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# SEED GERMINATION PATTERNS IN GREEN DRAGON (*ARISAEMA DRACONTIUM*, ARACEAE)[1]

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*Arisaema dracontium* (green dragon) is a perennial herb that is widely distributed in eastern North America. However, in Canada, at the northern edge of its distribution, the species is designated as ‘‘vulnerable’’ with respect to conservation status. In natural populations, seedlings are uncommon; the present study was undertaken in order to characterize seed and seedling properties in green dragon. Seeds were sampled from five sites, ranging from Ontario at the northern limit of the distribution range, to Louisiana in the south. Seed germinability ranged from 25 to 55%, depending upon source. Experiments indicated that neither the hard seed coat nor a water-soluble exudate from the seed was responsible for inducing or maintaining dormancy. Patterns of seed germination appear to reflect general climatic conditions at the sites where seeds had originated. Cold stratification at 3°C produced significantly greater relative germinability in all seed collections except the most southerly one, from Baton Rouge. These seeds also had a slower overall speed of germination. In contrast, germination of seeds from the most northerly site was promoted by cold stratification and occurred over a relatively brief period. Germination in alternating light and dark conditions decreased the speed of germination compared to germination in the dark, however exposure to light changed the phenology of germination by promoting development of adventitious roots and primary leaves in these seedlings.

**Key words:** Araceae; *Arisaema dracontium*; cold stratification; dormancy; population variation; seed germination.

The significance of the seed stage in plant population ecology has long been recognized (Harper, 1977; Silvertown and Lovett-Doust, 1993). Characters expressed early in the seed and seedling stage are particularly important, as early selection may be intense and is likely to affect the extent of phenotypic variance at subsequent stages in the life cycle (Harper, 1977). For example, the presence of dormancy that delays germination is often advantageous in a competitive or seasonal environment (Harper, 1977; Vleeshouwers, Bouwmeester, and Karssen, 1995). The germination response pattern of seeds is also regarded as a key characteristic in plant life history strategy (Angevine and Chabot, 1979; Mayer and Poljakoff-Mayber, 1989).

Since the early work of Turresson (e.g., 1922), ecophysiological studies have demonstrated that populations of a species may differentiate morphologically and physiologically (e.g., Hiesey and Milner, 1965; Baskin and Baskin, 1973; Lovett-Doust, 1981; Mayer and Poljakoff-Mayber, 1989). Germination behavior also may differ between regions, due to local adaptations to climate (Habeck, 1958; McNaughton, 1966; Winstead, 1971; Meyer and Monsen, 1991; Schutz and Milberg, 1997). These studies have all shown that species vary geographically in germination rate and degree of dormancy. The polymorphisms have been attributed to both genetic differentiation and to the contrasting environments in which seeds develop (Harper, Lovell, and Moore, 1970; Stebbins, 1971), although the causes of these polymorphisms remain contentious (Baskin and Baskin, 1973; Wang and Macdonald, 1991; Schutz and Milberg, 1997).

*Arisaema dracontium* (L.) Schott, green dragon, is a perennial aroid herb that inhabits wet bottomlands along rivers and creeks and forested clay floodplains in eastern North America. Clonal growth occurs via cormlets budding from the underground overwintering corm. Seed production occurs via fleshy fruits produced on a spadix. Sex expression in green dragon is phenotypically labile (Lovett-Doust and Cavers, 1982; Clay, 1993): in any single year, a flowering individual may be male or monoecious (bearing both male and female flowers). Typically, only large individuals are monoecious, and these develop a single infructescence bearing up to 150 berries (Lovett-Doust and Cavers, 1982), each berry containing 1–3 seeds.

Green dragon has low abundance in southwestern Ontario, where it exists at the margin of its range, but is relatively widespread in the eastern United States (Lovett-Doust and Lovett-Doust, 1995). The species is found where suitable habitat is available, but in southwestern Ontario and Quebec, in Canada, the species is listed as vulnerable by COSEWIC (1993) and is disappearing from locations where it had previously been collected (Gauvin, 1984). Demographic studies (Boles, 1996; Boles et al., unpublished data) suggest that recruitment of new seedlings is very low, so the present study was designed to consider the extent to which seed viability, dormancy, or germinability may be limiting recruitment.

Few recent investigations have studied seed germination in green dragon. MacDougal (1901) described the slow germination process of green dragon. Pickett (1913) demonstrated experimentally that germination in both *A. dracontium* and the closely related *A. triphyllum* takes 2–5 mo and indicated that in both species seedling growth was what he termed ‘‘blind,’’ that is, in the first year of

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TABLE 1. Geographic location and climatic data for green dragon populations that were the source of seeds used in this study as reported by Conway and Listton (1974) and the National Oceanic and Atmospheric Administration (1979).

| Location | Elevation (m above sea level) | Latitude | Longitude | Mean temperature (°C) |  | Mean humidity (%) |  |
|---|---|---|---|---|---|---|---|
|  |  |  |  | January | May | January | May |
| Clinton, Ontario | 115.5 | 43°39′ | 81°26′ | −7.7 | 11.0 | 77 | 55 |
| Toledo, Ohio | 203.9 | 41°37′ | 83°40′ | −3.3 | 14.4 | 69 | 51 |
| Cleveland, Ohio | 236.8 | 41°42′ | 80°50′ | −2.2 | 14.4 | 69 | 56 |
| New Albany, Indiana | 241.1 | 38°13′ | 85°53′ | 1.1 | 19.4 | 71 | 55 |
| Baton Rouge, Louisiana | 19.5 | 30°27′ | 91°11′ | 11.6 | 23.8 | 65 | 56 |

growth the embryo grew a corm and small roots were produced, and nutrients were transferred from seed to corm, all prior to the formation of any primary leaves or other photosynthetic organs. Rennert (1902) compared the morphology and anatomy of seedlings in *A. dracontium* and *A. triphyllum* and suggested that the slow germination of green dragon might be related to anatomical and physiological immaturity of the embryo, although the embryo appeared to be morphologically mature.

The following questions are addressed here: (1) what are the patterns of seed viability, dormancy, and germination in green dragon? (2) Do these seed-based phenotypes relate to the ecological and geographical conditions under which the seeds were produced?

## MATERIALS AND METHODS

***Pretreatments***—During August–September 1994, mature infructescences having ~ 70–150 berries/infructescence were collected at random from five populations in eastern North America, as described in Table 1. Populations ranged from Clinton, Ontario, at the northern limit of the distribution range, to near Baton Rouge, Louisiana, in the south. Individual fruits were allowed to air-dry and stored at room temperature (23°–26°C) until May 1995, when experimental pretreatments were initiated (storage in this manner did not affect the dormancy or viability of the seeds). For each population, seeds were mixed and then allocated at random, in three replicate petri dishes, each containing 30 seeds, to each pretreatment. Pretreatments follow.

*Cold stratification*—Seeds were soaked in distilled water for 3 d, wrapped in paper bags, and then stored in plastic bags in a refrigerator (3°C), for 25 d. During the period of imbibition, water was replaced twice a day.

*Scarification of the seed coat*—This was carried out in either of two ways: (1) abrasion by lightly grinding seeds in a mortar with a pinch of clean silica sand until the seed coat was broken; or (2) acid scarification, where seeds were immersed in 96% sulphuric acid for 5 min, and then rinsed thoroughly in running water for 30 min.

*Phytohormone immersion*—Seeds were immersed for 3 d in either a solution of gibberellic acid-3 ($GA_3$) or kinetin, at a concentration of 100 ppm for each phytohormone (Sigma Chemical Co., St Louis, Missouri). The selection of 100 ppm in each case was based on preliminary experiments indicating this concentration for both phytohormones as most effective in promoting germination.

***Germination***—Seeds that had undergone the pretreatments described above were placed on wet filter paper in glass petri dishes (9 cm diameter × 1.2 cm depth). These were then placed in a Conviron (Conviron, Winnipeg, Manitoba, Canada) germination chamber, set at 16 h of daylight at 20°C and 8 h of darkness at 14°C, to approximate general springtime field conditions. To ensure no systematic effects due to position within the chamber, petri dishes were re-arranged at random every 2 d. A second set of seeds was placed in light-tight canisters and set up under conditions of continuous darkness. Manipulation and observation of these dark-treated seeds were carried out in dim green light, and germination was recorded every 2 d for 60 d. Visible radicle growth was used to define germination. At the end of the test period, all ungerminated seeds were tested for viability using a tetrazolium chloride stain (Moore, 1962).

During preliminary studies it had been noted that a yellow, water-soluble material was exuded from soaking seeds. To examine the possible effect of this exudate on seed germination, a group of seeds was exposed to the exudate solution during the germination period, instead of clean distilled water.

***Seedling establishment***—For observation of seedling development, following radicle emergence, the seedlings were placed in soil and covered to a depth of 1 cm, in plastic pots (three replicates of 15 seedlings were used for each of the five populations) and raised under the alternating light and dark conditions given above. One group of seedlings was left in the light-proof containers (but watered regularly) as controls. The number of roots per seedling and the number of seedlings developing any primary leaves were assessed 90 d after initiation of the germination experiment, in order to determine what conditions were associated with ‘‘blind’’ germination.

***Data analysis***—All germination and seedling development data were transformed to percentage values and analyzed using analysis of variance (SYSTAT FOR WINDOWS, 1992). The following parameters were determined.

$$\text{Germinability} = \frac{\text{number of germinating seeds}}{\text{number of seeds initiated}} \times 100. \quad (1)$$

$$\text{Relative germinability} = \frac{\text{number of germinating seeds}}{\text{number of viable seeds initiated}} \times 100. \quad (2)$$

$$\text{Dormancy} = \frac{\text{number of ungerminated but viable seeds}}{\text{number of seeds initiated}} \times 100. \quad (3)$$

$$\text{Relative dormancy} = \frac{\text{number of ungerminated but viable seeds}}{\text{number of viable seeds initiated}} \times 100. \quad (4)$$

$$\text{Mortality} = \frac{\text{number of inviable seeds}}{\text{number of seeds initiated}} \times 100. \quad (5)$$

$$\text{Index of germination rate: IGS} = \sum G/t, \quad (6)$$

where $G$ is the relative germinability percentage, at 5-d intervals, and

TABLE 2. Overall seed germination qualities for five seed populations of green dragon, following storage for 8 mo at room temperature.

| Population | Germinability % (±SE) | Dormancy % (±SE) | Relative dormancy % (±SE) | Mortality % (±SE) |
|---|---|---|---|---|
| Clinton | 25.6 (±4.0) | 24.4 (±0.8) | 49.8 (±5.2) | 50.0 (±3.9) |
| Toledo | 41.1 (±6.4) | 41.1 (±6.4) | 50.0 (±3.9) | 17.8 (±0.9) |
| Cleveland | 48.9 (±4.1) | 32.2 (±4.8) | 39.6 (±4.5) | 18.9 (±0.8) |
| New Albany | 55.5 (±7.0) | 33.3 (±1.5) | 38.3 (±3.8) | 11.1 (±5.0) |
| Baton Rouge | 55.6 (±2.5) | 23.3 (±1.5) | 29.1 (±2.8) | 21.1 (±2.3) |
| Overall mean | 45.3 (±5.6) | 30.9 (±3.3) | 41.4 (±8.5) | 23.8 (±6.8) |

$t$ is total germination period. This parameter characterizes the pace of germination for particular seed replicates.

Mean number of days for 50% of seeds to have germinated (R). (7)

## RESULTS

***Seed quality in five seed collections***—Table 2 summarizes mean values for germinability, dormancy, relative dormancy, and mortality, prior to any pretreatment. The Clinton population had the highest level of mortality (50%), and the New Albany population had the lowest (11.1%). Overall, germinability of the five seed populations decreased with increasing latitude (see Table 1 for latitudes). Compared with the three geographically central populations, both the northernmost (Clinton) and the southernmost (Baton Rouge) had significantly lower dormancy rates (Tukey test, $P < 0.05$). However, the relative dormancy rate (which takes into account the proportion of dead seeds, in particular among the Clinton collection) had a gradual decrease with decreasing latitude (see Table 2).

***Effects of pretreatment on germination***—Seed from two populations, Toledo and Baton Rouge, having the highest and lowest values, respectively, for relative dormancy rate, were used to investigate the pretreatment effects. Subsamples of these seeds were either physically abraded or acid scarified, soaked in the yellow, water-soluble exudate produced by seeds, or treated with kinetin or $GA_3$. Figure 1a, b shows the relative germinability at day 30 for seeds from these two populations. For both populations the two scarification pretreatments did not raise the overall germinability compared to controls; $GA_3$ (100 ppm) and kinetin (100 ppm) both produced increased germinability. Figure 2a, b indicates that the yellow water-soluble exudate tended to slow the course of germination somewhat, but did not diminish the overall final germinability of seeds from either site.

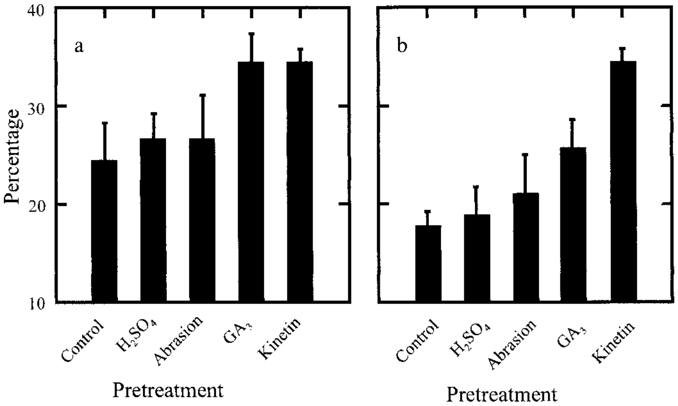


Fig. 1. Effects of scarification of the seed coat (by mechanical abrasion and immersion in 96% sulphuric acid for 8 min) and hormone pretreatment (kinetin and gibberellic acid-3, both at concentrations of 100 ppm), on germination in green dragon seeds from (a) the Toledo population and (b) the Baton Rouge population. Values are means (± SE) of three replicates (comprising 30 seeds each), measured on day 30 post-incubation.

The effects of pretreatment by cold stratification at 3°C are shown in Table 3 and Fig. 3a–e. Stratification at 3°C

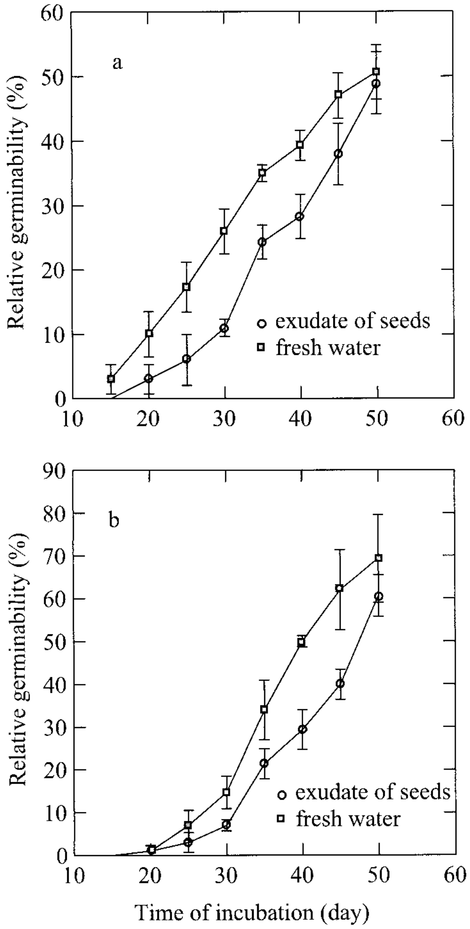


Fig. 2. Comparison of germination period for green dragon seeds collected from (a) the Toledo population and (b) the Baton Rouge population. Seeds were incubated in either distilled water or the exudate from soaked green dragon seeds. Values are means (± SE).

TABLE 3. Comparison of relative germinability (mean ± SE) for five seed populations following pretreatment at 3°C for 3 wk. Results shown are values at the 50th d of incubation. Different uppercase letters indicate significant difference between values in same row; different lowercase letters indicates significant difference between values in the same column (Tukey tests, $P < 0.05$).

| | Population | | | | |
|---|---|---|---|---|---|
| Treatment | Clinton | Toledo | Cleveland | New Albany | Baton Rouge |
| Control | 50.2 ± 4.6<br>B c | 49.5 ± 3.4<br>B c | 60.4 ± 5.6<br>AB b | 61.7 ± 4.7<br>AB b | 70.9 ± 5.9<br>A a |
| 3°C | 88.1 ± 2.1<br>A a | 86.8 ± 4.2<br>A a | 91.9 ± 4.0<br>A a | 87.4 ± 4.3<br>A b | 74.6 ± 4.2<br>B a |

significantly promoted overall germinability ($P < 0.05$), except for the Baton Rouge population where the increase in germinability following stratification at 3°C was not statistically significant. The increase in germinability for the other four populations is attributable to a decrease in the level of dormancy and was not associated with reduced mortality. While no effect of cold stratification was found for relative germinability of seeds collected from the Baton Rouge population, stratification at 3°C did raise the relative germinability ($t$ test, $P < 0.01$) of the remaining four seed collections to almost the same level (means for the relative germinability of cold-treated seeds did not differ significantly among the four populations).

Table 4 shows the index of germination speed for each population, and Fig. 4 shows the pattern of germination over the 50-d observation period. Seeds from the Baton Rouge population had significantly slower germination, and germination continued over a longer period. In contrast, seeds from the Clinton site germinated more rapidly and did so in a flush of germination that spanned just 10 d (days 25–35).

***Role of light in seedling establishment***—Light/dark alternation significantly promoted development of a primary leaf ($P < 0.001$); indeed no seedlings raised in the dark produced a green primary leaf during the study; the few primary leaves produced under dark conditions were chlorotic (Table 5). Light/dark alternation also promoted formation of adventitious roots (Table 6) and was particularly associated with cases where a green leaf had developed (Table 6). Green leaf development seemed to be favored by full exposure to light in the petri plate, rather than the partial exposure experienced by germinated seeds transferred to soil (Table 5). The proportions of seedlings that produced a green leaf followed a general geographic trend, with 23% of Clinton seedlings turning green, compared to 61% of Baton Rouge seedlings.

## DISCUSSION

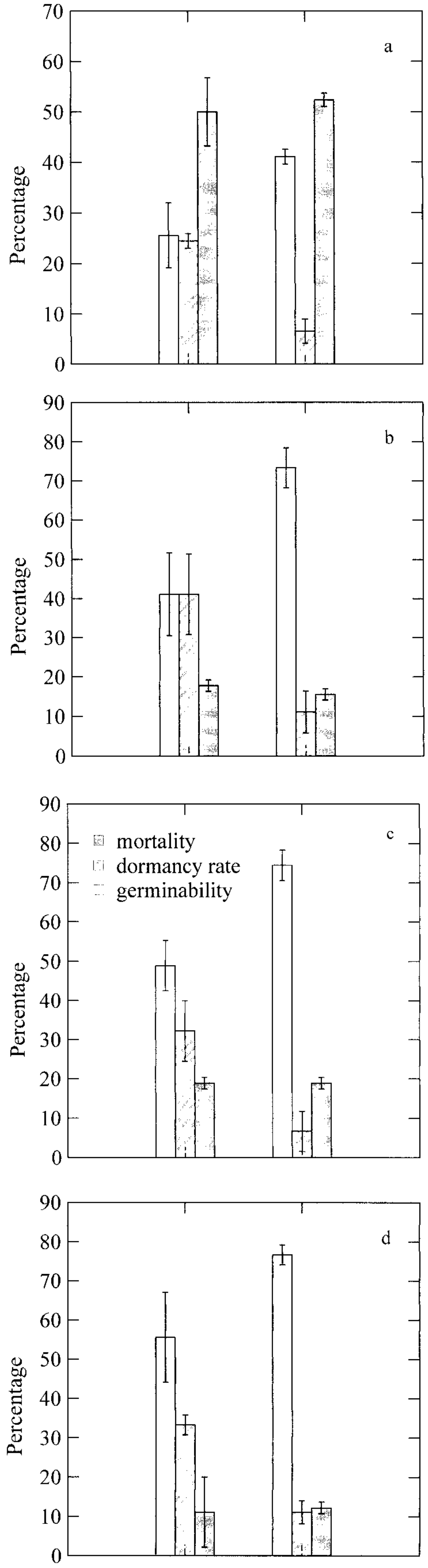
***Seed mortality***—Ontario seeds show the highest mortality rate and overall inviability. This may have played a part in the decline of Ontario populations or may at least explain low recruitment of new seedlings. At this point it is unclear whether the lower survival and germination of these seeds reflect lower genetic vigor or the prevalence of conditions unsuitable for germination and establishment of green dragon (for example, extreme flooding is very rare, due to strenuous monitoring of water levels and control of flood events by Regional Conservation Authorities).

***Dormancy in green dragon***—Pickett's (1913) study of germination in green dragon demonstrated that, even under conditions favorable for germination, only ~60% of seeds ultimately germinated, following incubation for as long as 4 mo. Results of the present germination experiment (e.g., Table 2) also indicate that after incubation for 50 d, the five seed collections had germinability ranging from 25 to 55%, depending upon site. On average, 30.9% of viable seeds did not germinate during the observation period, due to dormancy. Rennert (1902) reported that seed germination in green dragon took fully a month longer than in *A. triphyllum*. Furthermore, in comparing the seeds of the two closely related species, Rennert concluded that there were three distinct differences between the two species in terms of morphology and anatomy: (1) the wall of the outer row of cells of the testa in green dragon was larger and thicker and covered with a cuticle; (2) some of the cells below the outer row of the testa in green dragon contained ‘‘a red colored material,’’ presumed to be tannin, within them; and (3) the size of the embryo in green dragon seeds was smaller, and the procambium in the plumule of the embryo developed less vigorously. Rennert hypothesized that these three features of green dragon seeds were responsible for its slower germination, but no other reports testing these hypotheses have been published.

In the present study, the results of both scarifying the seed coat (Fig. 1) and immersing seeds in a solution containing exudate from seeds (Fig. 2) support Rennert's hypothesis that the hard seed coat and the exudate (possibly a mixture of tannin and/or other water-soluble compounds) contribute to the delay of germination in green dragon seeds. However, these factors are not responsible for dormancy in green dragon, because no significant difference in ultimate germinability was found between controls and these two pretreatments, following incubation periods of 30 and 50 d. In contrast, the exogenous application of two phytohormones significantly promoted early germination and broke dormancy in these seeds (Tables 2, 3). This suggests that a possible endogenous shortage of the two hormones, kinetin and GA3, which have been recognized to exert important effects on differentiation and growth in oranges and to promote general embryo development (Bidwell, 1974; Naylar, 1984; Mayer and Poljakoff-Mayber, 1989), may suppress seed germination, even under otherwise favorable conditions.

There are numerous indications in the literature that cold stratification is an effective measure for breaking seed dormancy (Davies, 1978; Mayer and Poljakoff-Mayber, 1989; Ferasol et al., 1995). In the case of green dragon, seeds from all populations except Baton Rouge showed an increase in relative germinability, from 25 to 40% (Table 3) after being exposed to low temperature (3°C) for 3 wk prior to being incubated. This suggests that a cold and wet period is a prerequisite for seeds to germinate in most of these North American populations, especially those located in the northern part of the distribution. Although we did not analyze seedlings for phytohormone levels in the present study, a decrease in levels of abscisic acid (ABA) and an increase in gibberellic acid concentration have been reported in stratified seeds in many other species (Davies, 1978; Mayer and Poljakoff-Mayber, 1989; Lin, Chen, and Lin, 1994; Bhardwaj and Masoodi, 1994). Embryo growth has also been described in cherry seeds by Pollock and Olney (1959). These authors observed that the embryonic axis increased in cell number, dry mass, and total length during moist storage at 5°C. If similar changes occur in green dragon seeds during wet-cold stratification, the present results would support one of the early predictions of Rennert (1902) that embryo immaturity in green dragon can lead to failure to germinate. However, neither pretreatment of green dragon seeds (e.g., the application of exogenous growth regulators and cold stratification at 3°C), nor pretreatment by combinations of these measures (J.Yang, personal observations) was able to induce germination by all viable seeds (Fig. 1; Table 3). The residual 10–25% of viable seeds that remained dormant despite these pretreatments suggest the existence of additional mechanisms that may keep seeds dormant in this species. (For example low endogenous levels of kinetin and $GA_3$ may inhibit germination.)

***Reaction to cold stratification in five seed populations***—The conditions required for effective cold stratification in general resemble the natural conditions to which seeds are exposed in winter and early spring (Mayer and Poljakoff-Mayber, 1989). Green dragon seeds develop in fall and then are subjected to lower temperatures during the winter months, when they are also exposed to moist conditions under leaf litter or in the soil. Stratifi-



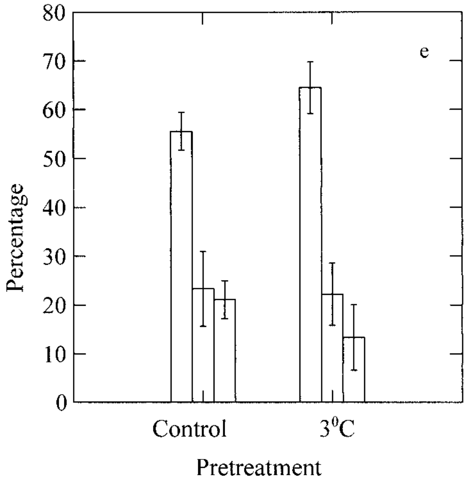


Fig. 3. Comparison of the effects of cold stratification (3°C) on germination, dormancy and mortality in seeds from (a) Clinton; (b) Toledo; (c) Cleveland; (d) New Albany; and (e) Baton Rouge. Values are means (± SE) of three replicates (comprising 30 seeds each).

TABLE 4. Comparison of the index of germination speed ($\Sigma G/t$) among five populations. Values are mean ± SE of ten replicates (30 seeds per replicate). All seeds used for the experiment were pretreated at 3°C for 3 wk.

| Mean of all five populations | Population | | | | |
|---|---|---|---|---|---|
| | Clinton | Toledo | Cleveland | New Albany | Baton Rouge |
| 8.1 ± 2.4 | 9.3 ± 1.8 | 8.5 ± 3.1 | 7.9 ± 2.1 | 8.9 ± 1.2 | 5.7 ± 1.7* |

* Compared with the other four populations, the value for the Baton Rouge population was significantly different ($P < 0.05$; Tukey test).

TABLE 5. Effects of alternating light and dark conditions (16 h light and 8 h dark) on emergence of first leaf in green dragon seedlings.[a] See Materials and Methods for the conditions of seed germination and seedling growth. Note that all leaf buds were chlorotic under dark conditions.

| | Treatment | | |
|---|---|---|---|
| | | Alternating light/dark | |
| Population | Dark water | Soil | Water |
| Clinton | 3.0 ± 1.3 | 8.0 ± 1.7 | 23.3 ± 5.9 |
| Toledo | 0.0 ± 0.0 | 16.0 ± 1.7 | 49.3 ± 3.1 |
| Cleveland | 2.0 ± 0.6 | 25.2 ± 2.8 | 42.1 + 3.8 |
| New Albany | 3.0 ± 1.0 | 20.5 ± 1.6 | 45.2 ± 3.1 |
| Baton Rouge | 1.0 ± 1.7 | 19.7 ± 4.2 | 61.3 ± 3.2 |

[a] Values in the table are number of seedlings with leaf bud, divided by number of seedlings tested, times 100.

cation temperatures are therefore likely to be different for seeds that overwinter in sites experiencing different winter temperatures. Overall, the present results support this. Following storage (23°–25°C) of the seeds for 8 mo, the relative dormancy rate declined with decreasing latitude of sites from which seeds were collected. This suggests that seeds developed in the warmer part of the species' distribution have little requirement for a low-temperature exposure prior to seed germination, whereas, in contrast, a low temperature is necessary to stimulate germination in seeds that developed in the colder parts of the species' distribution. Furthermore, as shown in Table 3, wet-cold stratification for 3 wk at 3°C significantly raised relative germinability of seeds collected from the three northernmost populations by breaking dormancy in those seeds (Fig. 3) and had no significant effect on germinability of seeds from the more southerly Baton Rouge population. For the four northern seed populations, the effect of 3°C was similar and raised relative germinability to similar levels. This association between seed dormancy and the requirements for breaking dormancy (in this case the winter temperatures at the source population) suggests that the difference in environmental conditions under which plants grow causes adaptive differentiation in ecophysiology between populations. This could even lead to the formation of distinct ecotypes, if such differentiation is genetically based (Baskin and Baskin, 1973; Mayer and Poljakoff-Mayber, 1989; Meyer and Monsen, 1991).

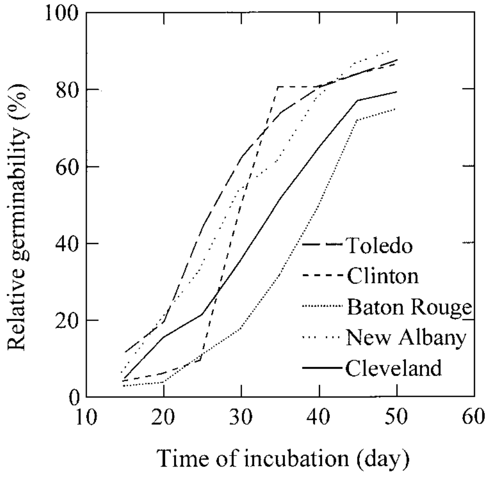


Fig. 4. Time course for germination of green dragon seeds from five populations (Clinton, Toledo, Cleveland, New Albany, and Baton Rouge). Graphs show relative germinability (number of germinating seeds/number of viable seeds). All seeds tested were stratified at 3°C for 3 wk before incubation. Values are means of three replicates (comprising 30 seeds each).

In addition to the difference in relative germinability, differences in germination speed and the period of germination are apparent among the five seed populations. The four northerly seed populations had both the fastest (Table 4) and the more concentrated flushes of germination (Fig. 4). The accelerated pattern of germination was most obvious for seeds from the most northerly population, Clinton. Ecologically, the speed and duration of germination can be adaptive, reflecting the extent of environmental heterogeneity at a site (Harper, 1977; Meyer and Monsen, 1991) or the typical duration of suitable conditions. At a more northerly site the available growing season is shorter, so there should be an advantage to rapid and early germination and establishment. In contrast, extending germination over a longer period could prevent eradication of the whole seed batch, due to adverse conditions that may follow germination. Thus, just as seeds from the most southerly population, Baton Rouge, have an extended germination period and slow germination suited to the warm climate there, so the seeds from the northern populations have a shorter germination period and relatively high germination speed in probable response to the cooler, shorter growing season at that latitude.

TABLE 6. Effects of alternating light and dark conditions (16 h light and 8 h dark) and leaf development on root growth in seedlings.[a] Values are mean % ± SE of three replicates of 20 seedlings per replicate, measured after 90 d of incubation. See Materials and Methods for the conditions of seed germination and seedling growth. For all five seed populations, there are significant differences between columns for the three values listed in same population (Tukey test, $P < 0.05$).

| | Treatment | | |
|---|---|---|---|
| | Dark | Alternating light and dark | |
| Population | Seedlings without leaf | Seedlings with leaf | Seedlings without leaf |
| Clinton | 6.3 ± 2.1 | 82.7 ± 4.2 | 38.7 ± 2.8 |
| Toledo | 9.3 ± 2.3 | 89.3 ± 5.2 | 45.0 ± 2.3 |
| Cleveland | 11.3 ± 2.0 | 85.1 ± 3.1 | 41.0 ± 2.1 |
| New Albany | 14.1 ± 4.1 | 83.1 ± 5.1 | 41.5 ± 5.1 |
| Baton Rouge | 13.3 ± 3.4 | 77.4 ± 8.3 | 53.3 ± 6.1 |

[a] Values in the table are number of seedlings with at least one adventitious root, divided by number of seedlings with at least one basal root, times 100.

***Effects of light on seed germination and seedling establishment***—Light is one of the environmental factors that may regulate seed germination and early establishment of seedlings (Arnim and Deng, 1996). With regard to their response to light, seeds can be divided into three broad groups: (1) those that require light for germination; (2) those in which germination is inhibited by light; and (3) those in which germination is indifferent to light (Mayer and Poljakoff-Mayber, 1989). In the case of green dragon, it seems that the seeds fall into the third group, as the final relative germination percentage did not differ significantly between the dark and the alternating light/dark treatment. However, light does have other effects on the germination of green dragon seeds. Light significantly slowed the rate of germination in all five seed collections, measured by the mean number of days for 50% of final germination to occur. For the more northerly populations, where rapid germination and a concentrated period of germination could be adaptive to the shorter growth season there, the delayed germination of some seeds by light would spread the germination process more evenly throughout the brief window of germination at that latitude. It may also create an environmentally induced polymorphism, in that light-exposed seedlings will germinate slowly, but will be more likely to develop a green leaf, whereas the remainder of the seeds will germinate ‘‘blind’’ (sensu Pickett, 1913) and produce photosynthetic tissue the following year.

Light also alters the phenology of seedling establishment. Although it did not influence emergence of the radicle from the seed coat, it did significantly promote the development of additional adventitious roots (Table 6). The photosynthetic effect of light on development of these roots and the first seedling leaf is possibly also exerted photomorphogenetically. For all five populations, only a small number (<3%) of seedlings that grew in the fully dark condition produced a green leaf bud. In contrast, under light conditions, even after being covered by a 1-cm layer of soil, ~18% of seedlings produced a green first leaf. When seedlings were fully exposed to light, on average ~45% of the seedlings produced an expanded green first leaf. This result is consistent with Pickett's observation (1913) that ~90% of viable seeds were ‘‘blind,’’ i.e., seedlings germinating from this kind of seed developed only a corm and primary root, without a leaf, when the seeds were allowed to germinate in sandy loam with 2 cm of cover. The ecological and evolutionary significance of light in promoting green dragon seedlings to develop a first leaf and adventitious roots seems clear, and the sensitive response of green dragon seedlings to light has an important implication for environmentally induced bet-hedging during germination and establishment.

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