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American Journal of Botany, 71:6 (1984), pp. 795-802. <http://www.jstor.org/stable/pdfplus/2443470.pdf>

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AMERICAN JOURNAL OF Botany

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Source: *American Journal of Botany*, Vol. 71, No. 6 (Jul., 1984), pp. 795-802

Published by: [Botanical Society of America](#)

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VARIATION IN SEED WEIGHT AND ITS EFFECTS ON GERMINATION IN *PASTINACA SATIVA* L. (UMBELLIFERAE)¹

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ABSTRACT

Pastinaca sativa (wild parsnip) produces seeds on the primary, secondary, and tertiary umbels of the flowering stalk. Within plants, variation in seed weight is about twofold. Secondary and tertiary seed weight is 73% and 50% of primary seed weight, respectively. Maximum variation in seed weight between plants is sixfold when tertiary seeds from a small plant are compared to primary seeds from a large plant. Within an umbel order, variation in seed weight between plants is correlated with plant size. Under autumn germinating conditions in the laboratory, final germination of seeds from different umbel orders does not differ but smaller seeds germinate more rapidly than larger seeds. Under spring germination conditions in the laboratory, significantly more primary and secondary seeds germinate than tertiary seeds and the rate of germination is independent of seed weight. Field germination of seeds from different umbel orders produces similar results except that in the spring both secondary and tertiary seed germination is lower than that of primary seeds. These results suggest that with respect to seed germination characteristics small seeds may have a competitive advantage over large seeds in the autumn because they germinate more quickly, but in the spring small seeds are at a disadvantage because they have lower overall germination. Because most germination in the field occurs in the spring, population recruitment from small seeds is likely to be substantially less than that from large seeds.

TRADITIONALLY, seed weight within a plant species is considered to be a remarkably constant characteristic (Salisbury, 1942; Harper, Lovell and Moore, 1970; Harper, 1977; Silvertown, 1981). However, numerous studies have demonstrated that seed weight within a species or even an individual plant can vary greatly (Salisbury, 1942; Black, 1959; Twamley, 1967; Harper et al., 1970; Janzen, 1977; Schaal, 1980; Gross and Soule, 1981; Thompson, 1984). Such variation in seed weight within a species may affect germination and/or seedling characteristics and, thus, population recruitment. Large seeds frequently have greater percent germination or emergence than small seeds and produce larger and more vigorous seedlings which may enhance survivorship (Black, 1956; Harper and Obeid, 1967; Twamley, 1967; Austenson and Walton, 1970; Anderson, 1971; Haskins and Gorz, 1975; Schaal, 1980). Also, seedlings from large seeds may be less susceptible to density stress (Harper and Obeid, 1967; Twamley, 1967). On the other

hand, small seeds may germinate more rapidly than large seeds and thus, gain a competitive advantage (Ross and Harper, 1972; Rabinowitz, 1978; Howell, 1981; Grime et al., 1981). Additionally, small seeds are likely to have greater dispersal capacity than large seeds and may be more effective at colonizing gaps in existing vegetation (Baker, 1972; Rabinowitz, 1978; Silvertown, 1981; Gross and Werner, 1982). They also may be less susceptible to seed predation (Smith, 1974).

In this study variation in seed weight within and between individuals of *Pastinaca sativa* L. (Umbelliferae) and the potential effect this variation has on germination under laboratory and field conditions are investigated. The study was initiated because in large individuals of *P. sativa* (basal stem diameter [BSD] of the flowering stalk > 12 mm) destruction of the primary (first) inflorescence by *Depressaria pastinacella* (Duponchel) (Lepidoptera: Oecophoridae) leads to increased seed set on tertiary inflorescences produced later in the growing season (Hendrix, 1979). Although total seed number does not differ between damaged and undamaged plants, seeds from tertiary inflorescences generally weigh less than the seeds they replace (Hendrix, 1979). Therefore, an analysis of the effects of herbivory on fitness in *P. sativa* must take into account potential differences in germination due to differences in seed weight.

¹ Received for publication 24 February 1983; revision accepted 12 March 1984.

I wish to thank K. Grove, L. McClaffin and M. Smith for assistance with the germination experiments and R. W. Cruden, E. J. Trapp, S. Bookman, and four anonymous reviewers for helpful comments on earlier drafts of this manuscript. This work was supported in part by NSF Grant BSR 82-05534.

The specific questions addressed are: 1) What is the variation in seed weight within and between plants? 2) Does seed size vary with plant size? And 3) Does the rate and/or overall germination of seeds from difference inflorescences (primary, secondary, and tertiary) differ under autumn and spring germination conditions?

MATERIALS AND METHODS—*Natural history of P. sativa*—*Pastinaca sativa* is a facultative biennial common in old fields, roadsides, and woodland edges in North America (Gleason, 1952). After a rosette stage, plants produce an erect, leafy stem terminating in the primary umbel (Thompson and Price, 1977). Lateral shoots terminating in secondary umbels are produced from the leaf axils of the main stem. Secondary shoots give rise to tertiary umbels and, in some cases, quaternary umbels develop on tertiary shoots (Hendrix, 1979). Secondary umbels mature about 10–14 days after the primary umbel and tertiary umbels mature about 10–14 days after secondary umbels. Each hermaphroditic flower produces two one-seeded mericarps commonly referred to as seeds. In Iowa, flowering begins in May and seeds are dispersed from August to October. Seeds germinate in both autumn and spring (Baskin and Baskin, 1979; S. Hendrix, pers. observ.). *Pastinaca sativa* does not reproduce vegetatively (Thompson, 1978).

Variation in seed weight—Mature seeds from each umbel order (primary, secondary, and tertiary, if available) were collected from 16 plants in an old field population in Johnson Co., Iowa (Lucas Twp., Sec. 20). Ten seeds from each umbel order of individual plants were randomly chosen and weighed to the nearest 0.1 mg. Performance curves of mean seed weight vs. number of seeds weighted for ten umbels indicates that a sample of ten seeds gives an estimate of seed weight within plus or minus 5% of estimates based on larger sample sizes (up to 50 seeds). The secondary umbels on two plants died in the flower stage and six plants did not produce tertiary seeds. Comparisons of seed weight were made with Student's *t*-test. The relationship between weight of seeds from different umbel orders and BSD of flowering stalk was determined by product-moment correlations.

Laboratory germination tests—Mature seeds from ten large individuals of *P. sativa* (BSD > 12 mm) were collected in late July 1981 from the same population as seeds used in the analysis of variation in seed weight. Large plants

were chosen for the germination studies because these plants show the increase in tertiary seed set following herbivory on the primary umbel and because only large plants produce sufficient number of seeds for the experimental design used. Ten seeds from each of the three umbel orders of each plant were weighed to the nearest 0.1 mg. The range of seed weights was 2.2 to 6.0 mg; this is nearly the full range of seed weights for plants of all sizes (see results). Preliminary germination tests in both the laboratory and field indicate that germination of secondary and tertiary seeds from damaged and undamaged large plants is statistically identical (Hendrix, unpubl. data). After collection, seeds were allowed to after-ripen in dry storage for 60 days. Freshly matured seeds were not tested because they have poor germination (Baskin and Baskin, 1979).

Prior to the germination tests, some of the after-ripened seeds were subjected to an additional treatment. In this treatment seeds were allowed to imbibe water for 72 hr and were then cold treated in the dark at 5 C for 30 days. This treatment was designed to approximate the cumulative conditions seeds would experience following dispersal in the autumn and subsequent overwintering.

Germination tests of after-ripened and after-ripened and cold treated seeds from each of the three umbel orders of the ten plants were conducted in triplicate. Sample size was 50 seeds per dish. Total sample size for each treatment was 4,500 seeds. Seeds were dusted with a fungicide and placed on two layers of moistened filter paper in 9-cm dishes. Dishes were sealed with Mylar plastic. Water was added every three days. All germination tests were conducted at 25 C/15 C (16:8 hr) with a 16-hr photoperiod. The light sources were cool fluorescent and incandescent light. Light intensity at seed level was c. 3,000 lux. Seed germination was determined at weekly intervals for 17 wk; protrusion of the radicle was the criterion for germination.

Following completion of the seed germination tests, seeds not filled with endosperm or attacked by an unidentified seed chalcid (Hymenoptera: Chalcidae) were removed. About 25% of all seeds were not filled with endosperm and 1% of all seeds were attacked by the chalcid. Seeds falling into these two categories were deleted from the total number of seeds per dish prior to statistical analysis. The remaining ungerminated seeds were tested for viability by staining with tetrazolium chloride (Moore, 1972).

The nested analysis of variance (ANOVA) (Sokal and Rohlf, 1969) was used in all com-

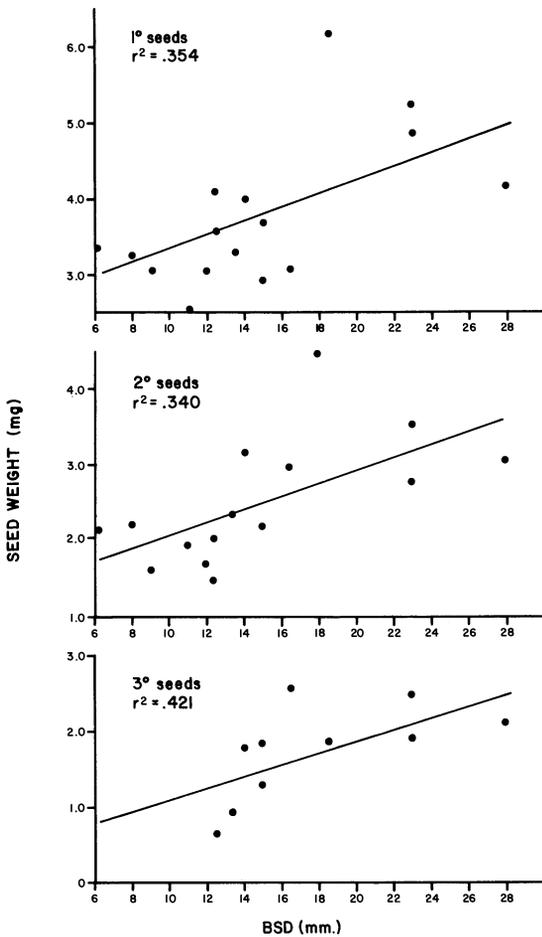


Fig. 1. Relationship between weight of seeds (mg) from primary, secondary, and tertiary umbels and basal stem diameter (BSD) of the flowering stalk. Primary seeds: $y = 0.098X + 2.294$; Secondary seeds: $y = 0.088X + 1.167$; Tertiary seeds: $y = 0.077X + 0.326$.

parisons of percent germination within treatments. An arcsine transformation was performed on percentages prior to all analyses. Means were compared with the Duncan multiple range test. Two-way analysis of variance was used to test for the effects of treatments, individual plants, and interaction of plants and treatments on final germination of seeds from primary, secondary, and tertiary umbels.

Field germination tests—The study site for field germination tests was an early successional field at the Oakdale Campus of the University of Iowa, located about 11 km west of Iowa City, Iowa. The species composition of this field is typical for other locations containing *P. sativa* and the closest natural population

of *P. sativa* is about 1 km away. *Pastinaca* seeds lose their viability within 1–2 yr (Jones and Rosa, 1928; USDA, 1967; Hendrix, unpubl. results) and since no *P. sativa* seedlings were found in the study site for two years prior to the start of the experiment, the potential problem of seedlings emerging from a seed bank can be discounted. In the study area 24 0.5-m × 0.5-m plots were established. Each plot was surrounded by a 0.25-m buffer zone. Plots were hand tilled and leveled prior to the introduction of seeds. This manipulation simulates the frequent occurrence of *P. sativa* on bare ground in natural populations.

Mature seeds were collected in late July from eight large individuals (BSD > 12 mm) of *P. sativa* from the same population used as a source of seeds for the other portions of this study. Plots were randomly assigned to receive seeds from a specific umbel order (primary, secondary, or tertiary) of each plant. In early August 1981, 300 seeds from each umbel order of each plant were hand sown into the plots. A total of 7,200 seeds were sown. Seedling establishment was monitored monthly from September to December 1981 and from May to July 1982. At each monthly period, newly emerged seedlings were individually marked with color coded picks.

RESULTS—Seed weight—Variation in seed weight between plants is positively correlated with plant size (primary seeds, $t_s = 2.78$, $P < 0.02$; secondary and tertiary seeds, $t_s = 2.68$ and 2.42, respectively, $P < 0.05$) (Fig. 1). The larger the plant (as measured by BSD of the flowering stalk), the heavier the seeds produced. Primary seeds weigh from 3–6 mg, secondary seeds weigh from 1.5–4 mg, and tertiary seeds weigh from 1–2.5 mg. Primary seeds from a small plant (BSD = 8 mm) weigh about the same as tertiary seeds from a large plant (BSD = 23 mm). The overall variation in seed weight between plants is about sixfold if tertiary seeds from a small plant are compared with primary seeds from a large plant.

Within plants, primary seeds were significantly heavier than secondary seeds (all t values > 2.30, $P < 0.05$) in 9 of the 10 plants and secondary seeds were significantly heavier than tertiary seeds (all t values > 2.30, $P < 0.05$) in 8 of the 10 plants. Secondary and tertiary seed weight was about 73% and 50% of primary seed weight, respectively, although individual plants show much variation in this characteristic. The range per plant of secondary seed weight relative to primary seed weight was 36.1–97.4%; for tertiary seeds the range was 15.8–83.2%.

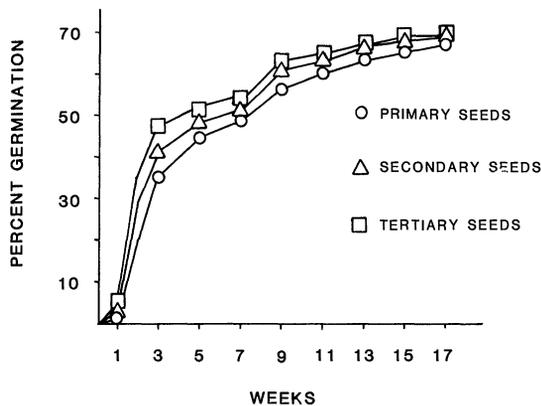


Fig. 2. Percent germination over time (weeks) of seeds from different umbels receiving an after-ripening treatment.

Laboratory germination of seeds—Different treatments resulted in different amounts and patterns of germination. Following the after-ripening treatment (Fig. 2) seeds from all umbels began to germinate after one week but from wk 2–5 the proportion of seeds from tertiary umbels which had germinated was significantly greater than the proportion of seeds from primary umbels which had germinated (Duncan multiple range test following nested ANOVA, all P values < 0.05). Germination of seeds from secondary umbels was intermediate during this time span and was not significantly different from the germination of either primary or tertiary seeds. From wk 6–17 the proportion of seeds germinated from different umbels did not differ. At the termination of the experiment about 68% of the primary seeds had germinated and about 69% of the secondary and tertiary seeds had germinated. About 25% of the ungerminated seeds (7.5% of all seeds) were still viable at the conclusion of the experiment. Different umbel orders did not differ significantly with respect to this characteristic (ANOVA, $F = 0.18$, $P > 0.75$).

Following the after-ripening and cold treatments (Fig. 3), seeds from all umbel orders began to germinate between the first and second week and by wk 5 nearly all seeds that were going to germinate had done so. From wk 3–17 the proportion of tertiary seeds germinated was significantly less than the proportion of primary and secondary seeds which had germinated (Duncan multiple range test following nested ANOVA, all P values < 0.05). At the termination of the experiment about 83% of the primary seeds, 81% of the secondary seeds, and 72% of the tertiary seeds had germinated.

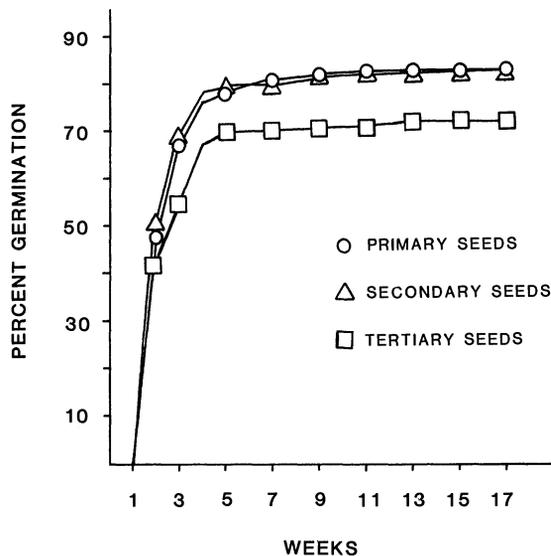


Fig. 3. Percent germination over time (weeks) of seeds from different umbels receiving an after-ripening and cold treatment.

About 30% of the ungerminated seeds (5% of all seeds) were still viable at the conclusion of the experiment. Different umbel categories did not differ with respect to this characteristic (ANOVA, $F = 1.44$, $P > 0.10$).

The number of days needed to attain 50% of final germination differed between treatments (Table 1). After-ripened seeds from all umbels required 26–40 days to reach 50% germination. Secondary and tertiary seeds required significantly fewer days to reach 50% germination than did primary seeds (Duncan multiple range test following nested ANOVA, $P < 0.05$). After-ripened and cold treated seeds required about 15 days to reach 50% germination and seeds from different umbels did not differ significantly (Duncan multiple range test following nested ANOVA, $P > 0.05$).

The two-way analysis of variance of final

TABLE 1. Number of days ($\pm SE$)^a required to attain 50% of final germination and seed wt

Umbel order	Treatment		Seed wt (mg) ^a ($\pm SE$)
	After-ripening only ^b	After-ripening and cold treatment	
1°	39.1 \pm 7.3	15.3 \pm 1.6	5.45 \pm 0.16
2°	28.7 \pm 7.0	14.5 \pm 1.1	4.06 \pm 0.17
3°	26.5 \pm 6.1	15.5 \pm 1.5	2.21 \pm 0.09

^a Mean of means per plant.

^b Primary significantly different from secondary and tertiary ($P < 0.05$).

TABLE 2. Two way ANOVA of final seed germination

Source of variation	df	MS	F ^a
PRIMARY SEEDS			
Treatments	1	0.508	33.59***
Plants	9	0.243	16.07***
Interaction	9	0.112	7.35***
Error	49	0.015	
SECONDARY SEEDS			
Treatments	1	0.234	7.17**
Plants	9	0.256	7.82***
Interaction	9	0.079	2.43*
Error	49	0.033	
TERTIARY SEEDS			
Treatments	1	0.006	0.25 ns
Plants	9	0.167	6.63***
Interaction	9	0.130	5.09***
Error	49	0.026	

^a *** $P < 0.01$; ** $P < 0.025$; * $P < 0.05$; ns, not significant.

germination (Table 2) indicates that for primary and secondary seeds but not tertiary seeds there is significant variation in the proportion of seeds germinated due to treatment with significantly more primary and secondary seeds germinating following the after-ripening and cold treatment (Duncan multiple range test following ANOVA, $P < 0.05$). All umbel categories show significant variation between plants and there is significant plant-treatment interaction.

Field germination tests—In the field, germination of seeds from primary umbels was far greater than germination of seeds from either secondary or tertiary umbels (Fig. 4). Of all seeds which germinated 44%, 27%, and 28% were from primary, secondary, and tertiary umbels, respectively. Absolute germination of seeds from primary, secondary, and tertiary umbels was 17.8%, 10.7%, and 11.4%, respectively.

Germination of seeds occurred mainly in the spring. During autumn about 1.3% of all seeds sown germinated and during the spring about 12.1% of all seeds germinated. Of all seeds germinating during autumn 35%, 20%, and 45% came from primary, secondary, and tertiary umbels, respectively. Overwintering success of seeds germinating in autumn was 53.7%. Of the seeds germinating in the spring, 45%, 29%, and 26% were from primary, secondary, and tertiary umbels, respectively.

DISCUSSION—Variation in seed weight—Between and within plant variation in seed weight

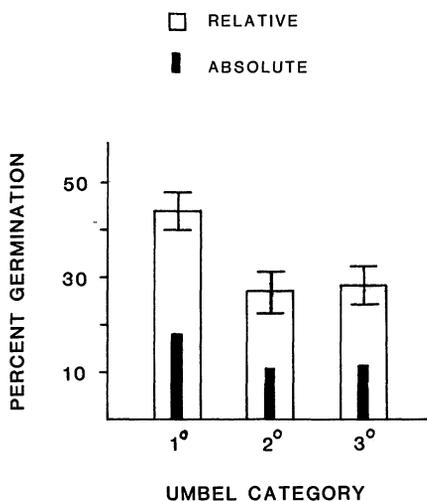


Fig. 4. Percent field germination (\pm SE) of seeds from different umbels.

in *P. sativa* is due to its pattern of growth and development. *Pastinaca sativa* is characteristic of plants which first go through a phase of indeterminate, vegetative growth followed by a determinate phase of reproduction culminating in the death of the plant (Harper et al., 1970). As in *Daucus carota* (Borthwick, Phillips, and Robbins, 1931), *P. sativa* initiates an excess of reproductive structures early in the year of flowering, but not all of these structures actually mature. Both the number of reproductive structures and their size is probably dependent in part on plant size. Hence, seeds from large plants weigh more than seeds from small plants.

Within plants there is competition between inflorescences for available nutrients (Harper et al., 1970). Primary, secondary, and tertiary seeds develop in succession over a 3–4-wk period and the seeds in late developing tertiary umbels are at a disadvantage in competing with early developing inflorescences for nutrients. This pattern of lower seed weight in late developing inflorescences has been noted for both sunflower and barley (Harper et al., 1970).

The variation in seed weight between plants in *P. sativa* falls within the range of seed weights reported for other species. Seed weight varies twofold in *Lotus corniculatus* L. and *Silene alba* (Miller) Krause (Twamley, 1967; Gross and Soule, 1981), fivefold in *Convallaria majalis* L. (Salisbury, 1942), and as much as 17-fold in *Trifolium subterraneum* L. (Black, 1959). Within plants, seed weight may vary 1.25-fold in *Helianthus annuus* L. (Harper et al., 1970) and fivefold in *C. majalis* L. (Salisbury, 1942).

Germination of seeds—The results of both the laboratory and field studies presented here indicate that the seeds of *P. sativa* are capable of germinating in both autumn and spring. However, in the laboratory experiments germination of seeds under autumn conditions was high but in the field autumn germination was less than 10% of total germination. Baskin and Baskin (1979) also found extensive germination of after-ripened seeds under laboratory conditions, but low field germination of seeds (about 4% of total germination) in 1973 in Fayette County, Kentucky. Likewise, Martin (1943) found no autumn germination of *P. sativa* seeds in Ames, Iowa, during the years 1934–36. In contrast to the above results, in some years autumn germination in Iowa may reach levels as high as 20–30% of total germination (Hendrix, pers. observ.).

The variation in autumn germination in the field is likely due to year to year differences in environmental conditions. While year to year variation in autumn temperatures or degree of temperature alteration may play a role in determining the level of germination in the autumn, the amount of rainfall during this time appears to be particularly important. During the years 1934–36, central Iowa was experiencing severe late summer droughts (U.S. Environmental Data Service, 1934–36) and rainfall for Lexington, Kentucky during the latter part of August through September was about 50% of normal (U.S. Environmental Data, National Survey, 1973). In contrast, the high levels of autumn germination in Iowa were in years when rainfall during August and September was greater than normal (C. Johnson, pers. comm.). The hypothesized effect of rainfall on autumn germination may be partially due to the presence of furanocoumarins in the seeds of *P. sativa* (M. Berenbaum, pers. comm.). These secondary chemicals act as seed germination inhibitors and must be leached out before germination can occur (Berenbaum, 1980). Under laboratory conditions, autumn germination of seeds from different umbels did not differ. Under field conditions germination of seeds from different umbels differed greatly, but this may have been due to the small sample size.

The results of the laboratory germination of after-ripened seeds following the simulation of overwintering indicate that this treatment differentially affected germination of seeds from different umbel orders. Both primary and secondary seeds but not tertiary seeds show increased germination (about 10%) relative to seeds from the same plants and umbels receiving only the after-ripening treatment. These

differences are not related to the inability of tertiary seeds to successfully survive the cold treatment since the proportion of ungerminated seeds still viable at the conclusion of the experiment was similar for all umbels. The results of the field germination tests are similar to those of the laboratory tests except that secondary seeds as well as tertiary seeds showed low levels of germination relative to primary seeds. The cause(s) of these differences in germination of seeds from different umbel orders following simulated or natural overwintering is not known but might involve hormonal balances (Evenari, 1965), utilization of endosperm (Stokes, 1965), or changes in the balance between germination promoters and inhibitors (Mayer and Poljakoff-Mayber, 1982). The decrease in germination of seeds from secondary umbels in the field experiments but not laboratory experiments suggests differences between simulated and natural overwintering, although the nature of these differences is not known.

The cold treatment of seeds from different umbels in the laboratory experiments had the additional effect of decreasing the number of days to 50% germination and shortening the time span needed for maximum germination. This effect of a cold treatment on days to 50% germination has not been previously reported for *P. sativa*, although it occurs in other species (Stokes, 1965).

A major difference between the laboratory and field studies of germination is that overall levels of germination in the field were much less than those in the laboratory. While part of the low field germination is likely due to the fact that a certain proportion of the seeds sown lacked embryos and/or endosperm (these could not be distinguished prior to sowing), other factors may be involved. Soil temperatures in Iowa during winter are often as low as -5°C during January and February; laboratory cold treatment of seeds at the same temperature for 30 days reduces subsequent germination to levels similar to that found in these field studies (Hendrix, unpubl. results). Also, seeds in the field may be more susceptible to fungal attack. It is possible that some of the ungerminated seeds would not have germinated until the next growing season, although carry-over germination in field experiments currently underway have been less than 10% of total germination (Hendrix, unpubl. results).

The results of the two-way ANOVA (Table 2) demonstrate that for all umbel orders there is significant variation between plants in final germination and significant variation due to the interactions of plants with treatment. The

variation due to plants indicates that some individuals are more likely to leave successful offspring than others. The differences in the reaction of plants to different environmental conditions suggest that there is strong selection pressure for variation rather than uniformity in germination requirements within populations of *P. sativa*. This is not surprising considering that *P. sativa* is a mid-successional species capable of long term occupation of habitats which change substantially over time. Differences within and between individual plants in either rate or overall amount of germination have been found in *Rumex crispus*, *R. obtusifolius*, and *Daucus carota* (Cavers and Harper, 1966; Hawthorn, Toole and Toole, 1962). Such differences may be common and whenever possible, seed germination studies should take into account potential differences between individual plants (Salisbury, 1965; Cavers and Harper, 1966).

The results of this study suggest that herbivore destruction of the primary umbel in large individuals of *P. sativa* by *D. pastinacella* reduces the fitness of these plants despite the fact that tertiary seed production increases and seed number itself is not reduced. In autumn, primary and tertiary seeds are at least ecologically equivalent and tertiary seeds may actually have a competitive advantage due to their more rapid germination. However, the majority of germination occurs during the spring when tertiary seed germination is lower than that of primary seeds. Therefore, overall recruitment from small seeds is likely to be less than that from large seeds.

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