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Intrapopulation variation in *Abutilon theophrasti* seed mass and its relationship to seed germinability

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Abstract

The relationship between seed mass variation and germinability in ten *Abutilon theophrasti* Medic. plants from a single agricultural population was examined under controlled environmental conditions. Seeds were collected in the autumn of 1995 and dry-stored in paper bags at 4°C until the start of trials in the spring of 1998. For each plant, between 549 and 1000 randomly selected seeds were separated into seven mass fractions based on individual seed mass, with classes ranging from <6.0 to >11.0 mg. Subjecting the seeds to a cold stratification (4°C) period for 7 d followed by a 21-d alternating day/night (25/14°C) temperature and 14-h photoperiod regime, resulted in 75% overall germination, 24% dormancy and 1% non-viable seeds. The majority of the seeds germinated within 7 d of being exposed to the alternating temperature/light regimes. There was a significant ($P < 0.001$) difference in mean seed mass between the ten plants, with mean mass ranging from 8.8 to 9.6 mg. For nine of the ten plants, the greatest proportion of seeds occurred in the 9.0–9.9 mg mass fraction, while the lowest proportion of seeds was generally found within the 6.0–6.9 mg mass fraction. Most seeds (96%) having a mass below 6.0 mg were non-viable and, of the viable seeds, none germinated. There was a significant ($P < 0.0001$) relationship between seed mass and total germination, but not rate of germination. Germination peaked for seed mass fractions comprising the greatest proportion of total seeds (8.0–9.9 mg) and was lowest for seeds with high or low mass. There was a weak trend of lower germinability for heavier seeds (>10.0 mg) compared with lighter seeds. Maternal source had a significant effect ($P < 0.05$) on total germination and germination rate. Findings from this study suggest that intrapopulation variation in *Abutilon theophrasti* seed mass and its influence on germinability of seeds may play a significant role in maintaining a variable germination pattern and persistent seed bank in this troublesome annual agricultural weed.

Keywords: ***Abutilon theophrasti*, intrapopulation variation, seed bank, seed dormancy, seed germination, seed mass, velvetleaf**

Introduction

Seed size plays an important role in determining the successful establishment of individual plants within a population (Roach and Wulff, 1987; Westoby *et al.*, 1992; Milberg and Lamont, 1997; Kidson and Westoby, 2000). Seed size variation may be due to trade-offs in resource allocation between seed size and number (Venable, 1992) or as a response to environmental heterogeneity (Janzen, 1977). Intraspecific seed size variation and its relation to seedling survival have been demonstrated in several plant species (Meyer *et al.*, 1995; Andersson and Milberg, 1998).

The ability of a seed to germinate is affected by several factors, including genetic origin, age and growing environment of the parent during seed maturation, and seed position on the plant (Bello *et al.*, 1995; Dekker *et al.*, 1996; Andersson and Milberg, 1998; Wright *et al.*, 1999). Germination and dormancy of seeds can also be influenced by seed size, shape and surface orientation (Harper, 1977; Moles *et al.*, 2000). Seed dormancy has generally been viewed as an important physiological adaptation to variable, unpredictable environments (Cohen, 1966; Fenner, 1985; Allen and Meyer, 1998).

Intrapopulation variation in seed mass and germination has been examined for a few species (e.g. Harper and Obeid, 1967; Stamp, 1990; Zammit and Zedler, 1990; Evans and Cabin, 1995; Milberg *et al.*, 1996). In species exhibiting seed dimorphism, such as

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Bidens pilosa and *Cakile edentula*, differences in seed mass correlated with differences in germination (Forsyth and Brown, 1982; Zhang, 1993). The relationship between seed mass and germination in plant species that do not produce dimorphic seeds is not as evident, and often the confounding effect of environmental factors on seed size and germination has further complicated matters (Milberg *et al*., 1996). The relatively few studies that have attempted to relate individual seed size fractions to viability and germination rates have provided inconsistent results, showing both that seeds of greater mass exhibit higher (Zammit and Zedler, 1990) and lower (Stamp, 1990) germination and rates of germination than seeds of lower mass. Milberg *et al*. (1996) reported that there were large variations in germination rate between nine seed mass fractions in *Lithospermum arvense* and *Anchusa arvensis*. Moreover, the relationship between germination and seed mass differed in both species and between populations of the same species. Large seeds of *Lithospermum* always germinated well, whereas small seeds generally had a poor percentage germination. However, for one of the *Anchusa* populations, germination tended to decrease with increasing seed mass. Research by Harper and Obeid (1967) on fibre and oil seed flax cultivars demonstrated that seeds of intermediate size germinated faster than seeds from extreme size classes. Few studies have examined intrapopulation germinability and dormancy characteristics of seeds from different size fractions for species exhibiting strong physical dormancy.

Abutilon theophrasti (velvetleaf) is a large, self-pollinated annual weed infesting maize and soybean crops, particularly in the mid-western and north-eastern regions of the United States, eastern Canada and the eastern Mediterranean regions. Each plant is capable of producing up to 17,000 seeds that exhibit a high degree of physical dormancy due to the presence of a thick, hard seed coat that is impermeable to water (Warwick and Black, 1988; Baskin and Baskin, 1989). Under optimal conditions for germination, hard seeds cannot imbibe water and are unable to germinate. However, physical scarification, resulting from regular cycles of freezing and thawing or from placement in boiling water for brief periods, disrupts the seed coat and increases germination in hard-seeded species (Lacroix and Staniforth, 1964; Zanin *et al.*, 1989; Li *et al*., 1999).

In work by Zhang and Hamill (1997), *Abutilon theophrasti* seeds, having a mass ranging from 4.8 to 11.7 mg, did not exhibit significant differences in germination and dormancy. Surprisingly, in that study, only 39% of seeds germinated, while a large portion of seeds (40%) were found to be non-viable. The remaining seeds (21%) were viable but dormant. Given the low viability of seeds in the Zhang and Hamill (1997) study, it was unclear whether the lack of a relationship between seed size and germinability of seeds in *Abutilon theophrasti* is a general feature of this species or is simply specific to the population tested. Moreover, no attempt was made to relate seed size variation to germinability for individual plants. This may be especially important given the numerous instances where within-plant variation in seed size contributes most to the total seed mass variation within a population (Pitelka *et al*., 1983; Thompson, 1984; Milberg *et al*., 1996). To date, the relationship between intrapopulation seed mass variation and seed germinability in *Abutilon theophrasti* is not well understood and requires further study.

Thus, the objectives of this study were: (1) to determine the variability in seed mass, total germination and rate of germination for the seeds of ten *Abutilon theophrasti* plants from a single agricultural population; and (2) to determine the relationship between seed mass, total germination and rate of germination for seeds from these ten plants.

Materials and methods

Mature capsules of *Abutilon theophrasti* were collected in late September 1995 from ten individually marked plants located within a 3 ha maize field at the Macdonald Campus Farm in Ste-Anne-de-Bellevue, Québec, Canada. Plants were selected randomly within the field but were at least 30 m apart from each other. Capsules were collected randomly on individual plants and were considered mature for harvest when their colour had changed from light green to dark black. Under typical growing conditions of south-western Québec, capsules mature from early August until early October. Thus, the late-September collection date permitted the harvesting of capsules that matured over the normal time period for this region. Capsules were dry-stored at 4°C in paper bags until the start of the experiment in spring 1998. Seeds from the ten plants were obtained by separating them from chaff by hand. The total number of seeds collected from each plant ranged from 549 to 1000, depending on the number of seeds produced by each plant and availability at the time of harvest. Seeds from each plant were then weighed individually to the nearest 0.1 mg and grouped into one of seven seed mass fractions. All seeds were placed on moistened filter paper in 9-cm-diameter plastic Petri dishes containing 8 ml of distilled water. No more than 50 seeds per mass fraction were placed within each Petri dish. Petri dishes were subsequently wrapped with Parafilm™ to prevent water evaporation during the experimental period. All seeds within Petri dishes were then subjected to a low-temperature (4°C) moist stratification treatment for 1 week in the dark. Seeds were subjected to this treatment because it simulated the early season, cold, moist soil conditions that seeds would typically experience under Québec conditions in March and April. At the end of the stratification period, seeds were incubated in a controlled environment chamber programmed to provide 25/14°C day/night temperatures, and a 14-h photoperiod at a photosynthetically active radiation (PAR) of 400 μmol m^{-2} s^{-1} using fluorescent lamps. These environmental conditions are typical of southwestern Québec field conditions in late May, when the first *Abutilon theophrasti* germination flush generally occurs. The number of germinated seeds having a radicle at least 2 mm long was recorded daily for a period of 21 days, and all germinated seeds were removed from the Petri dishes. At the end of the experiment, all non-germinated seeds were initially examined for viability by pressing them gently with forceps. Seeds that were crushed under this moderate pressure were considered to be dead. The remaining seeds were then placed in boiling water for 10 s, removed and placed on moistened filter paper, and returned to the original controlled environment conditions for a period of 48 h. All seeds that germinated following this additional germination period were characterized as being viable but dormant, while seeds that did not germinate during this 48-h period were considered to be dead. Placement of seeds in boiling water for a short period of time overcomes physical dormancy in this hard-seeded species (Lacroix and Staniforth, 1964; Zanin *et al*., 1989).

The mean time to germination was determined for each plant and for each of the seven seed mass fractions by first multiplying the total number of seeds germinating on the first day by 1, the total number of seeds germinating on the second day by 2, and so on. The average number of days that were required for seeds to germinate was then determined by dividing the sum of these terms by the total number of seeds that germinated (Milberg *et al*., 1996).

Germination, dormancy and viability data were square root transformed to homogenize variances prior to using the GLM analysis procedure in SAS (Cary, NC, USA). The analysis of variance (ANOVA) procedure was modified in order to take into account the potential heterogeneity of variances and lack of independence over time (from day 1 to day 21) of the temporal repeated measures of individual plants and seed mass (Dutilleul, 1998). The model used for the modified univariate ANOVA was derived by adding the time effects plus all the interactions to the terms of the standard ANOVA model and using the REPEATED statement of the GLM procedure. Most seeds below 6.0 mg were non-viable and thus were not included in the data analyses. Relationships between seed mass, germinability and dormancy were determined by both linear and non-linear regression analyses. The Kruskall–Wallis one-way ANOVA on ranks was used to determine differences in mean seed mass of plants.

Results

Seed mass variation between plants

For the ten plants combined, 75% of seeds had a mass within the 8.0–8.9 mg and 9.0–9.9 mg ranges, while only 1.5% of seeds had a mass within the two extreme seed mass fractions of <6.0 mg and >11.0 mg (Fig. 1). The variation in seed mass for each of the ten plants was large, with the greatest differences occurring for the 8.0–8.9 and 9.0–9.9 mg seed mass fractions (Fig. 1). Median seed mass differed significantly (P < 0.0001) among the ten plants, with seeds from individual 3 having the lowest median mass (8.8 mg) and seeds from individual 10 having the highest median mass (9.8 mg) (Fig. 2).

Between plant germination characteristics

After the 21-d experimental period, seed germination differed significantly (P < 0.05) among the ten plants (Table 1). For all plants and mass fractions combined, 75% of seeds germinated. In contrast, seed germination for individuals 6 and 8 were 57% and 92%, respectively (Fig. 3). Overall, 24% of *Abutilon* seeds did not germinate under the controlled environment conditions used, and 1.0% of seeds were non-viable.

Seventy-five per cent of seeds germinated within the first 7 d of the experiment, regardless of maternal source (Fig. 3). Germination declined sharply for all plants 10 d after the start of the experiment. The rate of germination differed significantly (P < 0.05) between plants (Fig. 4). Across all seed mass fractions, the average number of days required for seeds to germinate ranged from 3.2 d in individual 1 to 5.6 d in individual 7, with an overall population mean of 4.6 d. Seeds from individuals 6 and 4 exhibited the greatest and least variation in germination rate across the seed size fractions, respectively.

Relationship between seed mass and germination characteristics

Seed size had a highly significant (P < 0.0001) impact on total germination (Table 1). The highest germination levels (>85%) were observed for the 7.0–7.9 and 8.0–8.9 mg seed mass fractions, and the lowest levels for the lightest seed mass fraction (<6.0 mg), in which no seeds germinated. Only 58% of all seeds in the 6.0–6.9 mg seed mass fraction germinated. Most non-viable seeds (96%) had a seed mass below 7.0 mg. A weak positive trend was observed between mean seed mass and the number of

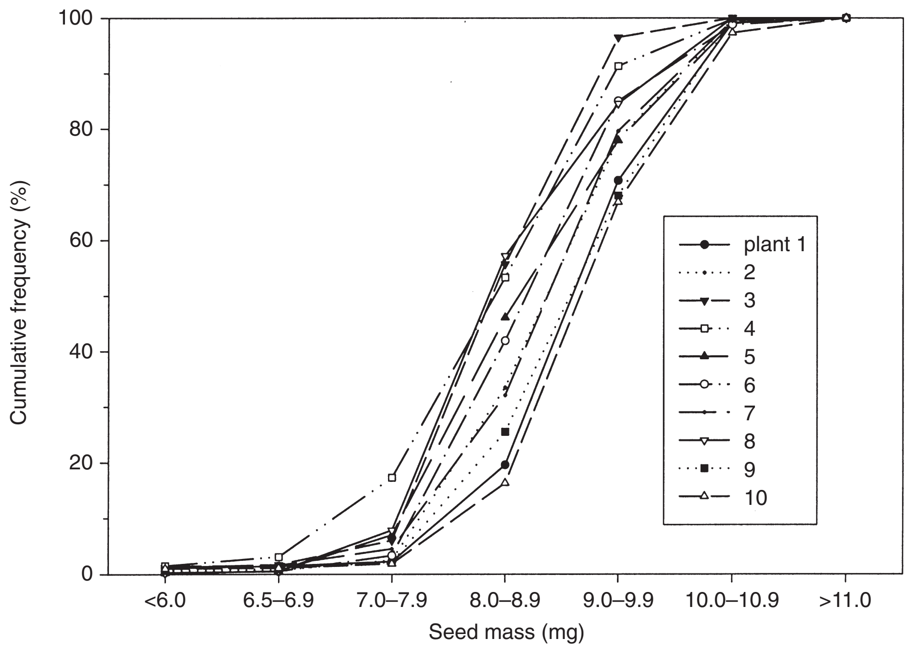

Figure 1. Cumulative frequency distributions of seed mass within seven seed fractions for ten *Abutilon theophrasti* plants collected from a single agricultural population. Curves are based on the individual masses of 1000 seeds, except for plants 1 (898), 5 (900), 8 (549), 9 (713) and 10 (820).

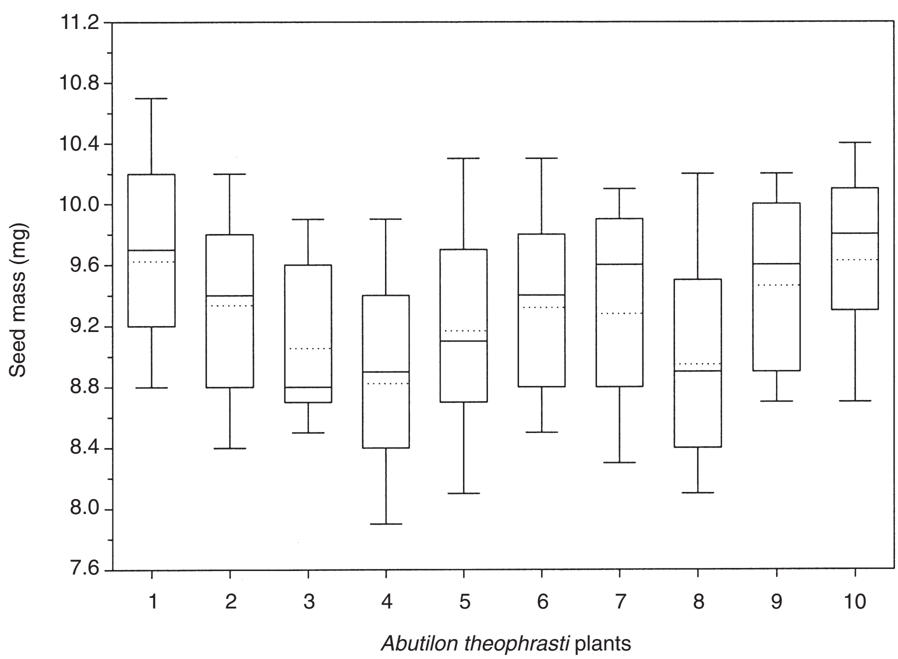

Figure 2. Median (solid line), mean (dotted line) and 25th and 75th percentiles of seed mass for each of ten *Abutilon theophrasti* plants from a single agricultural population. Bars above and below each box indicate the 90th and 10th percentiles, respectively.

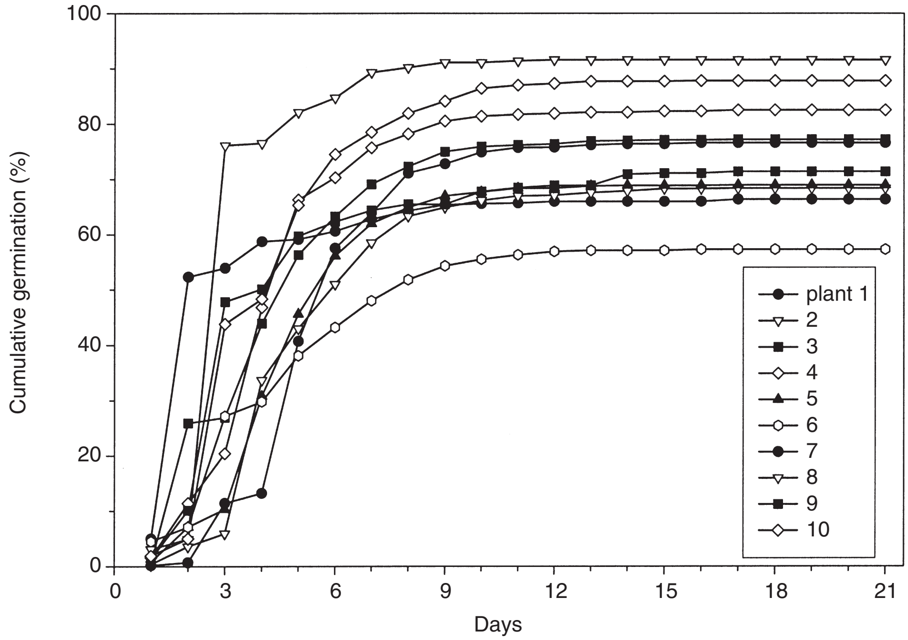

Figure 3. Cumulative germination (%) of *Abutilon theophrasti* seeds over a 21-d period for each of ten plants collected from a single agricultural population. A total of 549–1000 seeds were tested for each plant.

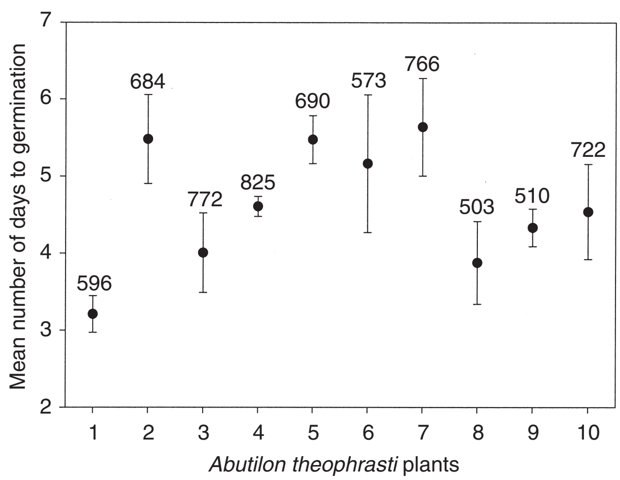

Figure 4. Mean number of days to germination for seeds collected from ten *Abutilon theophrasti* plants from a single agricultural population. Bars indicate ±SE of the means, and values above bars indicate the total number of seeds that germinated for each plant.

seeds not germinating when data for all ten plants were combined (Fig. 5).

The average number of days required for germination was not affected by seed mass (data not shown), although heavier seeds (>11.0 mg) did require, on average, 1.5 additional days to germinate. Interestingly, seeds germinating on the first day of the study had a substantially greater mass (9.7 mg) than seeds germinating during the following 12 days (Fig. 6). There was a trend of increasing time to germination for heavier seeds from day 4 to day 14 of the study (Fig. 6).

Discussion

The important differences in seed mass distribution found between the ten *Abutilon theophrasti* plants were likely due to a number of environmental effects rather than genotypic variation (Zhang and Hamill, 1997). It is plausible that the microenvironments in which the ten plants grew differed in their ability to supply essential resources such as nutrients and light. These differences would have resulted in plants producing seeds that were particularly large or small. It is also possible that the variation in seed mass observed among the ten plants may have been due to differential seed filling in seeds harvested from different branch locations on parental plants (Gutterman, 1992). Zhang and Hamill (1996) reported that mean seed weight in *Abutilon theophrasti* plants varied depending on population, maternal environment and their interaction. However, photosynthetic rate and number of leaves and flowers did not differ among the different populations. Baloch (2001) reported that, under favourable growing conditions, seed mass in *Abutilon theophrasti* was influenced by the branch location of capsules on

Table 1. Summary of ANOVA for *Abutilon theophrasti* total germination as affected by plant source, seed mass fraction and time of sampling (21 d)[a]. Seeds having a mass below 6.0 mg were omitted from this analysis as no seeds germinated

				Adjusted Prob>F[c]	
Source	df[b]	F-value	Probability	G–G	H–F
(a) Between-subject effects					
Plant source	9	2.16	0.0433		
Seed mass	5	22.89	<0.0001		
Error	45				
(b) Within-subject effects					
Time	20	28.11	<0.0001	<0.0001	<0.0001
Time × plant source	180	2.41	<0.0001	<0.0001	<0.0001
Time × seed mass	100	1.61	0.0003	0.0213	0.0062
Error	900				

[a]The Greenhouse and Geisser epsilon is a multiplicate factor by which the number of degrees of freedom of the F test for time-related effects are reduced in order to take the autocorrelation and heteroscedasticity over time into account (Dutilleul, 1998).
[b]df = Degrees of freedom.
[c]The G–G (Greenhouse–Geisser) and H–F (Huynh–Feldt) adjustment values are also shown, G–G = Greenhouse–Geisser epsilon = 0.3319; H–F= Huynh–Feldt epsilon = 0.5165.

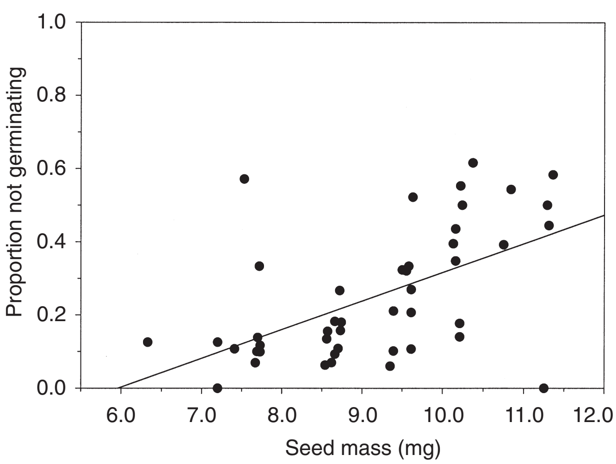

Figure 5. Relationship between the proportion of seeds not germinating and mean seed mass for seeds collected from ten *Abutilon theophrasti* plants from a single agricultural population. Data for seeds from only six seed mass fractions were used since, for the lowest fraction (i.e. <6.0 mg), most seeds were non-viable and no seeds germinated. Only mass fractions having more than five seeds were used in the analysis, $y = -0.47 + 0.08x$; $R^2 = 0.31$.

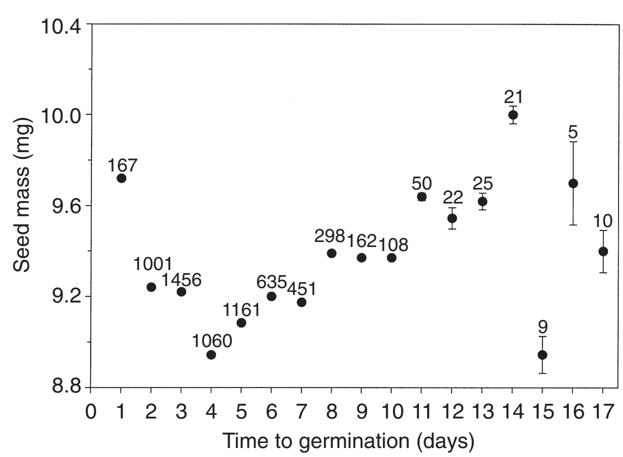

Figure 6. Mean mass (±SE) of *Abutilon theophrasti* seeds that germinated on each of the observed dates. No germination occurred after day 17. Data for the ten *Abutilon* plants were combined. Values near solid circles are the total number of seeds that germinated on that day.

parent plants. That is, seeds collected from early maturing capsules (basipetal) had greater mean weights than seeds harvested from late-maturing (acropetal) capsules. Interestingly, under the stressful conditions of fungal infection and high density, capsules harvested from different branch positions had seeds of similar mean weight. Plants grown under these conditions produced fewer capsules having a larger seed mass than plants grown in the absence of disease and at lower density. Vaughton and Ramsey (1998) also reported that mean seed mass in *Banksia marginata* was greater from early produced flowers lower down on the main stem than from later-produced flowers on the upper part of the main stem. Kane and Cavers (1992) noted that mean seed mass in *Panicum miliaceum* decreased over the growing season, both on individual panicles and all inflorescences of the plant. In contrast, Obeso (1993) observed no variation in mean seed mass at different fruit locations in *Asphodelus albus*.

Within the agricultural population sampled, the ten *Abutilon theophrasti* plants exhibited a large degree of variation in the germinability of their seeds (from 57 to 92%), despite a normal distribution in seed mass of the plants (data not shown). Hence, this variability in germination between the plants was likely not due to differences in seed mass frequency distributions. This finding suggests that differences in the maternal growing environment in this agricultural field (e.g. full sun versus shade) may have resulted in seeds from different plants having divergent germination abilities (Fenner, 1991; Bello *et al*., 1995). For instance, Bello *et al*. (1995) found that *Abutilon theophrasti* plants grown under full sunlight produced smaller-sized seeds that were 20% less likely to germinate under optimal environmental conditions than larger seeds produced from shaded plants. It was unclear from their study whether the decrease in seed dormancy for shaded plants resulted in fewer seeds having hard seed coats or whether some other dormancy mechanism was responsible. In the present study, variation in germination ability for the ten *Abutilon theophrasti* plants may also have been due, in part, to the harvesting of mature capsules on different branch positions. Research on other plant species has revealed large variability in germination of seeds collected from different branch positions on a single plant (Gutterman, 1992; Dekker *et al*., 1996). No attempt was made in the present study to harvest mature capsules from similar positions on each of the plants.

The rate of germination for seeds of the ten *Abutilon theophrasti* plants also differed over the 21-d experimental period. There was no obvious trend observed between the average amount of time required for germination and median seed mass for each of the ten plants. For instance, seeds of individual 1 had a median mass of 9.7 mg and required an average 3.2 d to achieve germination, whereas seeds of individual 7 had a similar median mass (9.6 mg) but required nearly 2.5 d more than individual 1 to achieve germination (5.6 d).

Zhang and Hamill (1997) reported no differences between the germination ability of *Abutilon theophrasti* seeds having a mass ranging from 4.8 mg to 11.7 mg. In the present study, there was a weak trend of lower germination ability for seeds having relatively high mass (i.e. >11 mg). The production of relatively large (>11.0 mg) dormant seeds may be an adaptive feature in *Abutilon theophrasti* because it provides a source of seeds for the soil seed bank that will likely produce competitively superior seedlings when the seeds eventually germinate (Roach and Wulff, 1987; Kidson and Westoby, 2000). Although the total number of large seeds (e.g. >11.0 mg) produced by individual plants may be relatively small (19% of the nearly 9000 seeds collected in this study), many of these dormant seeds may be responsible for the annual fluctuations in *Abutilon theophrasti* emergence patterns observed in the field (Warwick and Black, 1988; Cardina and Sparrow, 1997). Given that plants of this species may produce as many as 17,000 seeds per plant (Mitich, 1991), this would translate into approximately 3200 relatively large-sized seeds (>11.0 mg) produced per plant.

Variations in seed germinability and rate of germination between different plant populations of a species have been documented previously (e.g. Evans and Cabin, 1995; Schütz and Milberg, 1997). For example, Kane and Cavers (1992) reported that *Panicum miliaceum* seeds from two populations separated only by a road differed from each other in survival, germination and dormancy. Genetic uniformity within each population and heterogeneity in microenvironment were suggested as possible sources for the observed variations. Similarly, Milberg *et al*. (1996) reported that germinability and germination rate varied significantly between seed mass fractions in *Lithospermum arvense* and *Anchusa arvensis* and for different populations. Variability in parental growing environment was suggested to account for the differences in germination characteristics observed for the various seed mass classes. Hence, caution should be used when interpreting the results of the present study, given that seeds from only one agricultural population and for a single year were used (Andersson and Milberg, 1998).

Seeds of *Abutilon theophrasti* having a mass of less than 7 mg were largely non-viable (96%), although the proportion of these seeds for each of the plants was very low (i.e. 1–2% of the total number of seeds collected). These findings contrast with those of Zhang and Hamill (1997), where nearly 40% of the 1536 *Abutilon theophrasti* seeds collected were non-viable. Differences in growing environment, as well as duration and method of seed storage, may account for the observed disparity in results. That most *Abutilon theophrasti* seeds germinated within 7 d of being subjected to an alternating day/night temperature regime is consistent with other research (Zhang and Hamill, 1997). In the present study, heavier seeds generally required a longer period of time to germinate, although the effect was not significant. It is worth noting, however, that the mean mass of seeds (9.7 mg) germinating on the first day of the experiment was significantly greater than the mean mass of seeds germinating over the following 12 d. Thus, it would be expected that seedlings originating from these heavier seeds and first to emerge would have a competitive advantage over seedlings from lighter seeds that emerge later (Roach and Wulff, 1987; Gutterman, 1992; Lacey *et al*., 1997). However, Zhang and Hamill (1997) suggested that the adaptive advantage of *Abutilon theophrasti* plants produced from large seeds might not necessarily be reflected in the greater morphological and/or physiological performance of these plants, but rather to their enhanced deleterious impact on neighbouring plants. Zhang and Hamill (1996) found a significant interaction between *Abutilon theophrasti* population and cropping system with respect to seed mass and germination rate. Plants produced significantly heavier seeds with higher germination rates when grown with a maize crop as compared with seeds produced from plants grown with a soybean crop. It was suggested that the production of smaller-sized seeds in soybean versus maize was the result of a genetically based discriminative selection under these two crop management systems.

Variation in mean seed mass and germinability for different *Abutilon theophrasti* agricultural populations needs further investigation. Future research should also be directed towards understanding more fully the role that parental growing environment and capsule branch position play in determining seed mass variation and germinability in this troublesome annual weed.

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Seed Dispersal and Frugivory: Ecology, Evolution and Conservation

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