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Dormancy Implications of Phosphorus Levels in Developing Caryopses of Wild Oats (*Avena fatua* L.)

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Abstract. The element phosphorus made up 0.5% of the dry weight of dehulled *Avena fatua* caryopses 7 days after anthesis (DAA), half of it inorganic (P_i). Caryopses detached and pierced 7 DAA germinated in vitro with a rapid drop in P_i levels. By 15–20 DAA caryopsis dry weight had increased three- to fourfold, but phosphorus made up less than 0.04% of the dry weight of this enlarged caryopsis. Caryopses at this stage germinated readily without piercing if incubated in vitro. A further decrease in P_i accompanied by a marked increase in phytate phosphorus began about 15 DAA and continued during later seed maturation. By 20 DAA, when embryos were relatively mature and endosperm cell division had ceased, a decrease in caryopsis water content (as a percentage of dry weight) began, and seed dormancy became apparent. As starch and phytate reserves accumulated, P_i and water levels of the caryopsis diminished. Higher levels of endogenous P_i coincided with the anabolic events of initial seed formation and, to a lesser extent, with anabolic events of seed germination. Decreasing P_i levels coincided with accumulation of nutrient reserves, lowering of water content, and the initiation of dormancy. The data suggest that (1) enzymes associated with the formation and development of the embryo may be activated by the high P_i levels present during initial seed differentiation; (2) embryo quiescence and dormancy are facilitated by the drop of P_i levels which accompanies the accumulation of starch and phytate reserves; and (3) the increase in P_i which accompanies seed afterripening aids in the termination of dormancy and the resumption of germination.

Key Words. Seed dormancy—*Avena fatua*—Phosphorus—Maturation–Competition

The expression of primary (genetic) seed dormancy is subject to many constraints (Simpson 1990). Limited information is available on transient changes during development in key regulators, enzymes, and metabolites, which may influence the initiation of seed dormancy (MacNicol and Jacobson 1992). Nitrogen supply has been implicated in the establishing and breaking of dormancy in wild oat caryopses (McIntyre et al. 1996, Richardson 1979). An inverse relationship is suggested between seed dormancy and the amounts of inorganic phosphorus (P_i) available to the wild oat embryo (Jain et al. 1982, Quick and Hsiao 1984, Quick et al. 1982–1983). Within genetically uniform lines the duration of seed dormancy varies with the adequacy of phosphorus nutrition provided to the parental plants (Quick et al. 1982–1983). Dormant wild oat lines characteristically produce caryopses with lower P_i content than those produced by less dormant lines.

Seed components such as phytohormones also vary with dormancy, and the availability of P_i is not necessarily the cause of dormancy. However, changes in P_i level accompanying the development of the wild oat caryopsis suggest a regulatory role. P_i plays a role in phosphatase synthesis in cultured tobacco cells (Ueki and Sato 1977). Feedback inhibition of acid phosphatases (Duff et al. 1994) may be a general form of cellular regulation. ADP-glucose pyrophosphorylase, a key enzyme in starch biosynthesis, is subject to inhibition by P_i (Nakamura and Kawaguchi 1992). GA_3 appears to exert a control over synthesis or activation of enzymes involved in embryo and endosperm carbohydrate metabolism, thus influencing dormancy initiation or release (Foley et al. 1992, 1993). Exogenous P_i (50 mM) mimics the specific action of GA_3 in regulating the

Abbreviations: P_i, inorganic phosphorus; GA_3, gibberellic acid$_3$; DAA, days after anthesis.

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activity of certain enzymes in embryoless half-seeds of wheat (Saluja et al. 1987). These findings argue for a regulatory role for P_i in developing seeds and may be related to the observed increases in P_i which accompany the processes of afterripening and loss of dormancy in wild oat caryopses (Quick and Hsiao 1984). These observations, taken with the known involvement of reversible phosphorylation in regulating activity of some enzymes (Budde and Chollet 1988), suggest that more should be known of the relationship between dormancy induction and P_i levels. This paper details the levels of total, phytate, and inorganic phosphorus during wild oat caryopsis development and the effect on dormancy of competition for phosphorus within the panicle and the spikelet. Possible relationships of endogenous phosphorus to the imposition of dormancy in caryopses are discussed.

Materials and Methods

Seed Lines and Growth History

Caryopses of the genetically uniform line CS40 require a brief afterripening to overcome dormancy after abscission (Quick and Hsiao 1984). Plants were grown in peat/sand (50:50 v/v) in 15-cm pots. Water was supplied as needed, with 250 mL quarter-strength Hoagland's solution provided on alternate days (Hoagland and Arnon 1950). Light at upper leaf level was 400 μE m^{-2} s^{-1} with relative humidity at 40% and temperature at 20°C. Two experiments were run successively in the same growth chamber differing only in the time intervals at which panicles were harvested. Two tillers were retained.

Sampling

In the first experiment main shoot panicles were harvested 25 and 45 days after anthesis (DAA) of the upper florets of each main shoot panicle. The upper, middle, and lower sections of harvested panicles were separated, and an approximate DAA value was assigned to each set of bulked caryopses. The primary and secondary caryopses were also separated. Each seed sample was divided into two subsamples. In subsample 1, fresh and dry weights of dehulled caryopses were determined as well as phosphorus levels. Seed in subsample 2 was incubated in water and the P_i levels of the caryopses determined after 52 h.

In the second experiment, the main shoot panicles were harvested at 14, 20, 30, and 45 DAA of the terminal floret. Panicles were divided into upper, middle, and lower sections as in the first trial and an approximate DAA assigned to seeds. Primary and secondary caryopses within each sampling were analyzed separately for phosphorus components, and dormancy levels were assessed.

Germination Conditions

For each treatment three replicates of 50 seeds were placed, palea side down, in 9-cm Petri dishes containing one disc of Whatman No. 3 filter paper and 5.5 mL of distilled water. Incubation was in darkness at 20°C. Seeds ungerminated at day 10 were dehulled, pierced with a 1-mm needle at the top center (Raju et al. 1986), and held in darkness at 20°C for 7 days. For short term imbibition three replicates of 50 seeds were incubated for 24 h as for germination. Seeds were then dehulled and imbibed for the rest of the 52-h period. Caryopses were freeze dried to avoid breakdown of labile phosphorus compounds. As fresh caryopses were dehulled they were accumulated over a 5-min period in a Petri dish held at high relative humidity, weighed, lyophilized to constant weight, and desiccator stored until used.

Phosphorus Analyses

Dried dehulled caryopses were ground in a Wiley mill. Total phosphorus was determined (Anonymous 1965) following wet ashing with H_2SO_4. Triplicate analyses were performed for P_i and phytate phosphorus (Williams 1970).

Preparation of Figures

Each point represents the mean of three replicate values. The lines of best fit were determined using the spline interpolation option of SAS/GRAPH software (SAS Institute Inc. 1985). The lines of best fit in Figs. 1 and 3 pass through a series of joined triplets. The three joined points in each triplet are the mean values for caryopses of successively lesser physiologic age taken from upper, middle, and lower whorls of the panicles at each of the four sampling stages.

Results

Anthesis in the panicle followed described gradients (Raju 1990 and references cited therein). Anthesis in the upper third of the panicle preceded anthesis in the middle third by 4 ± 1 days and anthesis in the lowest third by 8 ± 2 days. Margins of error were due to acropetal gradients of development in the lateral branches. Dates of anthesis of secondary caryopses on the individual spikelets were 1–2 days behind the primary caryopsis.

Imposition of Dormancy during Development

Dormancy, indicated by a reduced ability to germinate after dehulling and piercing, first appeared at 18–20 DAA. Primary caryopses detached at 7 DAA germinated poorly when incubated on water (Fig. 1*A*), but if dehulled and pierced, most caryopses germinated. Intact primary caryopses samples 10–20 DAA germinated 10–15% after a 10-day incubation, a value unaltered by additional incubation (data not shown). Germination of these immature caryopses, if dehulled and pierced after the 10-day incubation, approached 90%. Over the period 10–20 DAA, water content of developing caryopses declined from 75 to 50% of fresh weight (Fig. 2, *A* and *B*).

Dormancy increased in caryopses harvested at later stages (Fig. 1, *A* and *B*). Dehulled, pierced primary caryopses 35–40 DAA germinated only 15%. Intact secondary caryopses were more dormant than primary caryopses. Dehulling and piercing treatments aided the germination of secondary caryopses but with less success in very early stages.

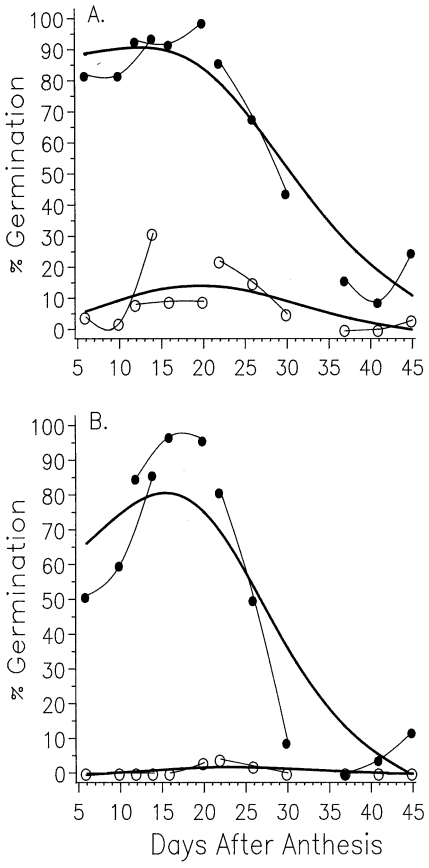

Fig. 1. Percent germination of primary (*A*) and secondary (*B*) wild oat caryopses harvested at various stages of maturity. Germination was recorded after 10 days of incubation of intact seeds (○) or on seeds given dehulling and piercing treatment at day 10 followed by another 7-day incubation (●) Each point represents a mean of three replicates. Caryopses at different stages of maturity from the same panicle are connected. A line of best fit is drawn for primary and secondary caryopses.

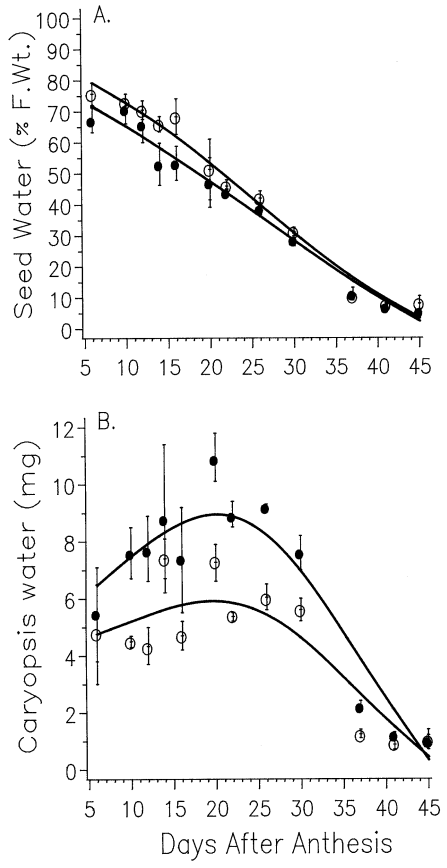

Fig. 2. Water content as percentage of fresh weight (*A*) or as mg of free water (*B*) of primary (●) or secondary (○) wild oat caryopses for up to 45 DAA. Means of three replicates ± S.E. are shown.

P_i Levels as Influenced by Position and Age of Caryopses

The levels of P_i in dehulled caryopses 7 DAA were very high. As much as 0.8% of the dry weight was P_i, with phosphorus itself accounting for up to 0.25% of the dry weight. Half of the total phosphorus present in caryopses at 6–10 DAA and 25% of that present at 14 DAA were in inorganic form (Table 1 and Fig. 3, *C* and *D*). Levels of P_i declined rapidly as maturation progressed (Tables 2 and 3; Figs. 3 and 4). This tendency was true whether P_i was expressed as μg of P_i/caryopsis (Fig. 3*B*) or as μg of P_i/g, dry weight (Fig. 4). Dormancy (a lessened germination response to dehulling and piercing) appeared 18–20 DAA (Fig. 1*A*) when P_i made up no more than 0.035% of the dry weight of dehulled caryopses and 10–15% of the total phosphorus present (Fig. 3; Tables 1 and 3). Caryopses 45 DAA were effectively mature under our conditions, and, at most, 4% of the total phosphorus present was P_i (Table 3 and Fig. 3*B*). The values for secondary caryopses followed the trends found for primary caryopses. At early developmental stages secondary caryopses on the spikelet had higher P_i levels (μg of P_i/g dry weight) than the corresponding primary caryopses, but by maturity at 45 DAA the secondary caryopses exhibited lower P_i levels than the corresponding primary caryopses.

Throughout the period of seed development the combined levels of organic and inorganic phosphorus remained between 4.5 and 5.5 mg of phosphorus/g dry weight, or about 0.5% of caryopsis dry weight. The proportion of phosphorus present in the form of organic phosphorus, especially phytate, increased steadily at the expense of P_i (Tables 1 and 3; Figs. 3, *C* and *D*, and 4). When immature (nondormant) caryopses were detached and incubated for 48 h on water the levels of P_i dropped appreciably. Total phosphorus values for imbibed and nonimbibed caryopses (Tables 2 and 3) indicated that the imbibed caryopses did not lose significant amounts of phosphorus due to leaching. Mature dormant caryopses 45 DAA incubated in a similar way showed no significant change in P_i level, nor did total levels of phosphorus

Table 1. Inorganic phosphorus (P_i) and phytate phosphorus (PA-P) as percentage of total P in developing wild oat caryopses (trial 2).

Estimated days after anthesis	Panicle whorl harvested[a]	Caryopsis dry weight (mg)	P_i	PA-P
Harvest 1: milk stage of upper whorl				
14	Upper			
	P	7.5	26.9	41.5
	S	3.9	33.5	39.8
10	Middle			
	P	3.2	43.3	27.3
	S	1.7	53.0	23.9
6	Lower			
	P	2.6	44.6	37.4
	S	1.5	48.1	40.2
Harvest 2: soft dough stage of upper whorl				
20	Upper			
	P	12.9	10.0	59.8
	S	7.3	14.8	48.5
16	Middle			
	P	6.3	24.2	35.1
	S	2.2	33.8	38.9
12	Lower			
	P	4.1	40.1	40.8
	S	1.8	44.7	45.6
Harvest 3: hard dough stage of upper whorl				
30	Upper			
	P	19.0	5.70	62.3
	S	12.3	4.32	56.6
26	Middle			
	P	14.7	9.76	60.7
	S	8.4	8.77	23.9
22	Lower			
	P	11.8	10.9	57.4
	S	6.3	13.5	51.8
Harvest 4: maturity				
45	Upper			
	P	20.1	3.38	69.7
	S	13.1	2.74	69.4
41	Middle			
	P	18.4	3.51	68.0
	S	11.0	2.04	68.0
37	Lower			
	P	18.0	3.41	65.6
	S	11.0	2.59	71.0

[a] P, primary caryopsis; S, secondary caryopsis.

or phytate show any marked change during the incubation period.

Discussion

A significant feature of the work described lies in the fact that the determinations of caryopsis mass, fresh and dry weights, phosphorus content, plus the seed incubation studies to establish the extent of primary dormancy, were carried out on the caryopses of known growth stage taken from plants of a single seed lot grown under uniform conditions. Comparisons of the type we attempt here are vulnerable to competition effects between seeds from different parts of the plant, even when the seeds have developed over corresponding periods of time (Fig. 3). Thus, caryopses developing on the upper whorl of a panicle accumulated biomass and phosphorus more effectively at a given chronological age than did caryopses of equivalent DAA located in lower panicle whorls (Fig. 3). The differences were considerable during the log phase of growth but diminished as the caryopses approached maturity. Terminal caryopses harvested at 30 DAA from the upper whorl of a panicle had a biomass and total phosphorus equal to or greater than the values determined for caryopses 38 DAA, which had been detached from the lowest whorl of a panicle at a time when the upper terminal caryopses were 45 DAA. These observations suggested that both caryopsis biomass and time from anthesis were related to the dormancy status and phosphorus levels of developing seeds and emphasized the importance of using caryopses from the same part of the panicle for any critical experiments on wild oat seed dormancy. Sufficient material was accumulated

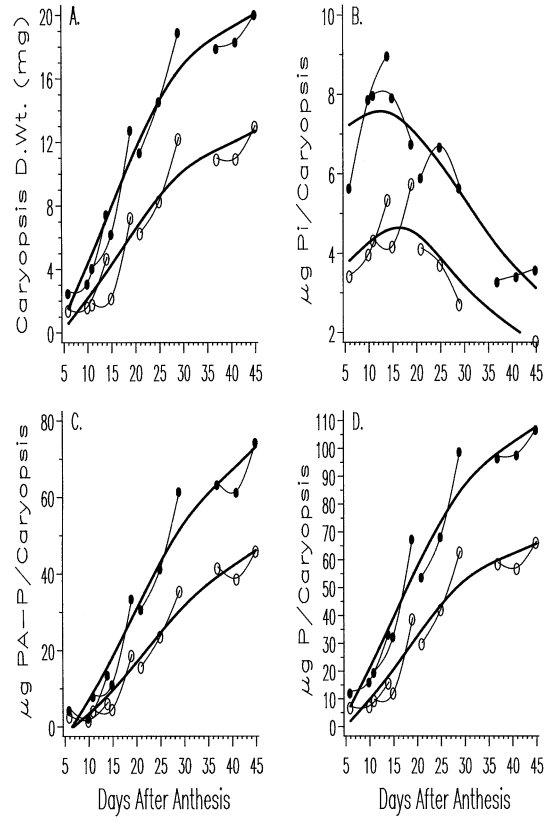

Fig. 3. Caryopsis dry weight (*A*), levels of P_i (*B*), PA-P (*C*), and total accumulation of P (*D*) in primary (●) or in secondary (○) wild oat caryopses at successive stages of maturity. Caryopses at different stages of maturity from the same panicle are connected. A line of best fit is drawn for primary and secondary caryopses.

at each development stage to assess the levels of P_i ions, phytate phosphorus, water content, and some interactions of these factors with the development of primary dormancy in the entire caryopsis.

Establishment of Dormancy during Caryopsis Development in Relation to Water Content

The low germination in caryopses less than 7 DAA was presumed to be due to embryo immaturity. The fact that piercing and dehulling greatly enhanced germination of caryopses at 7 DAA (Fig. 1, *A* and *B*) suggested that such procedures resulted in the loss of inhibiting substances in and around the caryopsis since water was unlikely to be a limiting factor at this stage. The embryos of caryopses detached 9 DAA were well differentiated (Raju 1990), and primary caryopses dehulled and pierced at this stage germinated well on water. The poorer germination of companion secondary caryopses (Fig. 1*B*) was understandable. The primary flower normally opened a day or so before the flower of the accompanying secondary caryopsis. A secondary caryopsis from a location that was assigned a provisional maturity level of 7 DAA might actually be only 5 DAA. The typical secondary caryopsis accumulated less biomass than did the primary caryopsis in the same spikelet, so dormancy was imposed more quickly (Fig. 1*B*). About 18–20 DAA a reduced germination response to dehulling and piercing appeared in the caryopsis, at a time when the water content of the immature caryopsis made up 50–55% of fresh weight or 100–120% of dry weight (Fig. 2, *A* and *B*). These caryopsis data agree with our earlier work (McIntyre and Hsiao 1985) reporting embryo water content values declining to 120% of dry weight by 18 DAA. We suggested at that time that an embryo water content of 120% of dry weight was a critical level that must be exceeded before embryo growth resumed. At 18–20 DAA the embryo was morphologically mature, and membranes about it appeared to be essentially complete at the time seed desiccation and dormancy induction began (Raju 1990). The water content (% dry weight) began to decline and over the next 20–25 days reached levels characteristic of the mature seed (Fig. 2, *A* and *B*). The ability of the maturing seed to germinate upon imbibition decreased over the same period. The initial rate of water uptake by the embryo in the mature caryopsis was inversely related to the depth of dormancy (Raju et al. 1988). Piercing increased the rate of water uptake. Piercing and imbibition studies on mature dormant seeds indicated that the start of germination was accompanied by a similar uptake of P_i as was found in precocious germination of young developing seeds. Breaching the integrity of the membranes about the endosperm affected both the phosphorus balance and the dormancy status of the caryopsis.

Table 2. Effect of imbibition[a] on P_i content of wild oat caryopses at immature and late stages of development (μg P/g dry weight).

Panicle position	25 days[b]		45 days[b]	
	Dry seed	Imbibed	Dry seed	Imbibed
Upper whorl				
Primary	517 ± 35[c]	221 ± 16	172 ± 11	201 ± 3
Secondary	603 ± 35	209 ± 11	147 ± 7	139 ± 13
Middle whorls				
Primary	753 ± 12	324 ± 33	170 ± 11	152 ± 14
Secondary	869 ± 27	321 ± 4	157 ± 2	139 ± 11
Lower whorls				
Primary	979 ± 57	406 ± 23	237 ± 17	197 ± 10
Secondary	1,320 ± 77	487 ± 28	165 ± 18	144 ± 6

[a] Caryopses imbibed 52 h; dehulled at 24 h. Sample size of 50 caryopses for each treatment.
[b] Days after anthesis of terminal floret.
[c] Values are means ± S.E. of triplicate analyses on two treatments.

Establishment of Dormancy during Caryopsis Development in Relation to Phosphorus

Phosphorus comprised approximately 5,000 μg of phosphorus/g dry weight during all stages of wild oat caryopse development. The initial high level of P_i in the immature caryopse (Figs. 3*B* and 4; Table 1) was converted to organic phosphate (largely phytate) as development progressed. A typical primary caryopsis 6 DAA contained 5.5 μg of P_i or 15 μg of phosphate ion and 6,000 μg of water (Figs. 2*B* and 3*C*). If uniform solution occurred, this was equivalent to a phosphate ion concentration of about 25 mM, which could have had a significant nutritional and osmotic effect. Such a proposal is not new. The accumulation of nitrate in the embryo of dormant caryopses was hypothesized (McIntyre et al. 1996) to increase water uptake and break primary dormancy in *Avena fatua.* Incubation in certain exogenous inorganic nitrogen salts hindered the development of skotodormancy in *Lactuca sativa* seeds (Hsiao and Quick, in press). Incubating intact *A. fatua* caryopses in phosphate solution did not appear to affect either primary or secondary dormancy (unpublished work), suggesting that seed membranes restricted the movement of phosphate ions more than was the case with nitrogen compounds. The embryo and endosperm of the developing caryopsis are known to retain some P_i (Fulchur 1986, Lolas et al. 1976). Changes in the level of P_i in the embryo from 18 DAA onward were not established in our study. We have already suggested that an increase of P_i levels in the entire caryopsis could prompt continued or resumed growth of the embryo (Quick and Hsiao 1984). Some germination resulted when immature caryopses 6 DAA were dehulled and pierced. Analyses on the limited incubation samples available suggested that total phosphorus values were unaffected, but P_i levels (dry weight

Table 3. Total phosphorus (P_t), inorganic phosphorus (P_i), and phytate phosphorus (PA-P) in wild oat caryopses during development.[a]

Caryopsis location	Caryopsis dry weight (mg)		P_t[b]		PA-P[b]		P_i[b]	
	Dry	Imbibed	Dry	Imbibed	Dry	Imbibed	Dry	Imbibed
25 DAA: terminal inflorescence								
Upper whorl								
Primary	16.6	17.0	78.0	86.4	40.8	43.7	8.02	3.49
Secondary	9.4	10.4	44.6	54.2	27.5	34.0	5.67	2.07
Middle whorls								
Primary	11.3	12.0	57.3	68.4	31.1	40.1	8.51	3.89
Secondary	6.6	6.7	33.1	38.4	17.1	25.5	5.74	2.15
Lower whorls								
Primary	10.4	10.4	53.9	58.6	29.0	33.7	10.18	4.22
Secondary	5.2	5.4	25.9	28.8	11.5	18.3	6.86	2.68
45 DAA: terminal inflorescence								
Upper whorl								
Primary	17.3	17.3	99.3	93.6	65.4	61.5	3.07	3.80
Secondary	11.0	10.8	60.8	57.8	44.1	38.5	1.70	1.49
Middle whorls								
Primary	17.0	16.5	88.4	88.3	61.7	61.8	3.10	2.82
Secondary	10.5	9.8	57.8	54.3	39.2	39.3	1.68	1.42
Lower whorls								
Primary	17.7	17.1	94.2	95.1	62.5	60.0	3.75	3.67
Secondary	10.6	10.2	59.0	58.7	40.1	40.3	1.71	1.49

[a] Values are means of triplicate replications (S.E. within 10%).
[b] Phosphorus (μg/g dry weight) present in each caryopsis as P_t, PA-P, and P_i.

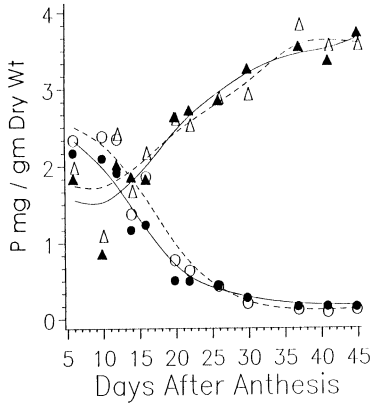

Fig. 4. Relationship between P_i (○) and PA-P (△) during the maturation of primary (empty symbols), and secondary (solid symbols) wild oat caryopses.

basis) were reduced greatly (Table 2). There was no appreciable leaching of P_i into the incubation medium, suggesting that, even at that time, membranes were complete and that the P_i present was converted to organic phosphates utilized in events leading to germination (Jain et al. 1983).

In addition to exerting some osmotic effects, it has been suggested that high levels of P_i inhibit synthesis of phytase in the scutellum (Biswas et al. 1982). Low levels of phytase might be of advantage in those stages of seed development when phytate reserves are being accumulated. Also, the high levels of P_i (μg of phosphorus/g dry weight) present during the initial time of seed formation should ensure no diversion to starch formation until embryo development is well under way (Nakamura and Kawaguchi 1992).

Interactions between Water Content and Phosphorus Content

The rapid decline in relative amounts of P_i in maturing caryopses with the accumulation of osmotically inactive starch and phytate (Fig. 4) is associated with the establishment of dormancy, whether as a cause or an effect. The events leading to germination occurred at times when both P_i and water content were abundant (Figs. 1, 2*B*, and 3*B*). Imbibition studies (Tables 2 and 3) suggested that at 16–17 DAA (lower whorl) and 21 DAA (middle whorl) the P_i pool was depleted rapidly during the first 2 days of imbibition and germination. Such a reduction in P_i was true even of very immature caryopses if they were pierced. The decline corresponded to results already established with mature nondormant caryopses (Hsiao et al. 1984). A similar decline in P_i was not found when dormant seeds were incubated unless they were first pierced and treated with GA_3. Afterripening dor-

mant seeds at room temperature restored their capacity for germination. The same process restored the P_i level within the caryopses (Quick and Hsiao 1984).

Uptake of water in developing barley grains leads to endosperm acidification and related metabolic changes (MacNicol and Jacobson 1992) which may influence the production or activation of a variety of phosphorylases within the endosperm (Nakamura and Kawaguchi 1992). Increase in water content (McIntyre et al. 1996, McIntyre and Hsiao 1985) and in P_i accumulating within endosperm or embryo might influence enzyme activation or inhibition (Saluja et al. 1987, Nakamura and Kawaguchi 1992, Ueki and Sato 1977) and a resumption of embryo differentiation. The low levels of P_i found in dormant, mature caryopses may be a device to maintain dormancy, since a number of plant enzymes require phosphorylation for activation or deactivation (Saluja et al. 1987). A possible role for the P_i that accumulates during afterripening would be to spark the ATP pump (Perl 1986) so that enzymes associated with continued embryo development might be synthesized or activated. Certain of these could utilize the abundant P_i released when phytases begin to degrade the phytate reserves in the germinating caryopsis. The ability of P_i at 50 mM to mimic GA_3 activity (Saluja et al. 1987) may provide another mechanism whereby P_i influences the dormancy level. Foley et al. (1992, 1993) suggested that GA_3 promoted the synthesis or the activation of enzymes involved in embryo or endosperm carbohydrate metabolism, thus providing sugar for breaking dormancy. Although other explanations may be advanced for the correspondence between P_i levels and dormancy levels, the ones we advance have the advantage of fitting the observed fluxes of P_i during the developmental and germination stages of the wild oat caryopsis.

References

Anonymous (1965) Official methods of analysis, 10th ed, Sec 6.064. Association of Official Agriculture Chemists, Washington DC

Biswas BB, Gosh B, Majumbar AL (1982) Myo-inositol polyphosphates and their role in cellular metabolism. In: Roodyn DB (ed) Subcellular biochemistry, vol. 10. Plenum Press, New York, pp 237–280

Biswas TK, Cundiff C (1991) Multiple forms of acid phosphatase in germinating seeds of *Vignia sinensis*. Phytochemistry 30:2119–2125

Budde RJA, Chollet R (1988) Regulation of enzyme activity in plants by reversible phosphorylation. Physiol Plant 72:435–439

Duff SMG, Sarath G, Plaxton WC (1994) The role of acid phosphatases in plant phosphorylation metabolism. Physiol Plant 90:791–800

Foley ME, Bancal M, Nichols MB (1992) Carbohydrate status in dormant and afterripened wild oat embryos. Physiol Plant 85:461–466

Foley ME, Nichols MB, Meyers SP (1993) Carbohydrate concentration and interactions in afterripening-responsive dormant *Avena fatua* caryopses induced to germinate by gibberellic acid. Seed Sci Res 3:271–278

Fulchur RG (1986) Morphological and chemical organization of the oat kernel. In: Oats: Chemistry and technology. American Association of Cereal Chemists, St Paul, MN, pp 47–74

Hoagland DR, Arnon DI (1950) The water culture method for growing plants without soil. Calif Agric Exp Stn Circ No. 347, pp 1–32 (Rev)

Hsiao AI, McIntyre GI, Hanes JA (1983) Seed dormancy in *Avena fatua*. I. Induction of germination by mechanical injury. Bot Gaz 144:217–222

Hsiao AI, Quick WA (1996) The roles of inorganic nitrogen salts in maintaining phytochrome- and gibberellin A_3-mediated germination control in skotodormant lettuce seeds. J Plant Growth Reg, in press

Hsiao AI, Quick WA, Jain JC (1984) Phosphorus containing compounds at comparable germination stages of caryopses of *Avena* species. J Exp Bot 35:617–625

Jain JC, Quick WA, Hsiao AI (1982) Studies of acid-soluble phosphorus compounds in genetically pure lines of *Avena fatua* with different dormancy characteristics. Can J Bot 60:2099–2104

Jain JC, Quick WA, Hsiao AI (1983) ATP synthesis during water imbibition in caryopses of genetically dormant and non-dormant lines of wild oat (*Avena fatua* L.). J Exp Bot 34:381–387

Lolas GM, Palamidis N, Markakis P (1976) The phytic acid-total phosphorus relationship in barley, oats, soybean, and wheat. Cereal Chem 53:867–871

MacNicol PK, Jacobson JV (1992) Endosperm acidification and related metabolic changes in the developing barley grain. Plant Physiol 98:1098–1104

McIntyre GI, Cessna AJ, Hsiao AI (1996) Seed dormancy in *Avena fatua*: Interacting effects of nitrate, water, and seed coat injury. Physiol Plant 97:291–302

McIntyre GI, Hsiao AI (1985) Seed dormancy in *Avena fatua*. II. Evidence of embryo water content as a limiting factor. Bot Gaz 146:347–352

Morris PC, Jewer PC, Bowles DJ (1991) Changes in water relations and endosperm abscissic acid content of wheat and barley grains and embryo during development. Plant Cell Environ 14: 443–446

Nakamura Y, Kawaguchi K (1992) Multiple forms of ADP glucose pyrophosphorylase of rice endosperm. Physiol Plant 84:336–342

Naylor JM (1983) Studies on the genetic control of some physiological processes in seeds. Can J Bot 57:3561–3567

Park HC, Van Etten RL (1986) Purification and characterization of homogeneous sunflower seed acid phosphatase. Phytochemistry 25:351–357

Perl M (1986) ATP synthesis and utilization in the early stages of seed germination in relation to seed dormancy and quality. Physiol Plant 66:177–182

Quick WA, Hsiao AI (1984) Changes in inorganic phosphate and seed germinability during afterripening of wild oats. Can J Bot 62: 2469–2471

Quick WA, Hsiao AI, Jain JC (1983–1983) Endogenous inorganic phosphate in relation to seed dormancy and germination of wild oats. Plant Sci Lett 28:129–35

Raju MVS (1990) Wild oat inflorescence and seed: Anatomy, development and morphology. Canadian Plains Research Center, University of Regina, pp 41–48

Raju MVS, Hsiao AI, McIntyre GI (1986) Seed dormancy in *Avena fatua*. III. The effect of mechanical injury on the growth and development of the root and scutellum. Bot Gaz 147:443–452

Raju MVS, Hsiao AI, McIntyre GI (1988) Seed dormancy in *Avena fatua*. IV. Further observations on the effect of mechanical injury on water uptake and germination in different pure lines. Bot Gaz 149:419–426

Richardson SG (1979) Factors influencing the development of dormancy in wild oat seeds. Can J Plant Sci 59:777–784

Saluja D, Berry M, Sachar RC (1987) Inorganic phosphate mimics the specific action of gibberellic acid in regulating the activity of monophenolase in embryo-less half seeds of wheat. Phytochemistry 26:611–614

SAS Institute Inc. (1985) SAS/GRAPH User's Guide, Version 5. SAS Institute Inc., Cary, NC, pp 1–596

Simpson GM (1990) Seed dormancy in grasses. Cambridge University Press, Cambridge, UK

Ueki K, Sato S (1977) Regulation of phosphatase synthesis by orthophosphate in cultured tobacco cells. Plant Cell Physiol 18: 1253–1263

Williams SG (1970) The role of phytic acid in the wheat grain. Plant Physiol 45:376–381