Phosphorus Utilization From Internal and External Sources In the Growth of Woody Ornamental Plants[1]

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Abstract. The influence of P applications on the growth of *Berberis* x *mentorensis* L. M. Ames, *Juniperus chinensis* 'Keteleeri' Cornman, and *Taxus* x *media* 'Hicksii' Rehd., was studied for 2 growing seasons. During one summer P was applied at varying rates to plants grown in containers and the growth and P content of various plant parts were determined. The following spring the roots of these dormant plants were washed free of the growing medium and the plants were grown in solution culture at varying levels of P labeled with P^{32}. The spring growth, the P content of all plant parts, and the % P coming from the solution into all plant parts during the spring were determined. Phosphorus applied during the summer caused little growth response except with young *Taxus* plants receiving a high P level. There were several significant growth responses during the spring due to P applications the previous season. A high P concentration during the spring increased the growth of some plants, but *Taxus* plants with a high internal P status showed little response. The P coming into the new spring growth from solution varied from 0 to 86% depending on the plant species used and the concentration around the roots. In *Berberis* the majority of the rest of the P moving into new growth originated from reserve P in the roots. In *Juniperus* the majority of the internally redistributed P came from the foliage and in *Taxus* both the foliage and roots were important sources of reserve P.

Woody plants undergo a period of rapid shoot expansion from dormant buds in the spring. This rapid growth needs considerable quantities of both inorganic and organic material which is derived from either externally absorbed material or internally redistributed material. Previous investigations (8) (10) have found that the new spring growth is greater in plants containing a high P content. These studies measured the P only in the readily accessible tissue and did not include an evaluation of the total plant P status. Meyer and Tukey (10) found differences of external P utilization during the spring depending on species, temperature of the solution, and P status of the plant. Harley et al. (6) found little transport of P into apple leaves from solution during early spring growth. The following experiments were performed to study internal P content of all tissues both before and after spring growth and to determine the relative contribution of various tissue sources of internal P and externally supplied P to the spring growth of woody ornamental plants.

Methods and Materials

Taxus x *media* 'Hicksii' Rehd., *Berberis* x *mentorensis* L. M. Ames, and *Juniperus chinensis* 'Keteleeri' Cornman, plants were potted in 3-liter containers in a 1:1:1 soil:peat:perlite medium on 14 July 1967. These plants were divided into 3 groups at random and each plant received either 0, 30, or 60 mg of P as KH_2PO_4 solutions every 2 weeks for 10 weeks. Sixty mg of N as NH_4NO_3 solution and 60 mg K as KH_2PO_4 and K_2SO_4 were applied every 2 weeks to all plants. The plants were grown in full sunlight with the containers resting on coarse gravel. The plants were allowed to go dormant naturally in the fall and were moved to an unheated cold frame until the following spring. Before growth started the roots of *Taxus* and *Berberis* were washed free of the medium and the plants were weighed. Some plants were separated into roots, stems, and foliage (where present) and the parts were analyzed for total P content. Phosphorus was determined after ashing as molybdovandophosphoric acid. Other plants were then grown in an 18°C greenhouse in aerated solution culture minus P according to Hoagland and Arnon (7). To each of the previous seasons P treatments for *Berberis* and *Taxus* 3 levels of P:0, 10^{-5}M, and 10^{-3}M H_2PO_4 labeled with P^{32} ($2 \times 10^{-4}\mu C 6\mu g$ P) were added making a 3 x 3 factorial experiment. There were 4 replications of one plant each per treatment. The solutions were changed every 2 weeks and the pH and P level including P^{32} were adjusted weekly. The *Juniperus* were treated similarly except they were raised in sand culture without P^{32} and fresh solutions were applied daily.

All plants were harvested after 6 weeks of growth and the new growth including stems and leaves was removed, dried, and weighed. The weight of this new growth of each plant was divided by the plants fresh weight before spring growth to give the new growth as mg dry weight per gram of fresh weight to take out variations in plant size. The plant parts remaining after removal of the new growth were again separated into roots, stems, and foliage. The total P concentration was determined for all the plant parts. The specific activity of P in *Berberis* and *Taxus* plant parts was determined by taking an aliquot of the ash solution used for total P, plating on a planchet, and counting on a gas flow GM counter. The % of P coming into various tissues of *Berberis* and *Taxus* plants from the solution was determined by the equation,

$$\frac{\text{Specific activity P in plant}}{\text{Specific activity P treating solution}} \times 100 = \% \text{ of P coming from solution in plant tissues.}$$

The following summer *Taxus* were again potted in soil:peat:perlite 1:1:1 and treated every 2 weeks with either 0 or 225 mg of P applied to the surface as dry 20% superphosphate and watered immediately. Nitrogen and K were supplied as in the previous experiments. These were given a total of 6 treatments starting 2 July 1968. They were then stored 1968-69 winter in a cold storage at 1°C. The following spring of 1969 the plants were analyzed and treated in solution culture as in the previous experiments; however, only 0 and 10^{-3}M P levels were used with P^{32} (1.2×10^{-3} $\mu C/\mu gP$) making a 2 x 2 factorial experiment. New white root growth was separated from older brown roots and analyzed for P. Six replications of one plant each were used for each treatment.

All data (except P from solution) in all experiments were compared according to Duncans New Multiple range test. In addition, an A.N.O.V. was computed for the spring growth data as a factorial experiment and significant main effects and interaction are noted where appropriate.

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Results and Discussion

Berberis. The weights of dormant plants of *Berberis* grown during summer 1967 and spring 1968 were not significantly different (Table 1). These plants were pruned to a vigorous bud before weighing. The P content of dormant *Berberis* stems increased significantly as 30 mg and 60 mg of P was applied every 2 weeks the previous summer, but there was no difference between these levels. The P content of the roots appeared to increase with P application; however, they were not significantly different.

The spring 1968 growth of *Berberis* was variable and no significant differences were observed for any treatment. There were significant increases in the P content of the spring growth as the concentration around the roots was increased from 10^{-5} to 10^{-3} M during this growth period regardless of the previous summer's treatments (Table 1). This increase in P content came directly from the solution and did not affect internal redistribution. In the new spring growth of plants grown in 10^{-3}M solution 40-56% of the P came directly from the solution. This was about the magnitude of increase in the P content of the new growth. In those plants receiving no P during the spring the P contents of the stems and roots decreased indicating transport from both of these structures into the new growth. There were smaller decreases in the roots at the 10^{-5}M concentration during the spring, however, 10-15% of the P in the roots was replaced from the solution indicating considerable transport from this tissue. The 10^{-3}M concentration during the spring significantly increased the P content of the roots. There was still movement of stored P from this tissue considering that 50-80% of the P content of these roots came directly from the solution.

Juniperus. There was no significant increase in either growth or P content of roots or shoots of *Juniperus* as P level was increased during the summer of 1967 (Table 2). The new growth during spring 1968 was significantly increased due to spring applied P. This was shown as a main effect by A.N.O.V., although Duncan's test does not show this significance. There was no effect of the summer P level on the following spring growth.

The P content of the new growth increased significantly as the solution level was increased from 10^{-5} to 10^{-3}M during spring. If the P contents of the old foliage and roots of plants given no P during the spring are compared to the starting levels in the dormant plants, it can be seen that most of the phosphorus comes from the older foliage with a small amount from the roots. This is in contrast to *Berberis* (Table 1) where considerable internally redistributed P comes from the roots. At the 10^{-3}M spring level, the P contents of the new growths and roots increase significantly, whereas, the P content of older foliage remains stable. The P appears to bypass the older foliage and go directly to the new growth, although considering the results with *Taxus* and *Berberis* there may be redistribution with the spring applied P replacing that moving out of the older tissue.

Taxus – Exp. 1. There were no significant differences in spring growth of *Taxus* caused by the P application the season it was applied (Table 3). There appeared to be increased P in the leaves and roots as the P application was increased during the summer, but differences were not significant. Growth the following spring was significantly increased by both the summer and spring P application as determined by A.N.O.V. There was no significant interaction between spring and summer applications. The P content in the new growth increased significantly as the P concentration of the solution was raised to the 10^{-3}M level during the spring and 40-50% of P in the new growth came from the solution. The 10^{-5}M treatment caused no significant increase in growth and only 4-5% of the P in the new growth came from this solution. The P content of the new

Table 1. Spring growth and P content of *Berberis* x *mentorensis* as influenced by P applications during two seasons[ab]

Summer 1967 P mg/pot.	0			30			60		
Growth g fresh wt	49.65 a			53.47 a			45.96 a		
% P stems	.194a			.230 b			.228 b		
% P roots	.466a			.485a			.541a		
Spring 1968 P Molarity									
Growth	0	10^{-5}	10^{-3}	0	10^{-5}	10^{-3}	0	10^{-5}	10^{-3}
mg dry wt/g fresh wt	43.82 a	43.91 a	61.22 a	48.39 a	56.52 a	55.52 a	46.88 a	45.98 a	45.03 a
% P in new growth	.191a	.210a	.362 b	.210a	.222a	.385 b	.214a	.234a	.330 b
% of P from solution in new growth	0	4.86	53.68	0	5.97	56.49	0	2.98	41.18
% P stems	.171a	.205abc	.218 c	.206abc	.215 bc	.246 cd	.193ab	.218 c	.275 d
% of P from solution in stems	0	2.74	35.74	0	2.84	32.92	0	1.66	21.43
% P from roots	.225a	.270ab	.490 cd	.276ab	.302ab	.590 d	.286ab	.340 b	.485 c
% of P from solution in roots	0	14.89	77.60	0	14.74	81.13	0	10.62	53.53

[a]Mean of 4 plants.

[b]Differences between means in the same row are significant at the 5% level when they have no common subscript letters.

Table 2. Spring growth and P content of *Juniperus chinensis* 'Keteleeri' as influenced by P applications during two seasons[ab]

Summer 1967 P Mg/pot.	0			30			60		
Growth g fresh wt	52.61a			52.96a			55.79a		
% P foliage	.201a			.204a			.206a		
% P roots	.155a			.163a			.161a		
Spring 1968 P Molarity	0	10^{-5}	10^{-3}	0	10^{-5}	10^{-3}	0	10^{-5}	10^{-3}
Growth mg dry wt/g fresh wt.	47.87a	50.81a	59.10a	48.76a	54.33a	55.80a	52.55a	55.52a	59.30a
% P new growth	.152a	.171ab	.265 c	.170ab	.196 b	.260 c	.160ab	.172ab	.280 c
% P older foliage	.129a	.138a	.200 b	.133a	.188a	.204 b	.131a	.148a	.190 b
% P roots	.124a	.138a	.555 b	.134a	.193a	.590 b	.168a	.154a	.638 b

[a]Mean of 4 plants.

[b]Differences between means in the same row are significant at the 5% level when they have no common subscript letters.

growth of plants receiving no P during the spring was related to the previous seasons P application. This P came from the older foliage and roots as evidenced by the decrease in P in these tissues (Table 3). The stems were not checked during this experiment. The older leaves on plants receiving 10^{-3}M P did not change in P content; however, as 23-30% of this P was from the solution there was some transport of stored P out of this tissue. If this new P is subtracted from these levels the P content remaining is approximately the same as that in plants receiving no P during the spring. This indicates that only a certain amount of P is available for redistribution and this leaves active absorption sites available.

Taxus – Exp. 2. Younger plants of *Taxus* were used and the level of P was increased during the summer 1968 over that in the first experiment. This increased P resulted in significant increases in the summer growth as measured by dormant fresh weight and increases in P content of plants receiving 225 mg P over those receiving 0 P during the summer (Table 4).

The spring 1969 growth of *Taxus* was significantly increased by P applied the previous summer regardless of the spring level and even when presented on a mg dry wt/g fresh wt basis (Table 4). There was a significant interaction: the high spring level of P increased spring growth significantly only when the level of P in the tissue was low due to low P the previous summer.

The P content of the new growth of plants receiving no P during the spring was significantly increased due to the previous season's P application. If the P concentration during the spring was raised to 10^{-3}M the P content of the new growth was significantly greater in low P status plants from the previous summer than the high P plants that received the 225 mg level. This was also shown by the % P coming from the solution into the new growth (Table 4). This indicates that considerable P is

Table 3. Spring growth and P content of *Taxus* x *media* 'Hicksii' in Exp. 1 as influenced by P applications during two seasons[ab]

Summer 1967 P mg/pot.	0			30			60		
Growth g fresh wt	31.48a			31.72a			31.86a		
% P leaves	.156a			.168a			.164a		
% P stems	.071a			.083a			.061a		
% P roots	.251a			.278 b			.268 b		
Spring 1968 P Molarity	0	10^{-5}	10^{-3}	0	10^{-5}	10^{-3}	0	10^{-5}	10^{-3}
Growth mg dry wt/g fresh wt	62.9 a	67.1 ab	73.0 ab	69.3 ab	77.4 bc	95.7 d	72.0 ab	71.0 ab	88.5 cd
% P new growth	.236a	.164a	.358 b	.245a	.273a	.365 b	.269a	.260a	.355 b
% of P from solution in new growth	0	3.93	40.57	0	5.09	50.71	0	3.91	44.63
% P older leaves	.116a	.129a	.139a	.121a	.131a	.167a	.131a	.124a	.166a
% of P from solution in older leaves	0	2.46	22.78	0	3.02	29.38	0	.236	26.23
% P roots	.187a	.238abc	.363 d	.192ab	.243 bc	.395 d	.215abc	.246 c	.389 d
% of P from solution in roots	0	14.25	45.81	0	17.74	56.54	0	13.87	56.18

[a]Mean of 4 plants.

[b]Differences between means in the same row are significant at the 5% level when they have no common subscript letters.

Table 4. Spring growth and P content of *Taxus* x *media* 'Hicksii' in Exp. 2 as influenced by P applications during two seasons[ab]

Summer 1968 P mg/pot.	0		225	
Growth g fresh wt.	18.14 a		22.16 b	
% P leaves	.095a		.256 b	
% P stems	.052a		.087 b	
% P roots	.084a		.270 b	
Spring 1969 P Molarity	0	10^{-3}	0	10^{-3}
Growth mg dry wt/g fresh wt.	14.30 a	25.82 b	62.94 c	64.82 c
% P new growth	.140a	.897 d	.303 b	.418 c
% of P from solution in new growth	0	86.39	0	40.50
% P older leaves	.054a	.562 b	.144a	.216a
% of P from solution in older leaves	0	81.47	0	21.98
% P new roots	.168a	.881 c	.396 b	1.275 d
% of P from solution in new roots	0	96.01	0	69.21
% P older roots	.062a	.204 b	.191 b	.466 c
% of P from solution in older roots	0	79.34	0	55.21
% P stems	.037a	.140 c	.086 b	.104 b
% of P from solution in stems	0	73.08	0	29.63

[a]Mean of 6 plants.

[b]Differences between means in the same row are significant at the 5% level when they have no common subscript letters.

taken up by both low and high P status plants during the spring; however, in the high P summer group of plants P was diluted by increased growth of plant material.

The P content of the new roots during the spring was increased both by previous season application and current season's concentration with the latter being more important. In the low P status plants almost all (96%) of P came from the solution into the new roots.

The P content of the older foliage and roots when compared to that before growth show, as in the first experiment, that there was considerable redistribution of P from the older leaves and roots into the new growth of both shoots and roots at the 0 spring concentration. The change in P content of the stems was minor and they could be considered as a minor source of stored P. The plants receiving 10^{-3}M P during the spring tended to redistribute about as much P into the new growth as those receiving 0 P. The increased P in the older tissue at the 10^{-3}M spring concentration came from the solution and replaced that which was transported out of the older tissue.

These experiments show the importance of internally stored P for spring growth of woody ornamental plants. The P stored in the roots of *Berberis* was the major contributor to new spring growth while P stored in the foliage of *Juniperus* and *Taxus* was also important. The stems contributed very little stored P to the new growth. When considering tissue analysis in response to P application the roots appear to show greater variation. Studies of growth responses to P applied the same season (2, 3, 4, 5) miss considerable growth response because considerable quantities of stored P are used in growth.

There were increases in growth due to spring applied P. This was greater in low P status plants. Phosphorus concentration at the 10^{-3}M level gave a response. Black (1) reported that the normal concentration of P in soil solution ranges from 10^{-5}M to 10^{-7} or less. Phosphorus moves very slowly in normal soils, so field applications in the spring, unless soils are very sandy, probably do not contribute to spring growth. Therefore, spring applied P would move down during the summer, then taken up and stored for the following season. Spring applied P, even that reaching the roots, would influence only those plants with a low P status. Meyer and Tukey (10) showed that low soil temperature during spring may also inhibit P uptake. With cold soils internally stored P would appear to be more important in spring growth than externally supplied P. This was shown for N material for some species (9) but other species appeared to differ (8). Phosphorus applications during the spring would benefit spring growth of some woody plants in light or warm soils, or in containers, if the previous season's P fertilization was not adequate.

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