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Priming Duration Influences Anatomy and Germination Responses of Parsley Mericarps

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Abstract. Germination studies indicated that increasing priming duration (–1.0 MPa at 20 °C for 7, 14, or 21 days) increased 'Moss Curled' parsley [*Petroselinum crispum* (Mill.) Nyman ex A.W. Hill] germination rate quadratically and seed moisture content linearly. A histological and anatomical study was conducted to identify and/or quantify principle mericarp organ or tissue volume changes influenced by priming duration. Embryo volume increased as priming duration increased from 7 to 21 days (0.014 to 0.034 mm^3), and this was due more to radicle (0.007 to 0.022 mm^3) than to cotyledon (0.006 to 0.011 mm^3) growth. Concomitant with increased embryo volume was increased volume of the depleted layer (space formation, surrounding the embryo), from 0.038 after 7 days to 0.071 mm^3 after 21 days, and increased hydrolysis of central endosperm (a thick-walled endosperm type). In nonprimed mericarps, central endosperm cells constituted 97% of the endosperm volume. The remaining 3% was comprised of 1% depleted layer and 2% distal endosperm (small, thin-walled, and irregularly shaped endosperm cells). During 7 or 21 days of priming, ≈10% or 40%, respectively, of central endosperm cells were hydrolyzed centrifugally around the embryo with a corresponding decrease in volume of central endosperm with thick cell walls. In addition, distal endosperm cells adjacent to the depleted layer, containing reserve materials, were digested of contents following 21 days priming, and sometimes, following 7 days priming. A long priming duration resulted in degradation of pericarp tissues, as indicated visually and by a decline in pericarp volume. We hypothesize that priming duration of parsley primarily influences radicle growth and centrifugal digestion and utilization of central and distal endosperm, resulting in a larger depleted layer required for embryo volume increases. Secondary events influenced by priming duration include cotyledon growth and degradation of pericarp tissues.

Seed priming is their exposure to sufficiently low water potentials to permit hydration but prevent radicle protrusion (see review by Pill, 1995). Priming of parsley mericarps (–1.2 MPa for 3 weeks at 15 °C) gave greater, earlier and more synchronous emergence (Ely and Heydecker, 1981). Pill (1986) noted that this same priming treatment gave earlier emergence and greater seedling shoot fresh weights but had no effect on emergence percentage of parsley. Akers et al. (1987), likewise, noted that priming (–0.5 MPa for 3 d at 25 °C, then –0.8 MPa for 1.5 d) speeded germination but had no effect on emergence synchrony or percentage. Embryo growth during priming (Dawidowicz-Grzegorzewska and Maguire, 1993; Gray et al., 1990; van der Toorn, 1989), and loosening of endosperm that is restrictive to embryo growth (Argerich and Bradford, 1989; Dahal et al., 1990; Guedes et al., 1981; Liptay and Zariffa, 1993; van der Toorn, 1989) were associated with increased germination rate of primed seed.

Austin et al. (1969) determined that carrot (*Daucus carota* L.) embryo length and volume increased after successive short duration water hydration treatments. Embryo volume of carrot (Gray et al., 1990) and parsley (Olszewski et al., 2004), and celery (*Apium graveolens* L.) embryo length (van der Toorn, 1989) increased as a result of priming. Embryo length increased with longer seed priming durations of carrot (Dawidowicz-Grzegorzewska and Maguire, 1993) or celery (van der Toorn, 1989).

Seed priming of lettuce (*Lactuca sativa* L.; Guedes et al., 1981) or tomato (*Lycopersicon esculentum* Mill.; Dahal et al., 1990) resulted in progressive loosening of endosperm tissue. Priming caused endosperm degradation at the distal end of carrot (Dawidowicz-Grzegorzewska, 1997) and celery (van der Toorn, 1989) mericarps. In response to priming of tomato seeds, a cavity formed around the cotyledons, and both seed volume and endosperm weakening increased (Argerich and Bradford, 1989). Liptay and Zariffa (1993) noted that priming of tomato seeds increased radicle growth and endosperm degradation. In earlier work we noted that increased germination percentage, rate, and synchrony of primed parsley mericarps (–1.0 MPa for 7 d at 20 °C) was associated with a doubling of radicle and cotyledon volumes and greater endosperm depletion adjacent to the embryo (Olszewski et al., 2004). Extending the priming duration from 4 to 7 d further increased the germination rate of parsley mericarps (Pill and Killian, 2000). The objective of this study was to identify and quantify anatomical changes influenced by priming duration of parsley mericarps, and relate these changes to germination performance.

Materials and Methods

Priming and germination. Parsley 'Moss Curled' mericarps (single-seeded dispersal unit of the schizocarp) and schizocarpic fruits were purchased as a single seed lot (Carolina Seeds, Boone, N.C.). Mericarps were separated from the schizocarps prior to seed testing and single mericarps were used for experiments within 6 months of purchase. Mericarps were primed in 125 × 80 × 20-mm transparent polystyrene boxes containing two layers of germination blotters (germination blotter No. 385; Seedburo, Chicago) and moistened with 15 mL polyethylene gylcol (PEG 6000) at 284 g•L^{-1}, equivalent to a nominal water potential of –1.0 MPa (Michel and Kaufmann, 1973). Priming was conducted in darkness at 20 °C for 0 (nonprimed), 7, 14, or 21 d. Each box

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contained ≈1 g (≈500 mericarps) mericarps spread as a single layer. To assure constant water potential, solutions were changed every 24 to 48 h during priming. During each change, mericarps were vacuum-surface dried before transferring to new blotters and PEG solution. After priming, mericarps were triple-rinsed in deionized water to remove PEG, and then dried at 21 °C and 45% relative humidity (RH) with air-flow for 7 d to seed moisture between 9.5% and 10.5%. Seed moisture, expressed on a fresh weight basis, was determined on three replicates of 0.2-g mericarps after oven-drying at 130 °C for 1 h (International Seed Testing Assn., 1985).

The germination assay was conducted in darkness at constant 20 °C. Nonprimed or primed mericarps were distributed onto double thickness germination blotters (germination blotter No. 385) saturated with 15 mL deionized water contained in 125 × 80 × 20-mm transparent polystyrene boxes. Each box (treatment) contained 50 mericarps, with four replications arranged in a completely randomized design. Germination (mericarps with visible radicles) was counted daily and germinated seeds removed from the box. From these counts, the angular transformation (arcsin of the square root) of final germination percentage (FGP) and days to 50% FGP (G_{50}, an inverse measure of germination rate) were calculated and subjected to analysis of variance.

Mericarp anatomy. A histological protocol similar to that of Jensen (1962) was used. Eight nonprimed mericarps and eight 7-d- or 21-d-primed mericarps were soaked in 10% buffered formalin phosphate for 2.5 weeks. To aid chemical infiltration, mericarps were cut transversely and centrally with a razor blade. Dehydration under vacuum used a 70% to 100% ethanol series followed by xylene infiltration, also under vacuum. Infiltration with paraffin was under vacuum for 8 to 12 d. Transverse sections were cut with an M1R rotary microtome (Shandon, Pittsburgh) at a setting of 6 μm; however, actual section thickness was estimated to be 7.1 μm using the "fold-method" (Bozzola and Russell, 1992). Sections were deparaffinized, stained with 0.5% safranin followed by 0.5% fast green, and permanently mounted.

Mericarp organ or tissue lengths were determined by multiplying section thickness by the number of transverse sections included in a given organ or tissue. Organ or tissue area was estimated on every fifth serial section by tracing its outline projected through a drawing tube attached to a Wild M20 microscope (Martin Microscope Co., Easley, S.C.), followed by referencing to a 0.25-mm^2 standard determined using a cut and weigh method (Bozzola and Russell, 1992). Each mericarp organ or tissue volume was calculated using the equation $V_o = (\Sigma a_e)t$, where V_o = mericarp organ or tissue volume; a_e = tissue area; and t = paraffin section thickness.

Results and Discussion

Priming and germination. Priming had no effect on germination percentage (mean = 86%) but decreased the G_{50} (Table 1). Increased germination rate is a common response to priming of parsley (Akers et al, 1987; Olszewski et al, 2004; Pill and Kilian, 2000). Increasing duration of priming resulted in a quadratic decrease in G_{50}, with most of the decrease occurring between 7 and 14 d. Pill and Kilian (2000) had noted decreased G_{50} as parsley priming increased from 4 to 7 d. A linear increase in seed moisture contents (41.0%, 42.9%, and 43.6% for 7, 14, and 21 d priming) was associated with decreasing G_{50} as priming duration increased. Brocklehurst and Dearman (1984) noted similar moisture contents of primed (–1.5 MPa for 2 weeks at 15 °C) mericarps of carrot (39.2%), celery (36.8%), leek (*Allium porrum* L., 46.9%), and onion (*A. cepa* L., 41.2%). Increased seed moisture content with priming duration may be due to osmotic adjustments necessary for effective priming (Bradford, 1986).

Table 1. Final germination percentage (FGP), days to 50% FGP (G_{50}), and mericarp moisture of nonprimed and primed (7, 14, or 21 d at 20 °C and –1.0 MPa) mericarps of 'Moss Curled' parsley.

Mericarp treatment	FGP[z]	G_{50} (d)	Mericarp moisture (% fresh wt)
Nonprimed	88% (70°)	7.6	7.5
Primed, 7 d	83% (66°)	4.5	41.0
Primed, 14 d	86% (69°)	2.7	42.9
Primed, 21 d	87% (69°)	2.5	43.6
$LSD_{0.05}$[y]	(8°)	(0.3)	1.2
Significance			
Mericarp treatment	(NS)	***	***
Priming, linear	(NS)	***	***
Priming, quadratic	(NS)	**	NS

[z]Angular transformation (arcsin square root).
[y]Least significant difference, $P \leq 0.05$.
NS, **, ***Nonsignificant or significant at $P \leq 0.001$ or 0.01, respectively.

Mericarp anatomy. Radicles were the primary source of embryo growth during priming, although cotyledon growth also occurred (Fig. 1A–C and Table 2). A large increase in radicle diameter was observed as priming duration increased (Fig. 1D–F). For nonprimed, 7-d-primed, and 21-d-primed mericarps, respective radicle volumes were 0.005, 0.007, and 0.022 mm^3, while respective cotyledon volumes were 0.004, 0.006, and 0.011 mm^3. An increase in priming duration (0 to 8 d) resulted in increased embryo length of carrot (Dawidowicz-Grzegorzewska and Maguire, 1993). Higher priming osmotic potential and longer priming duration resulted in increased celery embryo length (van der Toorn, 1989). In earlier work (Olszewski et al., 2004), we established that parsley embryo volume, but not length, increased with 7 d priming. We believe that this is the first report showing a direct relationship between priming duration and radicle and cotyledon volumes.

Surrounding the embryo is the depleted layer which is a space containing no endosperm cells or cell remnants (Fig. 1A–F). Primed mericarps had greater depleted layer volume than nonprimed mericarps, and increasing the priming duration increased the depleted layer volume (Table 2). Depleted layer volumes for nonprimed mericarps, 7-d-primed mericarps, and 21-d-primed mericarps were 0.021, 0.038, and 0.071 mm^3, respectively. Argerich and Bradford (1989) hypothesized that free space formation around the embryo was beneficial to germination because it allowed increased water uptake and greater turgor pressure, resulting in weakening of embryo restrictive endosperm tissues. In the present study, mericarp moisture content (Table 1) and depleted layer volume (Table 2) both increased with increased priming duration.

Exocarp and mesocarp tissues (Fig. 1B) of the pericarp were increasingly degraded as priming duration increased to 21 d (Fig. 1C). Pericarp and seed coat tissues contained sclerified cells (identified by intense staining with safranin red) at the distal end of the mericarp, which could provide a barrier to radicle protrusion. Pericarp, as a percentage of mericarp volume, was 46%, 44%, and 26% for nonprimed, 7-d-primed, and 21-d-primed mericarps. Pericarp volumes were 1.469, 1.046, and 0.612 mm^3, respectively, for nonprimed, 7-d-primed, and 21-d-primed mericarps (Table 2). This indicated that 7-d priming did not greatly affect pericarp volume while 21-d priming resulted in considerable loss of tissue.

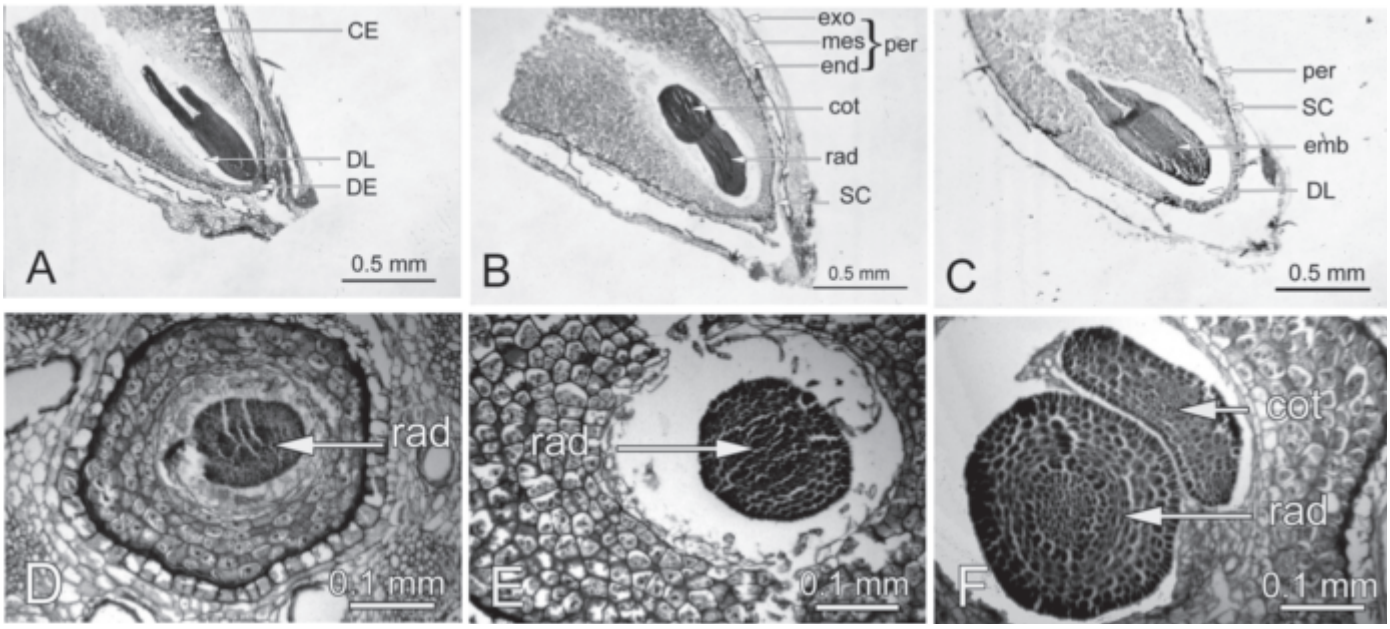

Fig. 1. Parsley embryonic organs, associated mericarp tissues, and space formation of: (**A**) nonprimed mericarp in longitudinal section indicating the three primary regions of the endosperm; (**B**) 7-d-primed mericarp in longitudinal section indicating embryonic organs and associated mericarp tissue; (**C**) 21-d-primed mericarp in longitudinal section showing well-developed embryo and expanded depleted layer as well as a loss of exocarp and mesocarp tissue; (**D**) nonprimed, (**E**) 7-d-primed, and (**F**) 21-d-primed mericarp in transverse section showing relative growth differences of the radicle. The cotyledon is inverted in (F), an unusual occurrence where the cotyledon grows towards the distal end of the mericarp. CE = central endosperm; cot = cotyledon; DE = distal endosperm; DL = depleted layer; emb = embryo; end = endocarp; exo = exocarp; mes = mesocarp; per = pericarp; rad = radicle; SC = seedcoat.

Table 2. Organ or tissue volumes of nonprimed or primed (7 or 21 d at 20 °C and –1.0 MPa) 'Moss Curled' parsley mericarps.

Mericarp organ or tissue	Mericarp treatment		
	Nonprimed	Primed for 7 d	Primed for 21 d
	Organ or tissue volume [mean ± SE (mm³)][z]		
Embryo	0.009 ± 0.002	0.014 ± 0.002	0.034 ± 0.006
Cotyledon	0.004 ± 0.001	0.006 ± 0.001	0.011 ± 0.002
Radicle	0.005 ± 0.001	0.007 ± 0.001	0.022 ± 0.005
Endosperm (total)[y]	1.674 ± 0.056	1.279 ± 0.117	1.665 ± 0.149
Central endosperm	1.629 ± 0.059	1.136 ± 0.104	0.979 ± 0.272
Depleted layer	0.021 ± 0.005	0.038 ± 0.006	0.071 ± 0.011
Pericarp	1.469 ± 0.171	1.046 ± 0.083	0.612 ± 0.127

[z]n = 8.
[y]Total endosperm = depleted layer + central endosperm with thick cell walls + residual endosperm.

Parera et al. (1993) also noted pericarp degradation in primed celery. Parsley germination inhibitors (Kato et al., 1978) occur in seed coverings and can be removed by scarification (Hassell and Kretchmen, 1997). This study is thought to be the first to quantify loss of pericarp and relate it to priming duration.

In nonprimed mericarps, central endosperm comprised 97% of the total endosperm volume; the remaining 1% was depleted layer and 2% was distal endosperm (Table 2). Thick-walled endosperm, a type of endosperm found in monocotyledonous and dicotyledonous seed, usually serves as a carbohydrate reserve for the developing embryo (Werker, 1997) and are characterized by having thick-walled endosperm type with distinct middle lamellae (Fig. 2A). In contrast to central endosperm, distal endosperm cells were small with thinner cell walls (Fig. 2B–C) and occurred at the micropylar region as well as regions flanking the radicle. Following 7- and 21-d priming, respectively, central endosperm with thick cell walls (Fig. 2A) declined to ≈90% and 60% of the total endosperm volume (with 10% and 40% with digested cell walls) while the depleted layer increased to 3% and 4 % of the total endosperm volume (Table 2). Loss of central endosperm was quantified by determining remaining volume of thick-walled endosperm, which comprised 1.629, 1.136, and 0.979 mm^3 in nonprimed, 7-d-primed, and 21-d-primed mericarps, respectively (Table 2). Although length differences for whole mericarps were minimal (average lengths for eight replicates of nonprimed, 7-d-primed, and 21-d-primed mericarps were 2.89 ± 0.13, 2.68 ± 0.08, and 2.82 ± 0.11 mm, respectively), endosperm volume for 7-d-primed mericarps was unexpectedly low. This may have been due to degradation of endosperm during the priming process. Similar volumes for nonprimed and 21-d-primed central endosperm (Table 2) may have been due to cell wall expansion resulting in increased cell size during long-term priming; however, this remains speculative as no detailed cell size measurements were taken. Also, weight differences between mericarps from different umbel positions (Thomas, 1996) may result in volume variation in a commercially purchased mericarp lot. The sequence of endosperm cell degradation is related to the location of digestive enzymes present within the seed (Werker, 1997). Celery endosperm degradation may originate from embryo-derived gibberellic acid that signals the endosperm to produce autolytic enzymes resulting in a centripetal pattern of endosperm degradation (Jacobsen and Pressman, 1979). Dawidowicz-Grzegorzewska (1997) and Dawidowicz-Grzegorzewska and Maguire (1993) observed that carrot endosperm changes during priming were limited to regions near the radicle. The sequence of central endosperm mobilization was centrifugal (radial progression of endosperm digestion), with cells nearest the embryo digested first. Cell walls of primed central endosperm were depleted to the extent that only inner walls of the central endosperm cell wall remained and, consequently, intercellular spaces formed in place of digested endosperm wall (Fig. 2D). The inner walls of

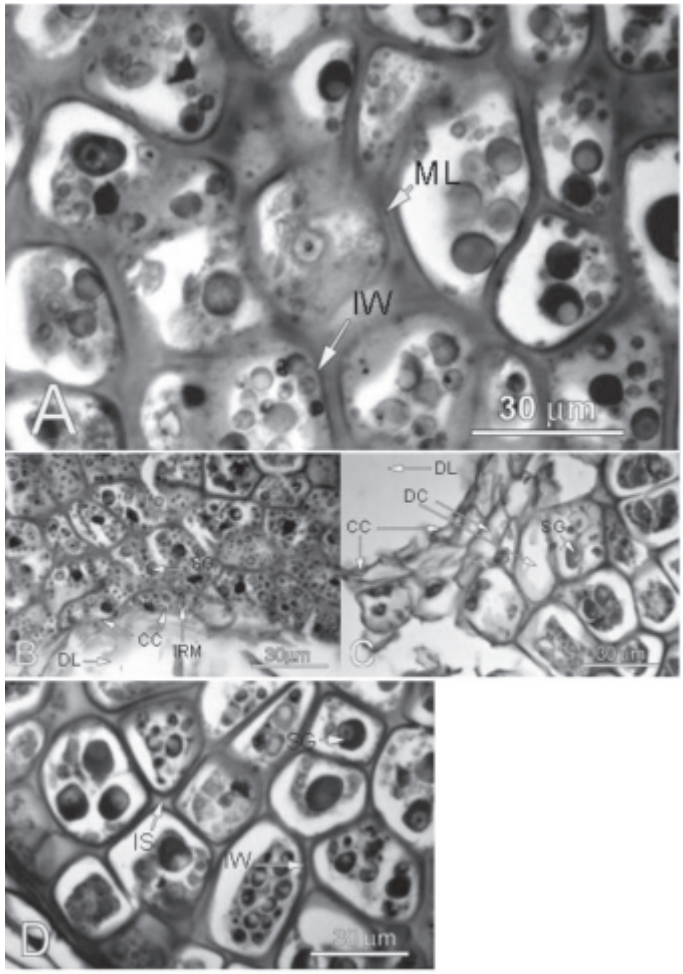

Fig. 2. Views of parsley endosperm. (**A**) nonprimed central endosperm cells were identified by large cell size, thick cell wall, and distinct middle lamellae, the nacreous nature (smeared appearance) is due to the thick primary cell wall; (**B**) nonprimed distal endosperm cells were identified by small cell size, thin cell wall, and irregular shape, the depleted layer is a space formation surrounding the embryo that likely becomes filled with water during hydration and may cause the compressed appearance of adjacent cells; (**C**) 21-d-primed distal endosperm illustrating the centripetal nature of digestion, with the initial digested cells being those nearest to the depleted layer and embryo and expanding in a radial direction; and (**D**) 21-d-primed central endosperm illustrating the results of thick cell wall digestion including complete digestion of materials between inner cell walls and intercellular space formation, starch grains were large in central endosperm but occurred in both distal and central endosperm. CC = compressed cell; DC = digested cell; DL = depleted layer; IRM = intracellular reserve materials; IS = intercellular space; IW = inner wall; ML = middle lamella; SG = starch grain.

adjacent cells came closer together as materials in the endosperm cell wall were depleted (Fig. 2D).

Distal endosperm cells adjacent the depleted layer contained intercellular reserve materials but following 21-d priming, and sometimes 7-d priming, cells were digested of their contents (Figs. 1D–F and 2B–C). Both before and after priming, cells adjacent to the depleted layer were crushed or compressed in appearance (Fig. 2B–C), possibly due to the force exerted by embryo growth and/or the water-filling of the cavity. Since many small seeded species contain no starch (Taylor, 1997) including carrot (Dawidowicz-Grzegorzewska, 1997), and transient amounts in celery (Jacobsen and Pressman, 1979), the presence of starch grains in parsley endosperm (Fig. 2B–D) and embryos (not shown) is surprising; however, the significance of this fact remains unknown. Although starch is often a temporary reserve material in many species (Werker, 1997) it was persistent in parsley (Fig. 2B–D). It is interesting to note that celery endosperm changes are light-dependent (Jacobsen and Pressman, 1979) while parsley endosperm changes occur in darkness.

We theorize that the increased germination rate of parsley mericarps with increasing priming duration could be attributed, in part, to greater radicle development that was dependent on the amount of endosperm storage cells that was mobilized for this purpose. Radicle development involved cell maturation since 24-h-imbibed primed mericarps had increased vacuolization, intercellular space formation and meristematic activity compared to 24-h-imbibed nonprimed mericarps (Olszewski, 2004). Associated with increased germination rate with extended priming, was an increase in depleted layer volume that may have been associated with increased mericarp moisture content, and a decrease in pericarp volume visible as degradation that may have reduced mechanical resistance to radicle penetration or may have eliminated germination inhibitors through a leaching effect.

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