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ONLY SEED SIZE MATTERS FOR GERMINATION IN DIFFERENT POPULATIONS OF THE DIMORPHIC *TRAGOPOGON PRATENSIS* SUBSP. *PRATENSIS* (ASTERACEAE)[1]

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Many studies have focused on the ecology of seed dimorphism, the production of two seed types by a single plant. Morphology and seed size are usually correlated, but how morphology affects germination percentage and seedling growth is poorly understood. Here we explicitly separate these effects for nine populations of the dimorphic species *Tragopogon pratensis* subsp. *pratensis*. Larger seeds yielded higher germination percentages, yet seed morphology had no additional direct effect on germination. Neither seed size nor seed morphology affected seedling growth. Neither germination nor seedling growth varied among populations, but seed head varied significantly. Results show that germination is mainly controlled by seed size rather than by seed morphology. This study is one of the few to distinguish explicitly between seed size and seed morphology effects on ecological characteristics and suggests that seed dimorphism may exert its ecological effects predominantly through its correlated size.

Key words: Asteraceae; germination; The Netherlands; population; seed dimorphism; seed morphology; seed size; seedling growth.

Seed dimorphism is the phenomenon in which a single plant produces two seed types with different morphology and/or behavior. Seed dimorphism is common in Asteraceae (Harper, 1977) and may, for instance, be characterized by differences in embryo size or presence of a pappus (Venable and Levin, 1985). In several species, differentiation in morphology is accompanied by a difference in seed size (Maxwell et al., 1994; Imbert et al., 1997). Besides the difference in size and/or morphology, the two seed types can also differ in dispersal characteristics, dormancy, and germination requirements (McEvoy, 1984; Venable and Levin, 1985; Maxwell et al., 1994; Zhang, 1994). In Asteraceae, reduced dispersability and delayed germination are ascribed to peripheral, sometimes dark-colored, relatively heavy seeds, whereas distant dispersal and quick germination are associated with the central, pale, and lighter seeds (McEvoy, 1984; McGinley, 1989; Maxwell et al., 1994; Imbert and Ronce, 2001). According to Imbert (2002) seed polymorphism is used by plants to cope with differences in their microhabitats; central and peripheral seeds of *Salicornia europaea* (L.), for instance, respond differently to salt concentration.

In spite of the large number of studies, it remains unclear to what extent seed size and seed morphology independently affect ecological characteristics such as germination and seedling performance (Zhang, 1993). Many studies have focused on the effects of seed size: e.g., on germination and seedling characteristics between species (Leishman et al., 1995; Jakobsson and Eriksson, 2000), on colonization ability (Lopez et al., 2000; Gibson, 2001), and on variation within species (Thompson, 1984; Wulff, 1986). However, we find no studies

on dimorphic seeds that distinguish between the effects of seed morphology and the effects of seed size on the behavior of these seeds. Zhang (1993) is one of the few who investigated whether seed morphology or seed mass has a greater impact on germination percentage and seedling growth of *Cakile edentula* (Bigelow) Hook., but unlike for many other species, they found no differences in relation to seed morphology or mass.

Metapopulation models suggest that in some landscapes, selection pressures against short-distance dispersal may lead to lighter seeds. In severely fragmented landscapes, the reverse selection pressure can be found: all seeds that disperse from the safe site can be considered lost (Olivieri et al., 1995). Some models suggest that a stable coexistence of high- and low-dispersal phenotypes can develop due to these conflicting selection pressures on competition and dispersal (Ronce and Olivieri, 1997; Mathias et al., 2001; Mathias and Kisdi, 2002). Seed dimorphism may provide a solution to these demands (Imbert, 2002). Moreover, differences in the degree of dimorphism between populations can be expected because populations face different environmental conditions, such as variation in fragmentation or density. Whether variation in seed size and morphology separately affect population performance under different environmental conditions also remains unknown.

This study addresses whether seed size or seed morphology itself is the main factor that causes variation in germination percentage and seedling growth between two seed morphologies. *Tragopogon pratensis* subsp. *pratensis* (L.) was used as a model species because it produces dimorphic seeds that are relatively easy to distinguish. Complete seed heads were collected from nine populations of differing size, spatial isolation, and habitat to investigate population differences. We hypothesize that both seed size and seed morphology influence germination percentage and subsequent seedling growth. Germination and seedling growth were examined on both nutrient-poor and nutrient-rich soils and under both low and high ratios of red : far red light (R : FR) because some effects of seed

TABLE 1. The location, habitat, effective population size (number of flowering individuals), and estimated degree of isolation (distance to next population) are shown per population of *Tragopogon pratensis*.

| Site | Coordinates | | Habitat | Effective population size | Estimated degree of isolation |
	N	E			
B1	51°53′17″	05°51′27″	Roadside	50–100	±250 m
B2	51°53′33″	05°51′55″	Roadside	50–100	±250 m
BD	51°51′36″	06°05′17″	Meadow/dike	>700	>1000 m
Cr	51°53′33″	05°51′55″	Dike	50–100	±500 m
Ma	51°49′36″	05°48′25″	Roadside	50–100	±500 m
NR	51°49′41″	05°17′06″	Meadow	>2500	>1000 m
Ph	51°49′51″	05°49′20″	Roadside	<50	±500 m
W1	51°49′21″	05°43′23″	Roadside	<50	±500 m
W2	51°49′31″	05°43′04″	Roadside	50–100	±500 m

size or morphology may become apparent only under unfavorable conditions (Gross, 1984; Maranon and Grubb, 1993; Leishman and Westoby, 1994; Vaughton and Ramsey, 1998).

MATERIALS AND METHODS

Plant material—*Tragopogon pratensis* subsp. *pratensis* (L.) occurs on roadside verges, dikes, and ruderal places on different soil types, from clay to sand and gravel (Weeda et al., 1991). The species is monocarpic and flowers from the end of May until the end of July. *Tragopogon pratensis* produces two seed types that differ in color and shape. The dark seeds are slightly curved, and their surface is rough. The pale seeds are straighter, and their surface is smoother. Dark seeds are produced on the peripheral ridge of the seed head, and pale seeds are produced in the central part. Both seed types are dispersed by wind, with the aid of a large pappus. The seeds used in this study were collected from nine populations in June 2002 (Table 1). The populations differ in size and degree of isolation (i.e., distance to the closest neighboring population). From each population, one seed head from 10 different individuals was collected.

Experimental setup—The seeds were weighed individually, without the pappus, on a Sartorius M2P microbalance (with an accuracy of 0.001 mg) and assigned to the ''dark'' (dark colored with a rough surface) or the ''pale'' morphology (light colored with smooth surface) or to the ''empty'' class (not developed, small pappus). The dark and pale seeds were stored individually in paper envelopes at room temperature. The number of ripe seeds per seed head ranged from 31 to 76. For each of five seed heads per population, 12 dark and 12 pale seeds were selected for the germination experiment in July 2002; the seeds closest to the average mass of the morphology type of that seed head were selected.

Six trays containing 96 pots (9 cm³) were filled with sand (nutrient-poor substrate), and another six trays were filled with potting compost (nutrient-rich substrate). In each tray, 45 dark and 45 pale seeds, one dark and one pale from each seed head. were placed randomly on the surface of the pots. The trays were then placed in a climate chamber maintained at 19 ± 1°C, with 16 h light and 8 h dark per day. Three trays filled with sand and three trays filled with potting compost were put under white light in combination with far-red light (light bulbs; Paulmann Schwarzlicht, 75 W); the remaining trays were put under white light (light bulbs; Philips TLD 36 W/840). The R : FR ratio of the far-red light bulbs in combination with white light was 0.2, the R : FR ratio of the white light was 9, and the light intensity was 80 μmol · m⁻² · s⁻¹. A light-impermeable screen was placed between the Far-Red (FR) and white (wt) light group. A Plexiglas plate was placed under the light bulbs to prevent heating the seeds. Germination was recorded daily for 20 d. Seeds were considered to have germinated as soon as cotyledons emerged above the soil. The seeds, and later the seedlings, were watered regularly. Starting 3 d after germination and continuing at least every other day, the length of the longest leaf of each seedling was measured.

Data analysis—To determine whether the seeds were dimorphic with respect to seed mass, a one-way analysis of variance (ANOVA) was performed for each of the nine populations. Whether the proportion of the three classes (dark, light, and empty) varied among populations and whether dark and light seed types differed in seed size between populations was also tested with a one-way ANOVA. The effect of the light treatment on germination was evaluated with a χ^2 test. A logistic regression, using seed mass as a covariable, was used to determine the effects of seed morphology, soil type, and population on germination percentage.

Differences in stem length were tested with ANCOVA using seed mass as a covariable. The main effects where soil type, population, seed head, and morphology. Seed head was considered nested within population. All tests were carried out with SAS, version 6 (SAS Institute, 1990).

RESULTS

Seed dimorphism—All nine populations produced dimorphic seeds with respect to seed size, and the dark seeds were heavier than the pale seeds (Fig. 1A). The individual seed masses on a seed head showed a bimodal distribution (data not shown) comparable to the distribution patterns of *Tragopogon dubius* seeds (McGinley, 1989). This pattern was found in all seed heads of all populations. Only occasionally was the difference between dark and pale seeds not obvious and an intermediate form was observed: a pale color, but a rough surface. We excluded these seed heads from further analyses.

Seed size differed greatly among populations with respect to dark and pale morphologies ($F = 58.84$, $P < 0.0001$ and $F = 90.67$, $P < 0.0001$, respectively). The average mass of pale seeds of some populations was similar to the average mass of dark seeds of other populations (Fig. 1A). Differences in seed size were not related to population size or distance to the next population.

The proportion of dark seeds on a seed head did not differ among populations and averaged 42.1% ± 0.81 ($F = 1.67$, $P > 0.05$; Fig. 1B). The proportions of pale and empty seeds, however, varied significantly among populations ($F = 3.97$, $P < 0.001$ and $F = 2.40$, $P < 0.05$, respectively). No relationship was found between seed size and seed number per seed head (data not shown).

Germination—Germination percentage in white light was 47.1% after 20 days, but only 0.74% germinated under light with low R : FR ratio ($\chi^2 = 88.64$, $P < 0.0001$; Fig. 2A). Because so few seedlings (only four) grew in the FR group, this group was excluded from further analysis. The far-red light bulbs were switched off at the end of the experiment to
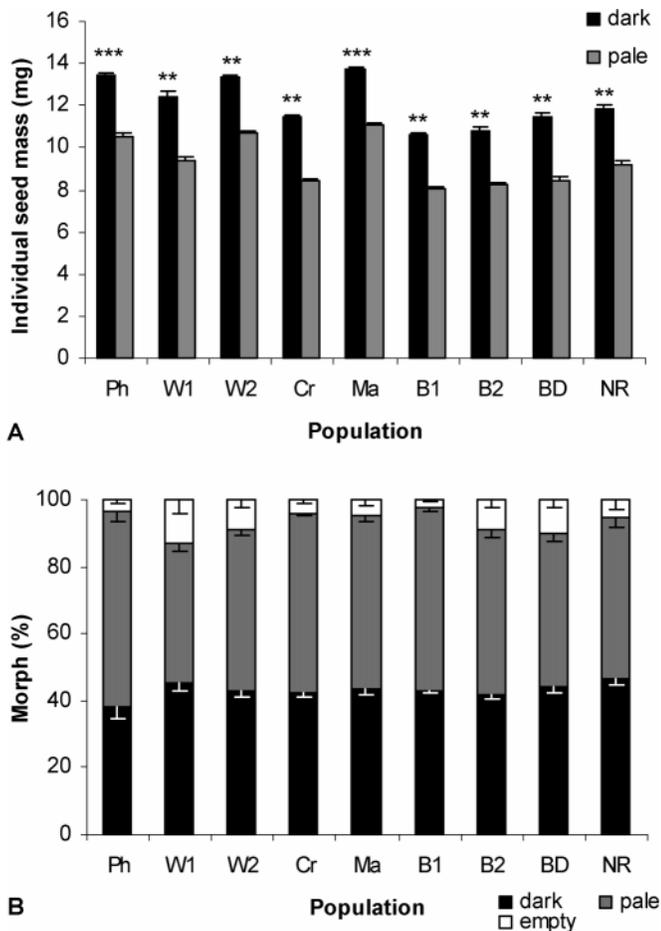
A

B

Fig. 1. Seed characteristics of nine populations of *Tragopogon pratensis*. (A) The average seed mass (± SE) of both dark and pale morphologies per population. Seed dimorphism with respect to seed mass is significant between all populations ($P < 0.01$ **, $P < 0.001$ ***). Populations are arranged from small (Ph) to large (NR) (see Table 1). (B) Percentage (± SE) dark, pale, and empty seeds averaged for all seed heads ($N = 10$) per population. Percentage dark seeds is constant at 42.9% ± 0.79 ($F = 1.67$, $P > 0.05$).
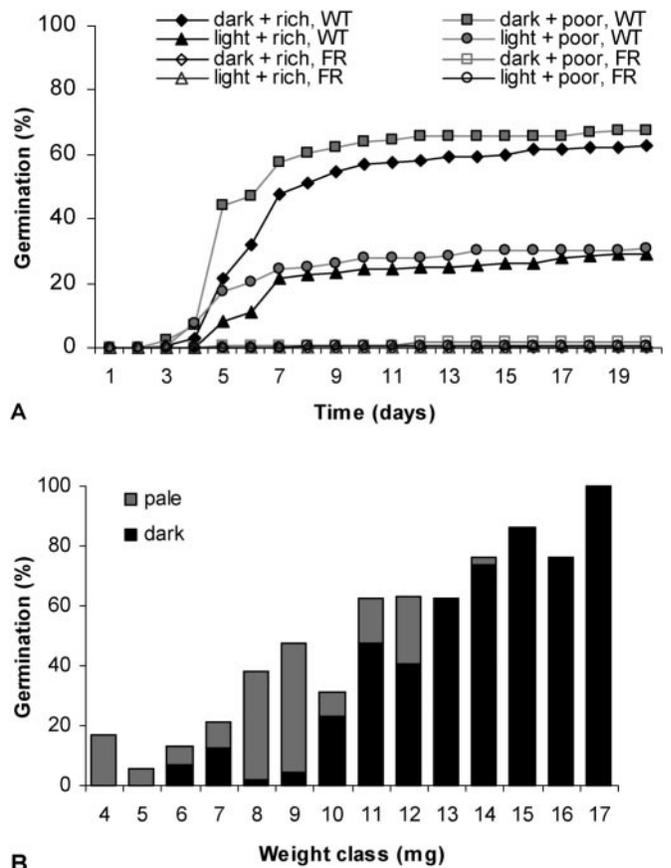

A

B

Fig. 2. (A) Germination rate of dark and pale seeds from the dimorphic *Tragopogon pratensis* sown on nutrient-rich and nutrient-poor soils and under white (wt) and far red (FR) light in a growth chamber ($N = 12$ of each morph per seed head, $N = 5$ seed heads per population). Seeds hardly germinated under FR light. (B) Total germination percentage per seed mass class of all populations on both soil types under white light are shown per morphology. Germination percentage increased with seed size ($\chi^2 = 10.37$, $P < 0.005$).

test whether the seeds in the FR group were viable, and 40 d later, 61.3% had germinated.

In white light, dark seeds had a higher germination percentage than pale seeds, 65.5% and 29.7%, respectively Fig. 2A). This effect could be entirely attributed to seed size; seed morphology did not influence germination percentage (Table 2). The probability of germination thus increased with increased seed size (Fig. 2B).

Seed head, however, did influence germination (Table 2), indicating that seeds from different individuals (mother plants) had different germination percentages, independent of seed size. Population had no significant effect on germination; differences between populations could be explained entirely by differences in seed size.

Growth—Seedlings remained shorter on nutrient-poor than on nutrient-rich soil (Fig. 3, Table 2). The first true leaf overgrows the cotyledon on nutrient-rich soil after 15 d. This leaf is also formed on nutrient-poor soil, but it does not overgrow the cotyledon. Furthermore, seedling length was not affected

by seed size, morphology, or population (Table 2). Seed head, however, did significantly affect seedling length. In addition, all interactions with seed heads significantly affected seedling growth, indicating that seedlings arising from seeds from different individuals (mother plants) behaved differently with respect to growth. These differences between individuals vary between the two soil types and morphologies. Thus, seedlings originating from one individual may grow taller on nutrient-rich soil than seedlings from another individual. Furthermore, for some seed heads, seedlings from pale seeds grew taller than seedlings from dark seeds and vice versa. However, no pattern in these differences emerged.

DISCUSSION

Although much work has been done on seed dimorphism, it is largely unknown to what extent seed size and seed morphology separately affect germination percentage and seedling growth and how this differs among populations of the same species. Here we show for *Tragopogon pratensis* subsp. *pratensis* that variation in seed size is the main causal agent affecting germination behavior and that morphology has no effect.

TABLE 2.   Statistical analysis of the effects of different parameters on germination (logistic regression) and seedling length (ANCOVA) of *Tragopogon pratensis*. Seed head is nested in population only for the ANCOVA and not for the logistic regression. The interactions with seed head are not tested for germination, because only a limited number of interactions are possible for the logistic regression.

	Germination			Seedling length			
Parameters	df	χ^2	P	df	Mean square	F	P
Seed size	1	10.37	0.001	1	117.57	0.3	0.584
Soil	1	0.00	0.967	1	226 213.24	330.07	<0.0001
Population	8	13.00	0.112	8	1308.80	1.53	0.185
Seed head (population)	36	54.56	0.024	34	858.21	2.2	0.001
Morphology	1	0.01	0.916	1	32.32	0.04	0.851
Morphology × population	8	5.59	0.693	7	848.96	0.93	0.509
Morphology × seed head (population)				17	912.86	2.34	0.004
Soil × population	8	10.92	0.206	8	685.35	0.52	0.828
Soil × seed head (population)				26	1309.96	3.35	<0.0001
Morphology × soil	1	0.00	0.958	1	732.89	0.45	0.524
Morphology × soil × population	8	8.14	0.420	7	1626.46	1.79	0.195
Morphology × soil × seed head (population)				10	908.44	2.33	0.015
Error				128	390.61		

In *Tragopogon pratensis*, dark (i.e., peripheral) seeds were heavier than pale (i.e., central) seeds within seed heads. The proportion of dark seeds was remarkably constant within as well as among populations. A few other studies did find a relationship between proportion of a certain morphology and environmental stress (Imbert and Ronce, 2001, and references therein). Differences in proportion of morphologies could be expected for *T. pratensis* because the populations differed in size and degree of spatial isolation. Selection pressures for different seed morphologies may have been similar in different environments, or *T. pratensis* may not be plastic in its distribution of morphologies, as is the case for other dimorphic species (Imbert, 2002).

Light conditions had a dramatic effect on germination percentages. Cresswell and Grime (1981) found that *T. pratensis* seeds can germinate in the dark, but our results show that the seeds do not germinate under light with a low R : RF ratio. This is consistent with the pattern found in many species (Brunvatne, 1998; Van Hinsberg, 1998; Shichijo et al., 2001; Yirdaw and Leinonen, 2002). Although dark seeds germinated
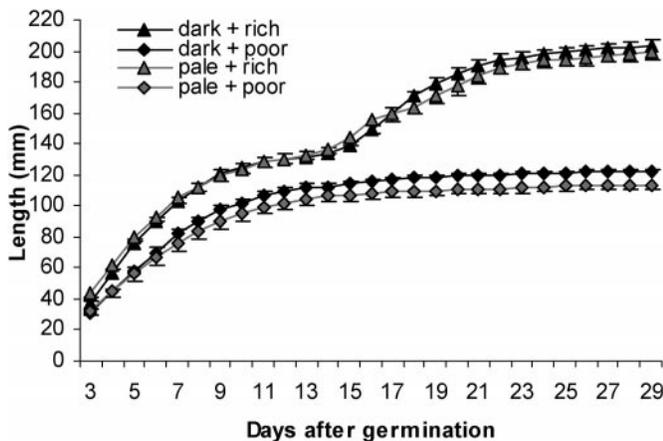

Fig. 3.   Length of seedlings from dark or pale seeds of the dimorphic *Tragopogon pratensis* on nutrient-rich and nutrient-poor soils (mean for all populations). Error bars do not exceed the symbols. Seedlings on nutrient-rich soil grew significantly taller (F = 330.07, P < 0.0001), but morphology had no significant effect.

better than pale seeds, this was only because dark seeds are larger. Seed size is the main factor determining germination percentage, as has frequently been reported for nondimorphic species (Winn, 1985; Hendrix and Trapp, 1992; Vaughton and Ramsey, 1998; Parciak, 2002). Differences in germination percentage between dimorphic seeds reported in previous studies (Venable and Levin, 1985; Venable et al., 1987; Imbert, 1999; El-Keblawy, 2003) may have resulted from differences in seed size rather than seed morphology. In addition to seed size, only seed head had a significant effect on germination percentage. This effect probably reflects genotypic (maternal) variation, because only one seed head was collected per individual plant.

According to Roach and Wulff (1987), maternal tissues surrounding the embryo, such as differences in the seed coat, can influence germination. Differences in seed content, such as starch and proteins, could also play a role in germination differences because physiological processes are involved in breaking dormancy and/or onset of germination (Vleeshouwers et al., 1995; Dyer, 2004). However, we are aware of only one laboratory study (Kristensen, 2003) that showed a negative relationship between mean germination time and protein content in *Hordeum vulgare* (L.), but it did not relate protein content to seed size. To our knowledge, why larger seeds have higher germination rates than smaller seeds is mostly unknown, and this certainly applies to the larger morphs in dimorphic seeds.

Seedling growth differed between the two soil types and among seed heads. No population, seed size, or seed morphology effect was found for seedling growth. Thus, although seed size is very important for germination, it does not affect seedling growth. This is different from many other species, in which larger seeds produce larger seedlings (Venable and Levin, 1985; Zhang, 1993; Maxwell et al., 1994). Imbert et al. (1997) found an effect of size only when seedlings were grown under competition. To simulate a stressful environment, we included a nutrient-poor treatment in our experiment, but seedling growth did not differentiate among seed sizes in this treatment either. In all the studies that did find an effect, embryo size of the seeds differed. Perhaps embryo sizes in *T. pratensis* are similar for different seed sizes, and the main component of variation in seed size is the pericarp, as in *T. dubius* (Maxwell et al., 1994). It could also be that seeds differ in endo-

sperm content. Roach and Wulff (1987) argue that the female parent may play a more important role in determining endosperm characteristics than the male parent. Potential differences in endosperm content in *T. pratensis* seeds may therefore account for the differences in growth between seed heads.

Implications—The lack of effects of seed morphology on germination and seedling growth raises the question why *T. pratensis* produces dimorphic seeds at all. To maintain seed dimorphism, there must be an ecological difference between morphologies (Imbert et al., 1997). Seed morphology should therefore have ecological impacts other than on seedling growth or germination. Predation rates, for instance, may differ between the dark and pale seeds, but we are unaware of studies that have investigated this. Geritz (1998) proposed that if the attack rate of predators is related to seed size, seed size variation within an individual is favored. Consistent with this model, the dimorphism may also be an evolutionary stable strategy to maintain variation in morphology. The morphologies of *T. pratensis* differ in color as well as structure, as in *T. dubius* (Scop.) (Maxwell et al., 1994), which may require different handling and searching strategies for predators, e.g., dark seeds are less visible on a dark surface than pale seeds, and vice versa.

Alternatively, seed dimorphism may arise from ontogenetic constraints as described by Imbert (2002). The hypothesis of developmental constraints arising from the morphology of the floral axis (McGinley, 1989) of the seed head is consistent with our observation that the proportion of dark (or peripheral) morphologies is fixed among populations, in spite of seed size differences. However, developmental constraints do not exclude that there is, or has been, an adaptive value of seed dimorphism. Seed dimorphism may solve conflicting demands on dispersal (Ronce and Olivieri, 1997) and the risk of predation. It may also be that seed dimorphism has been advantageous in the past and that developmental constraints have simply conserved it.

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