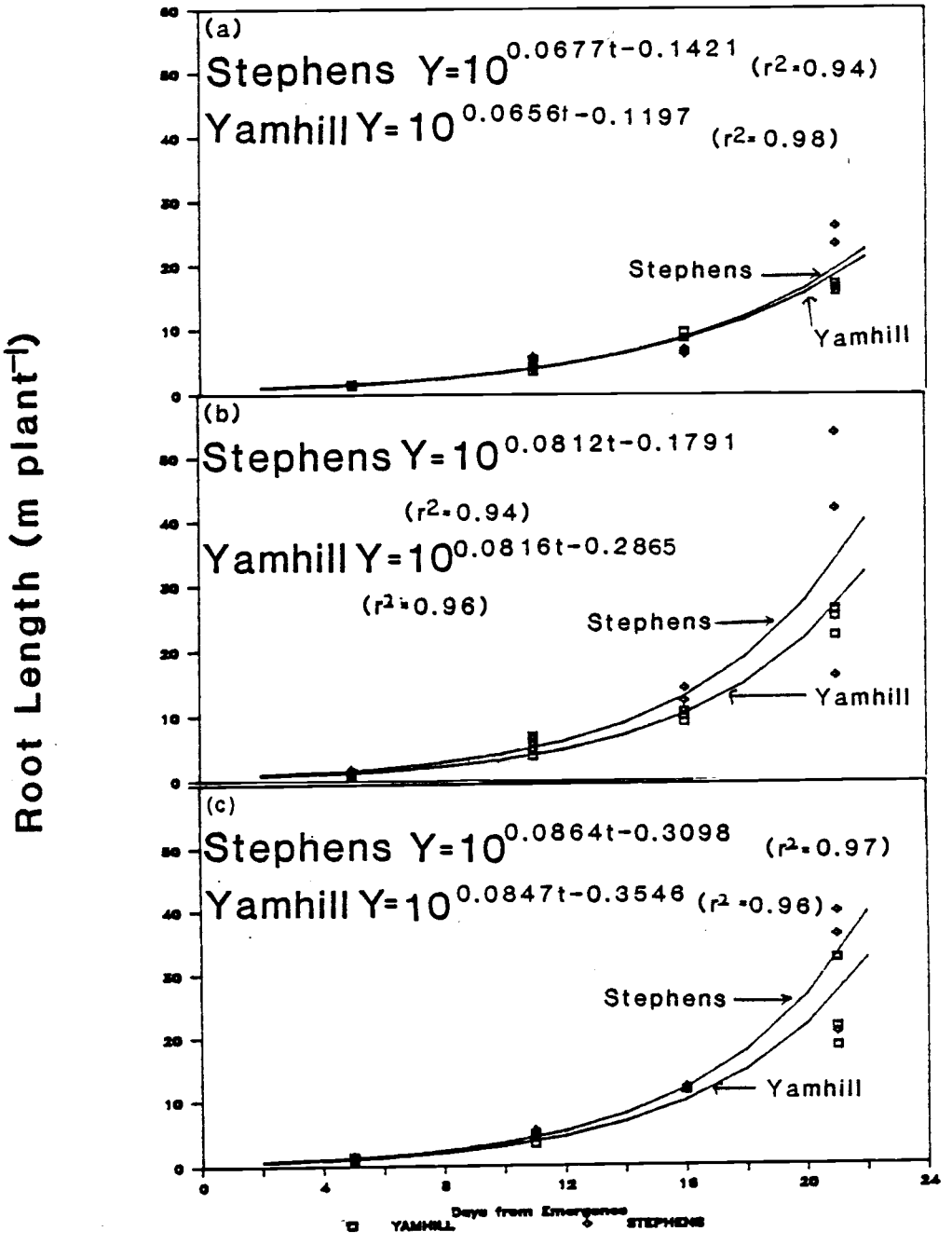

Figure 3. Root length as influenced by plant age, P treatment and cultivar (Experiment 3, data in Appendix Table 4). (a) 0 ug P g^{-1} soil, (b) 25 ug P g^{-1} soil and (c) 100 ug P g^{-1} soil.

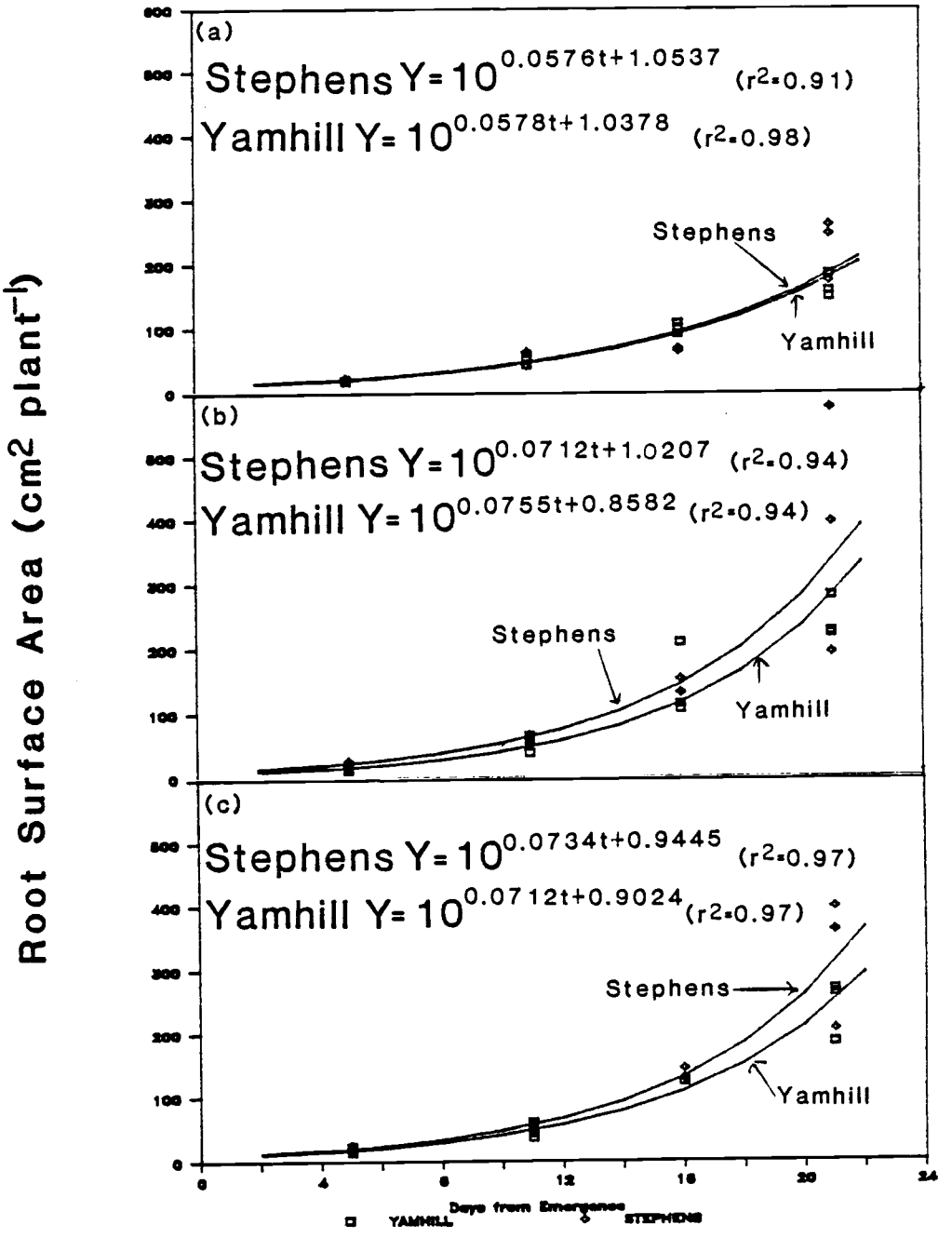

Figure 4. Root surface area as influenced by plant age, P treatment and cultivar (Experiment 3, data in Appendix Table 5). (a) 0 ug P g^{-1} soil, (b) 25 ug P g^{-1} soil and (c) 100 ug P g^{-1} soil.

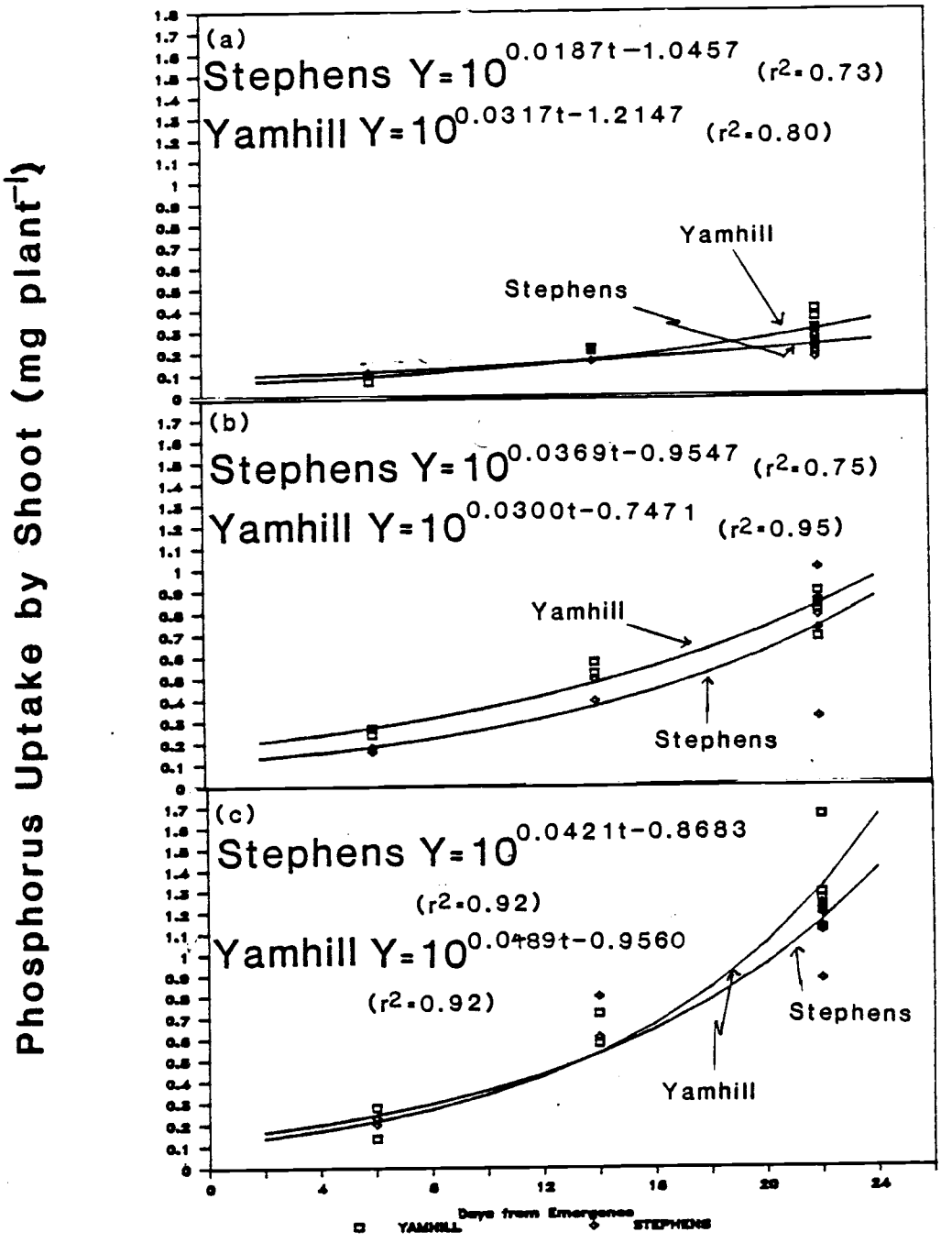

Figure 5. Phosphorus uptake by shoot as influenced by plant age, P treatment and cultivar (Experiment 2, data in Appendix Table 6). (a) 0 ug P g^{-1} soil, (b) 25 ug P g^{-1} soil and (c) 100 ug P g^{-1} soil.

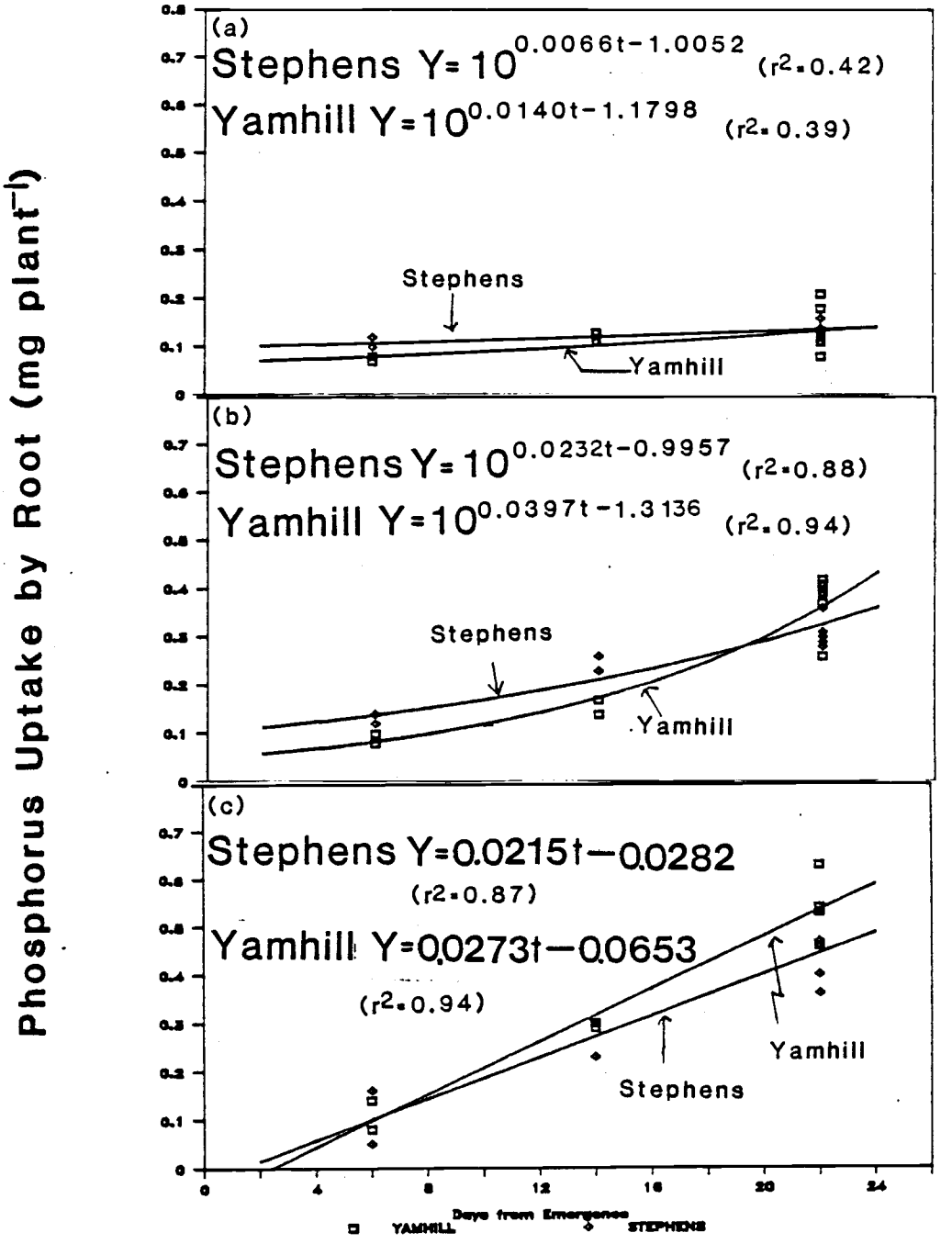

Figure 6. Phosphorus uptake by root as influenced by plant age, P treatment and cultivar (Experiment 2, data in Appendix Table 7). (a) 0 ug P g^{-1} soil, (b) 25 ug P g^{-1} soil and (c) 100 ug P g^{-1} soil.

DISCUSSION

Although there were many significant treatment interactions, plant age had the most significant effect on plant growth and P uptake as indicated by the large F values in comparison to others. P treatment also had a significant effect on plant growth but somewhat depended on plant age. Cultivar differences in P uptake and plant growth became apparent after about 10 to 14 days from emergence.

Ningping and Barber (1985) reported the root growth rate of wheat which was pre-germinated in moistened paper towels and transferred into a solution culture and grown for 42 days. They found that the relation between root length and time (day) was log $y = 0.069t + 1.85$ ($r^2 = 0.95$). Even though roots grow differently in a solution culture and soil, the cultivars also showed exponential growth and the cultivars on the P1 level had similar growth rate as Barber's finding. The cultivars on the P2 and the P3 levels demonstrated steeper growth curve than wheat growing in a solution culture. Furthermore as the wheats grew, Stephens had greater root length. Moreover, Stephens had larger root surface area than Yamhill. Since root mean radius was comparable for the cultivars, varietal difference was due to Stephens' greater root length.

The results were not consistent between experiments 2 and 3. In experiment 2, the root dry weight of Yamhill exceeded that of Stephens whereas in experiment 3 Stephens outyielded Yamhill in root dry weight. In experiment 2, several plants grew in a pot

while one plant was growing in a pot in experiment 3. Despite the different number of plants growing per pot, the same amount of nutrients were added to a pot in both experiments. Therefore, in the case of experiment 2, the plants might have experienced competition between roots. As a result of the competition, the plants allocated more metabolites into roots to urge root growth. The higher root:shoot ratio in the experiment 2 showed the different root growth patterns between two experiments. Therefore, the observed root dry weight difference between cultivars might be caused by root competition within a pot rather than the difference between cultivars. According to Dittmer (1937) using winter rye, the plant showed more extensive root growth when one plant grew in a pot than several plants grew together.

With no added P (P1), P uptake of shoot and root increased only slightly and was nearly linear with time. In contrast, at the P2 level, the P uptake curve was exponential with time. Since phosphorus is strongly adsorbed on soil surfaces, has low concentration in soil solution and slow diffusion rates, roots can only absorb phosphorus which is very near the root surface. The exponential root growth rate on the P2 level increased root contact with phosphorus in soil, which might have increased available P to roots as roots grew. On the other hand, phosphorus concentration in the P3 treatment was higher and may have resulted in a constant supply of P from the soil which may account for the steeper linear uptake of P by roots with time. It was found that Stephens tended to have higher P concentration with the high P

soil (P3).

Stephens and Yamhill did not show differences in dry matter yield and P uptake when no P was applied to the soil which is consistent with a previous report (Sullivan, 1981). Wheat might need to grow longer before showing any differences in tolerance to low phosphorus. When P was applied, Yamhill showed higher P uptake rate than Stephens but Yamhill had less extensive root systems than Stephens. Considering the results of this investigation and the observed performance of the cultivars in the field (Sullivan, 1981), Yamhill's tolerance to low phosphorus soil might be the result of factors other than size or morphology of the root system. These factors include possible differences in (a) mycorrhizal association, (b) root hairs, and (c) phosphorus uptake kinetics. Each is discussed in turn.

It is known that Vesicular-Arbuscular mycorrhiza increase availability of phosphorus for plants grown on low phosphorus soil. Young et al.(1985) investigated the infection of endomycorrhiza on Stephens and Yamhill before harvest on Hyslop farm, where extractable P varied from 70 to 119 mg kg^{-1} and pH from 4.3 to 6.3. No cultivar difference was found for root length colonization rate. Susceptibility of the wheats to specific species of VAM fungi depended on soil treatment and year. Nevertheless, Azocon and Ocampo (1981) reported that spring wheat varieties showed different susceptibility to VAM colonization. Winter wheat varities also might have a variable responses to infection by VAM fungi.

There is no information about effects of root hairs of

Stephens and Yamhill. According to Dittmer (1949), length and radius of root hairs within species are relatively constant. Itoh and Barber (1983) reported length and radius of root hairs of wheat (Triticum aestivum L.) vary from 0.17 to 0.31 mm and from 0.0050 to 0.0057 mm, respectively. A study done by Bole (1973) on wheat showed root hair density changed with phosphorus concentrations. Therefore, cultivar differences of P uptake might be the result of differences in root hair length or density.

Information about phosphorus uptake kinetics of wheats is limited. The study includes root morphology, nutrient uptake characteristics by roots and nutrient supply mechanism by soil. In order to understand cultivar differences in tolerance to low phosphorus soil, further investigations are necessary.

Finally, there were some advantages and disadvantages in using a growth chamber for the study. One of advantages was the the ease in maintaining a uniform environment in terms of temperature and light intensity. Supplying water to plants by capillary action made watering easy without overwatering. Also, it helped to minimize drainage out of the pots. The disadvantages of the growth chamber were limited space and limited experimental time. Since only 500g of growth medium was used, the size of pots would be a limiting factor for root growth if the wheat plants grew more than three weeks. Larger pots may be necessary if root morphology of wheat grown longer than three weeks is to be measured.

SUMMARY AND CONCLUSIONS

The soft white winter wheats Stephens and Yamhill were grown in the growth chamber with a 16 hour light period at 22° C and an 8 hour darkness at 16° C for three weeks. The soil was sandy loam and pH of 6.4 to 6.6. Phosphorus was added as phosphoric acid (H_3PO_4) at rates of 0, 25 and 100 ug P g^{-1} soil. The cultivars were separated into shoots and roots at harvest and phosphorus uptake was determined. Root characteristics such as root length, mean root radius and root surface area were compared between the cultivars.

The conclusions drawn from this investigation were as follows,

(1) Stephens produced more extensive root systems than did Yamhill when grown in soil free of aluminum toxicity and root competition.

(2) Yamhill took up more phosphorus from soil than did Stephens.

(3) Increasing phosphorus treatment increased phosphorus uptake and phosphorus concentration in plants. Stephens tended to have higher P concentration in shoot and root when P was applied.

(4) Stephens had higher root:shoot ratio throughout the experiment. Without phosphorus application to the soil, Stephens had the highest root:shoot ratio, suggesting greater allocation of photosynthates to root growth by Stephens.

Superior P uptake ability of Yamhill to Stephens can not be explained in terms of root size. Yamhill's greater ability to

recover P from soil might be caused by other factors such as differences in mycorrhizal association, root hair length or density and P uptake kinetics.

BIBLIOGRAPHY

Anghinoni, I., V. C. Baligar and S. A. Barber. 1981. Growth and uptake rates of P, K, Ca and Mg in wheat. J. of Plant Nutr. 3:923-933.

Azcon, R., and J. A. Ocampo. 1981. Factors affecting the vescular-arbuscular infection and mycorrhizal dependency of thirteen wheat (Triticum vulgare) cultivars. New Phytol. 87:677-685.

Barber, S. A. 1984. Soil Nutrient Bioavailability. A Wiley-Interscience Publication. John Wiley and Sons. New York.

Barley, K. P., and A. D. Rovira. 1970. The influence of root hairs on the uptake of phosphate. Commun. Soil Sci. Plant Anal. 1:287-292.

Bole, J. B. 1973. Influence of root hairs in supplying soil phosphorus to wheat. Can. J. Soil Sci. 53:169-175.

Bolger, M. C. 1980. Influence of phosphate and lime application on root growth and grain yield of two winter wheat cultivars (Triticum aestivum, L em thell). M.S. Thesis. Oregon State University., Corvallis.

Cholick, F. A,. J. R. Welsh, and C. V. Cole. 1977. Rooting patterns of semi-dwarf and tall winter wheat cultivars under dryland field conditions. Crop Sci. 17:637-639.

Classen, N., and S. A. Barber. 1976. Simulation model for nutrient uptake from soil by a growing plant root system. Agron. J. 68:961-964.

Dittmer, H. J. 1937. A quantitative study of the root and root hair of a winter rye plant. Am. J. of Botany. 24:417-420.

_____. 1949. Root hair variations in plant species. Am. J. of Botany. 36:152-155.

Foy, C. D., A. L. Fleming, G. R. Burns, and W. H. Arminger. 1967. Characterization of differential aluminum tolerance among varieties of wheat and barley. Soil Sci. Soc. Am. Proc. 31:513-521

Foy, C. D. 1974. Effects of aluminum on plant growth. In the plant root and its environment, ed. E. W. Carson, pp 601-642. University Press of Virginia, Charlottsville.

Gregory, P. J., M. McGowan, P. V. Biscoe, and B. Hunter. 1978. Water relations of winter wheat. 1. Growth of the root system. J. Agri. Sci. Camb. 91:91-102.

Itoh, S., and S. A. Barber. 1983. Phosphorus uptake by six plant species as related to root hairs. Agron. J. 75:457-461.

Lipsett, J. 1964. The phosphorus content and yield of grain of different wheat varieties in relation to phosphorus deficiency. Aust. J. Agric. Res. 15:1-8.

Maclean, A. A., and T. C. Chiasson. 1966. Different performance of two barley varieties to varying aluminum concentrations. Can. J. Soil Sci. 46:147-153.

Mengel, K., and E. A. Kirkby. 1981. Principles of plant nutrition. International Potash Institute, Bern.

Moore, D. P. 1974. Physiological effects of pH on roots. In The plant root and its environment, ed. E. W. Carson, pp 135-152. University Press of Virginia, Charlottsvile.

Neenan, M. 1960. The effect of soil acidity on the growth of cereals with particular reference to the different reaction of varieties thereto. Plant Soil. 12:324-328.

Ningping, L., and S. A. Barber. 1985. Phosphorus uptake and growth characteristics of wheat roots. J. Plant Nutr. 8:449-456.

Oregon State University Agricultural Experiment Station. 1985. Wheat Cultivar Abbreviations. Corvallis, Oregon

Oregon State University Extension Service. May 1986. Winter Wheat Varieties for 1986. Corvallis, Oregon.

Palmer, B., and R. S. Jessop. 1977. Some aspects of wheat cultivar response to applied phosphate. Plant Soil 47:63-73.

Sullivan, D. M. 1981. Phosphorus response and critical phosphorus levels of winter wheat varieties in western Oregon. M.S. Thesis, Oregon State University., Corvallis.

Taylor, R. G., T. L. Jackson, R. L. Powelson, and N. W. Christensen. 1983. Chloride, nitrogen form, lime, and planting date effects on take-all root rot of winter wheat. Plant Disease 67:1116-1120.

Tennant, D. 1975. A test of a modified line intersect method of estimating root length. J. Ecol. 63:995-1001.

Young, J. L., E. A. Davis, and S. L. Rose. 1985. Endomycorrhizal fungi in breeder wheats and triticate cultivars field-grown on fertile soil. Agron. J. 77:219-224.

APPENDICES

Appendix Table 1. Plant tissue concentration of potassium, calcium and magnesium.

Cultivar	Shoot	Root
	Mg, %	
Yamhill	0.32	0.37
Stephens	0.34	0.29
	Ca, %	
Yamhill	0.49	0.31
Stephens	0.55	0.29
	K, %	
Yamhill	3.97	1.27
Stephens	4.01	1.89

Standard error of means Mg for shoot = 0.016 (40 error df)
for root = 0.009 (40 error df)
Standard error of means Ca for shoot = 0.024 (40 error df)
for root = 0.008 (40 error df)
Standard error of means K for shoot = 0.096 (40 error df)
for root = 0.062 (40 error df)

Appendix Table 2. Dry weights of shoot per plant (Experiment 2)

Days from emergence	Cultivar	Reps.	P treatment*		
			P1	P2	P3
			mg		
6	Yamhill	1	27.9	49.4	47.2
		2	32.5	45.8	40.8
	Stephens	1	28.6	48.5	36.3
		2	33.7	42.6	32.0
14	Yamhill	1	120.7	166.3	183.0
		2	122.2	168.1	179.1
	Stephens	1	79.3	159.6	117.2
		2	122.7	135.2	185.8
22	Yamhill	1	215.3	523.3	502.9
		2	260.2	468.6	549.8
		3	228.0	451.1	592.8
		4	202.0	478.5	503.8
		5	265.7	462.3	496.7
		6	185.7	487.4	587.6
	Stephens	1	207.0	409.4	536.9
		2	206.2	395.1	397.7
		3	302.3	500.2	376.5
		4	219.0	427.9	472.8
		5	171.3	475.1	365.3
		6	208.3	359.7	399.2

* P1, P2 and P3 = 0, 25 and 100 ug P g^{-1} soil, respectively.

Appendix Table 3. Dry weights of shoot per plant (Experiment 3).

Days from emergence	Cultiver	Reps.	P treatment* P1	P2	P3
			mg		
5	Yamhill	1	17.5	23.8	15.3
		2	24.5	20.0	25.4
		3	15.1	11.6	29.0
	Stephens	1	22.8	20.8	17.4
		2	20.5	24.1	7.9
		3	19.9	19.8	19.7
11	Yamhill	1	84.0	115.8	83.8
		2	77.0	126.3	154.6
		3	98.5	75.9	82.6
	Stephens	1	82.3	112.4	104.6
		2	69.8	75.4	106.9
		3	89.0	93.9	114.7
16	Yamhill	1	222.2	338.3	409.6
		2	248.1	318.8	427.0
		3	229.6	360.0	392.2
	Stephens	1	131.3	311.2	336.7
		2	93.2	325.4	348.1
		3	112.2	301.0	349.0
21	Yamhill	1	361.1	794.5	959.7
		2	423.0	912.2	774.8
		3	468.0	736.6	699.8
	Stephens	1	428.0	917.7	803.4
		2	556.5	816.7	579.3
		3	280.1	913.4	802.5

* P1, P2 and P3 = 0, 25 and 100 ug P g^{-1} soil, respectively.

Appendix Table 4. Root length per plant (Experiment 3).

Days from emergence	Cultiver	Reps.	P treatment* P1	P2	P3
			m		
5	Yamhill	1	1.5	1.3	0.8
		2	1.3	1.1	1.1
		3	1.6	1.0	1.5
	Stephens	1	1.4	1.8	1.6
		2	1.4	1.4	1.1
		3	1.6	1.6	1.0
11	Yamhill	1	3.5	5.9	3.4
		2	5.2	7.0	4.4
		3	4.9	3.9	4.3
	Stephens	1	5.8	6.6	5.2
		2	4.0	4.9	5.4
		3	5.7	5.8	4.7
16	Yamhill	1	9.6	10.7	11.6
		2	9.6	9.2	11.6
		3	8.6	10.8	11.6
	Stephens	1	6.2	12.5	11.5
		2	6.9	14.4	12.1
		3	6.5	11.0	11.6
21	Yamhill	1	17.1	25.4	21.5
		2	15.9	26.4	32.3
		3	16.5	22.5	18.5
	Stephens	1	26.1	54.0	39.6
		2	23.2	42.0	20.6
		3	16.4	16.2	36.0

* P1, P2 and P3 = 0, 25 and 100 ug P g^{-1} soil, respectively.

Appendix Table 5. Root surface area per plant (Experiment 3).

Days from emergence	Cultiver	Reps.	P treatment*		
			P1	P2	P3
			cm^2		
5	Yamhill	1	21	19	14
		2	18	16	18
		3	21	12	23
	Stephens	1	24	27	25
		2	22	25	18
		3	23	24	21
11	Yamhill	1	44	60	36
		2	53	66	60
		3	56	39	43
	Stephens	1	62	67	59
		2	42	53	55
		3	64	60	50
16	Yamhill	1	109	108	124
		2	102	115	124
		3	92	210	124
	Stephens	1	66	133	129
		2	70	154	145
		3	68	131	131
21	Yamhill	1	150	224	270
		2	160	282	264
		3	187	226	186
	Stephens	1	262	576	398
		2	248	396	207
		3	175	193	362

* P1, P2 and P3 = 0, 25 and 100 ug P g^{-1} soil, respectively.

Appendix Table 6. Phosphorus uptake by shoot (Experiment 2).

Days from emergence	Cultivar	Reps.	P treatment*		
			P1	P2	P3
			mg		
6	Yamhill	1	0.07	0.27	0.28
		2	0.10	0.24	0.14
	Stephens	1	0.11	0.18	0.23
		2	0.11	0.16	0.20
14	Yamhill	1	0.22	0.52	0.58
		2	0.21	0.57	0.72
	Stephens	1	0.16	0.49	0.61
		2	0.21	0.39	0.80
22	Yamhill	1	0.28	0.89	1.20
		2	0.31	0.84	1.26
		3	0.36	0.68	1.66
		4	0.24	0.81	1.21
		5	0.40	0.83	1.29
		6	0.20	0.83	1.12
	Stephens	1	0.22	0.78	1.11
		2	0.27	0.84	1.19
		3	0.30	1.00	1.13
		4	0.23	0.84	1.13
		5	0.17	0.85	1.24
		6	0.20	0.72	0.88

* P1, P2 and P3 = 0, 25 and 100 ug P g^{-1} soil, respectively.

Appendix Table 7. Phosphorus uptake by root (Experiment 2).

Days from emergence	Cultivar	Reps.	P treatment*		
			P1	P2	P3
			mg		
6	Yamhill	1	0.08	0.10	0.08
		2	0.07	0.08	0.14
	Stephens	1	0.10	0.14	0.16
		2	0.12	0.12	0.05
14	Yamhill	1	0.11	0.14	0.29
		2	0.13	0.17	0.30
	Stephens	1	0.11	0.26	0.23
		2	0.13	0.23	0.30
22	Yamhill	1	0.13	0.40	0.46
		2	0.21	0.41	0.53
		3	0.12	0.26	0.54
		4	0.11	0.37	0.54
		5	0.18	0.42	0.54
		6	0.08	0.39	0.63
	Stephens	1	0.16	0.29	0.53
		2	0.16	0.31	0.36
		3	0.13	0.28	0.46
		4	0.14	0.31	0.46
		5	0.11	0.39	0.47
		6	0.14	0.30	0.40

* P1, P2 and P3 = 0, 25 and 100 ug P g^{-1} soil, respectively.