Effects of seed release timing on plant life-history and seed production in a population of a desert annual, *Blepharis sindica* (Acanthaceae)

Kenji Narita

Graduate School of Environmental Science, Hokkaido University, Sapporo 060, Japan

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Abstract

Growth, phenology, survivorship, and seed production were observed in a population of a desert annual, *Blepharis sindica*, with reference to the variation in the timing of seedling emergence. The population consisted of several cohorts induced by rain-cued seed release within a growing season. The fate of 100 individuals of six cohorts was monitored throughout the growing season. Earlier-established cohorts had significantly larger plant sizes and higher reproductive outputs than later cohorts. The time and duration of each phenological stage varied among the cohorts, and they were also influenced by plant size. Mortalities at the seedling stage, vegetative stage, and reproductive stage increased with the delay of seed release. Seed release was concentrated in the early growing season. Fecundity was highest in the earliest cohort and decreased monotonically in later cohorts. The results suggested that even in temporally varying environments, the superiority of early emergent plants was evident. The seed release patterns in temporally fluctuating desert environments are discussed as a compromise between 'diversified bet-hedging' and an optimal timing for maximizing the reproductive success in a growing season.

Introduction

Natural environments are inevitably fluctuating in space and time, and changes in various factors such as water availability, air temperature, and predator activity affect survivorship, growth, phenology, and reproductive success of plants (Schaffer 1974). In fluctuating environments, timing of germination is a critical trait affecting other life-history traits because plants with different emergence timings may experience different environmental conditions (Lacey 1982; Ruhren and Dudash 1996). For example, a cohort of a wild poppy, *Papaver dubium*, that germinated in autumn in England suffered high mortality during winter, but the plants that survived produced at least 10 times as many seeds as did plants of a spring cohort (Arthur et al. 1973). When the length of the growing season is restricted, size superiority of early-emergent plants is a common phenomenon observed in many populations (Miller 1987). For example, in successive cohorts of *Rumex crispus*, plants that attain a large size earlier often have lower mortality, begin to reproduce at a

younger age (Weaver & Cavers 1979), and achieve higher fecundity than do smaller neighbours of later cohorts (Harper 1977; Lee & Hamrick 1978; Cook 1980; Roach 1986; Rees 1994).

In desert environments, life-history traits of plants are greatly determined by rainfall events that fluctuate greatly in quality and quantity among years. Even within a growing season, the occurrence of rainfall is usually unpredictable and heterogeneous (Evenari 1985), and this creates highly variable environments for plants on a short time-scale. Under such conditions, individuals having different timings of emergence within a season experience different environments, which results in differences in the growth rate, phenology, and survivorship among cohorts within a population.

Much attention has been concentrated on the fractional seed germination pattern of desert annuals, with most of the studies being concerned with the variance in seed physiology (reviewed by Baskin and Baskin 1989). Theoretical studies have been developed about delayed germination beyond one year as

a 'bet-hedging' adaptation to the unpredictability of desert environments (Cohen 1966, 1967; MacArthur 1972; Venable & Lawlor 1980; Brown & Venable 1986; Venable 1989; Rees & Long 1992; Philippi 1993a,b). Intraspecific competition for resources is considered another reason for the spreading of germination within a year in desert environments (Leon 1985; Pantastico-Caldas & Venable 1993). Both the unpredictability of environments and the degree of the superiority of early-emergent cohorts would determine the distribution pattern of seed germination. Strong temporal variation in life-history traits and competition among cohorts are expected to affect the long-term fitness of individuals. However, it is still unclear whether the superiority of early-emergent cohorts exists in highly unpredictable desert environments.

To evaluate the effects of emergence timing within a year on reproductive success under highly fluctuating desert conditions, life-history characters among cohorts released and germinated in different rainfalls were observed in a natural population of a desert annual, *Blepharis indica* T. Anders. The aims of this paper are to answer the following questions: How variable is the timing of seedling establishment within a population? Are there differences in survival and fecundity among cohorts that have different emergence timings? And if so, do early-emergent cohorts have an advantage within the population?

Material and methods

Plant material

Blepharis indica is a lignified annual that grows on gravelly and/or sandy ground in the Thar Desert, India. Each inflorescence containing 1–20 flowers becomes a spiny cone with hard bracts retaining woody capsular fruits in the fruiting season (Bhandari 1990). Because of their lignified tough woody stems, branches and roots, plants of this species can remain standing on the ground surface for more than one year after death. Each woody capsular fruit contains two seeds on a short pedicel enveloped in persistent large bracts.

Seed release of *B. indica* is cued by heavy rainfall. First, hard bracts and persistent sepals open in response to rainfall. When a sufficient amount of water infiltrates into the apex of capsular fruits, the capsules tear suddenly and two disk-shaped seeds are thrown away a few meters by hook-shaped structures attached to a pair of capsules (Guterman et al. 1967). In preliminary studies, I observed that about 90% of the

released seeds germinated rapidly, i.e., within 5 hours when sufficient water was given. A fraction of the seeds on a plant remains within the cones even after several rainfall events, and some seeds are kept in capsular fruits even until the next monsoon season. This seed-holding mechanism establishes a persistent aerial seed bank on dead mother plants.

Because of the rain-induced, fractional release and its rapid germination feature, a population of *B. indica* consists of several cohorts induced by different rainfall events within one growing season.

The study site

The study was carried out in an arid grassland (26°59' N, 71°19' E) located in the Indian part of the Thar Desert. There are three distinct seasons: dry summer (from March–June), monsoon season (from July to September), and winter (from October to February). The plant growing season is the monsoon season and the subsequent early winter. Average annual rainfall during the period 1900–1981 was 150 mm, and the rain was mainly concentrated in the monsoon season (Figure 1). The rainfall occurs as a storm and usually continues for less than one hour, and the distribution pattern varied among years. In summer, the air temperature remains around 40 °C, sometimes exceeds 50 °C due to an intensive heat wave, and the minimum temperature sometimes decreases to as low as 0 °C in winter (Shanker 1983). The experimental field has been fenced for more than 30 years to prevent grazing by large herbivores. The grassland community is sparse and dominated by a perennial grass, *Lasiurus indicus* Henr, and an annual herb, *Indigofera cordifolia* Heyne.

Dynamics of cohorts

Ten 50 cm × 50 cm quadrats were established randomly with at least five meter distance in the experimental field immediately after the first rainfall of the monsoon season on 29 June, 1994. Seed release is restricted to short periods of rainfall and released seeds germinate rapidly. Here, 'cohort' is defined as a group of individuals that originated from seeds that were released and germinated because of the same rainfall event. Within the 10 quadrats, the number of dispersed seeds was measured for six cohorts (hereafter Cohort 1 to 6 in release order) released by six of 12 rainfall events. For each of the six cohorts, 100 seeds were marked by small tags within 24 h after release, except for Cohort 6, which was marked

Figure 1. Yearly rainfall pattern in the Thar Desert of northwestern India during 5 years (1990–1994). Values are total precipitation per month.

one week after release. A census of marked seedlings was made twice a month until the beginning of January when all plants were dead. At each census, the number of living plants, basal diameter of stems, and phenological events (i.e., seed, seedling, vegetative, pre-flowering, flowering, and seed setting stages) were recorded. The seedling stage was determined as the time between sprouting of the main stem and flushing of the first leaf. The initiation of the reproductive stage was determined by the time of appearance of the first inflorescence and the flowering stage was determined by the time of first flowering. The initiation of seed set was recognized by the change of fruit color. Plant death was determined by the color and toughness of stem and bracts. Timing and duration of each stage, and survival rate at each stage were evaluated in each cohort. The numbers of flowers and fruits were counted at each observation, and fecundity of each plant was obtained after all plants had died. The relationship between seed release timing (days from first rainfall) and survival rate at each growing stage, and the relationship between the seed survival rate and the

amount of rainfall and the seed densities in 10 quadrats were analyzed by Pearson's correlations. The difference in the basal diameter of the stems at the same time after emergence among cohorts was analyzed by one-factor ANOVA. The difference in phenology among cohorts was analyzed by one-factor ANOVA.

Results

During the surveyed season, 12 rainfall events were observed between 29 June and 13 September; 11 of the 12 rainfalls occurred in June and July (Figure 2a). The timing of seed release was totally concordant with the timing of rainfall (Figure 2b). Most of seeds were released during the early rainfalls in the season, while a few seeds were released in later rainfalls. Even after the last rainfall in the season, a fraction of the seeds remained on dead plants.

Growth in the basal diameter of the stem showed significant variation among the cohorts (Figure 3). Clear increases in the diameter one month after release were observed in the earlier three cohorts. Such a pattern was not observed in the later cohorts. The stem diameters of the three earlier cohorts (Cohorts 1–3) did not differ among each other, and were greater than those of the later three cohorts (Cohorts 4–6) throughout the growing season ($P < 0.05$, Scheffe's F test). Seedling size decreased significantly with the delay of the release timing among the cohorts ($r = 0.582$, $P < 0.0001$, $N = 481$). There was a strong positive relationship in plant size between the seedling and mature stages ($r = +0.790$, $P < 0.0001$, $N = 342$). These results showed the superiority of earlier-emergent individuals.

Both the timing of occurrence and duration of each phenological stage differed significantly among the cohorts (Figure 4). The timing of first flowering and seed-setting significantly differed among the cohorts ($P < 0.001$, respectively, ANOVA). The duration of the pre-flowering stage of the earlier three cohorts were significantly longer than those of Cohort 4. ($F = 10.23$, $P < 0.0001$, Scheffe's F test). Cohort 6 differed from the other five cohorts in its phenological features: it took less than half of the time to start reproduction than the other cohorts, and a few individuals initiated reproduction even when they had cotyledons.

Plant size also affected the phenology in this species, i.e., larger plants started earlier and had longer reproductive stages (Table 1). The timing of each phenological event was negatively correlated with both

Figure 2. The precipitation, and minimum and maximum air temperature of the growing season in 1994 (a), and the number of dispersed seeds per unit ground area ($/\text{m}^2$) in observed cohorts of *Blepharis sindica* (b). Each numeral in the figure indicates the cohort number. Mean number of seeds (open circles) is indicated with standard error (vertical bar, $N = 10$).

Figure 3. Growth pattern of basal diameters of each cohort of *Blepharis sindica*. Mean values are shown at each census time. Cohorts with the same letters within each time indicate non-significant differences by Scheffe's F-test ($P > 0.05$).

Figure 4. Phenological sequence of six cohorts within the population of *Blepharis sindica*. See text for classification of phenological events. Cohort 6 did not set any seeds. *** $P < 0.001$, * $P < 0.05$, NS not significant.

Table 2. The relationship between phenological events (time and duration of each event) and reproductive success. Correlation coefficients between phenological parameters and the number of seeds per reproductive individuals ($N = 200$).

	Time	Duration
Pre-flowering	-0.399***	+0.201*
Flowering	-0.092	+0.015
Seed-setting	-0.060	+0.274***

* $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$.

timing of emergence and seedling size. The duration of each phenological stage was affected negatively by the emergence timing, and positively by plant size.

The fecundity of each individual showed a significant size dependence. Both the number of flowers and capsular fruits per plant showed an exponential increase with stem diameter (Figure 5). Among the phenological traits, the initiation time of the reproductive stages had a negative relationship with fecundity, and the duration of the pre-flowering and seed setting stages had positive relationships with fecundity, i.e., plants that initiated earlier and continued longer reproduction produced more seeds (Table 2).

Due to the strong positive relationship between plant size and seed production, and the distinct differences in plant size among the cohorts, the fecundity varied among the cohorts. When plants that were successful in seed production were compared, the

Figure 5. The relationships between plant size and reproductive output of *Blepharis sindica*. Both the number of flowers (a) and fruits (b) per plant increase exponentially with plant size expressed as stem basal diameter.

mean number of fruits produced per plant decreased monotonically as the release was delayed (Figure 6a). On the other hand, the mean number of fruits produced

Table 1. Standardized partial regression coefficients of phenological parameters for the multiple regression with the timing of seed release and the seedling size (basal diameter of stem).

Phenological parameters	Standardized partial regression coefficients		<i>P</i>	<i>R</i> ²	<i>N</i>
	timing of release	Seedling size			

<i>Time</i>					
Pre-flowering	−0.775***	−0.591***	<0.0001	0.483	347
Flowering	−0.424***	−0.330***	<0.0001	0.208	241
Seed-setting	−0.271**	−0.293***	<0.0001	0.110	200
<i>Duration</i>					
Pre-flowering	−0.245**	+0.154 [‡]	<0.0001	0.098	241
Flowering	−0.081 ^{NS}	+0.106 ^{NS}	0.1099	0.012	200
Seed-setting	−0.068 ^{NS}	+0.273**	0.0001	0.079	200

[†] *P* < 0.05, * *P* < 0.01, ** *P* < 0.001, *** *P* < 0.0001, NS not significant.

Figure 6. Mean fruit production per plant that succeeded in seed production (a), and per released seed at the initial stage (b) in each cohort of *Blepharis indica*. Cohorts with the same letters indicate non-significant differences by Scheffe's F-test (*P* > 0.05). Vertical bars show standard error.

per released seed at the initial stage of this census (100 plants per cohort) did not differ among the earlier three cohorts (Figure 6b).

The survival rate at each growth stage differed among the cohorts (Figure 7). Cohorts 1 and 4 had lower seed survival rates than did the other cohorts, i.e., ca 40% of the seeds died on the ground surface

before germination. Seed survival in the other cohorts was very high (> 90%). Neither seed density nor the amount of rain triggering the seed release affected seed survivorship ($r = +0.591$, $P = 0.294$, $N = 10$; $r = +0.605$, $P = 0.280$, $N = 6$, respectively). Cohorts 1 to 4 had similar mortality patterns in the course of development of phenology after germination. Cohort 5 had high mortality at the seedling stage, but had the same survival curve as the earlier four cohorts after the vegetative growth stage. The survival rate of Cohort 6 showed a constant decreasing pattern throughout growth after germination, and none of the individuals survived until seed-setting. The cumulative mortality at seed-setting differed among cohorts, and there was a negative correlation between emergence timing and mortality ($r = 0.886$, $P < 0.0476$, $N = 6$). Plant size had a significant effect on the survival, i.e., there was a positive correlation between seedling size and life span of individuals (after removal of the individuals that died at the seed stage) ($r = +0.593$, $P < 0.0001$, $N = 405$).

Discussion

The population of *B. indica* observed in this study consisted of cohorts that emerged at each rainfall event, and the growth period of each cohort overlapped the growth periods of all the other cohorts. Even 10-days delay in emergence created a significant difference in growth, phenology, survivorship, and seed production among the cohorts. Individuals of the early cohorts had greater mean diameters than

Figure 7. Cumulative survival rates in the course of development of phenology in each cohort of *Blepharis sindica*. Cohort 6 was observed only from the seedling stage. Stage 1: release–germination; Stage 2: germination–seedling; Stage 3: seedling–vegetative growth; Stage 4: vegetative growth–pre-flowering; Stage 5: pre-flowering–flowering; Stage 6: flowering–seed-setting.

those of later cohorts. The small stem diameters in the later cohorts may be caused by suppression by larger plants in the earlier cohorts. In addition, later-established plants may suffer from a lower capacity of water uptake by smaller root systems because the frequency of rainfall decreases with the progress of the growth season which results in a lower growth rate. The same kind of advantage due to the larger plant size of early-emergent plants has been reported in other studies (Ross & Harper 1972; Cook 1980).

Larger plants started each phenological stage earlier and had a longer duration of each stage than did smaller plants. Earlier flowering and a longer reproductive period resulted in higher seed production. Thus, seed release timing has a strong effect on seed production in this species. Such size-dependent reproductive success has been observed in other desert annuals (Samson & Werk 1986).

The cumulative mortality at seed-setting showed a highly positive correlation with release timing expressed as the number of days after the rain event. The fact that most of the seeds were released in the earlier part of the season may be explained by both the high survivorship and the superiority of earlier emergence for fecundity. Similar kinds of advantages of early established cohorts have been observed in some perennial herbs (Lee & Hamrick 1978; Cook 1980; Tremlett et al. 1984) and colonizing weeds (Weaver & Cavers 1979). Although intraspecific interference or competition sometimes plays an important role in survivorship

of desert annuals (Inouye 1980; Kadmon 1995), at least in this study, density-dependent mortality was not observed within a cohort.

Seed mortality after release varied among cohorts but was independent of release timing, seed density, and amount of rainfall, suggesting the importance of seed predators such as rodents (Wada et al. 1995). Some released seeds were also eaten by ground beetles and ants at this site (unpublished data). The variation of seed mortality among cohorts partly decreased the advantage of early establishment in Cohort 1 in this season.

Cohen (1967) suggested that if there is a predictable environmental cue associated with a good year, environmentally-cued seed germination would evolve under temporally fluctuating environments. The earlier rain-cued seed release observed in this species is considered as an adaptation to the periodic occurrence of a favorable seasons. Because there were no significant relationships between precipitation at the time of seed release and the released seed number, survival or fecundity, the timing of rainfall within a year could be more reliable information for favorable conditions than the amount of rainfall.

Why does this species release a fraction of seeds at each rainfall event in spite of the high survival and fecundity in early-established cohorts? One possible explanation for the fractional seed release is a diversified bet-hedging strategy against year-to-year variation in rainfall patterns (Venable 1985; Philippi

& Seger 1989). For example, if there is a long interval between the first germination and the next rainfall, the cohort will suffer from high risk of extinction and/or low reproductive success due to drought stress. Such discontinuity of favorable conditions should favor fractional seed release. The variable rainfall patterns of the last five years (Figure 1) and the fact that seed mortality was independent of release timing partly support this prediction. A trade-off between the higher reproductive output of earlier-emergent plants and the risk-spreading adaptation to year-to-year fluctuation of rainfall patterns is considered to be important in determining when and what portion of seeds should disperse within a growing season.

Another possible explanation for the fractional distribution of seeds is competition among plants. Leon (1985) developed a mathematical model of optimal continuous germination schedules within a year, introducing competition by the making growth rate proportional to the limiting resource availability *per capita*, and to the size already attained at reproduction. He predicted that spreading seed germination over time is an evolutionarily stable strategy (ESS) when the resources are not abundant. Although the results of this study did not provide direct evidence of competition among plants for resources, spreading of the timing and duration of growth among cohorts may help to decrease the resource competition, i.e., fluctuating and limited water availability may enhance the spreading of seed release over many rainfall events.

In summary, the timing of seed release has a significant effect on the survivorship and reproductive success in *B. sindica*. The fact that the seeds are predominantly released early in the season is explained by the high reproductive success of earlier cohorts through the superiority of larger plants. Both the fluctuations of rainfall pattern among years and seed mortality within a season may explain the spread of seed release within a season as a 'diversified bet-hedging strategy' in desert environments. A fraction of seeds remains on dead plants even after one growing season; this suggests that *B. sindica* may reduce the risk of extinction not only within a year but also between years. The seed release pattern within a season may be affected by this inter-year 'bet-hedging strategy', the fraction of seeds that remain on the dead plants can offset the risk of extinction of all cohorts in one growing season.

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References

- Arthur, A. E., Gale, J. S. & Lawrence, K. J. 1973. Variation in wild population of *Papaver dubium*: VII. Germination time. *Heredity* 30: 189–197.
- Baskin, J. M. & Baskin, C. C. 1989. Physiology of dormancy and germination in relation to seed banks. Pp. 53–66. In: Leck, M. A., Parker, V. T. & Simpson, R. L. (eds), *Ecology of soil seed banks*. Academic Press, San Diego.
- Bhandari, S. 1990. *Flora of the Indian Desert*. MPB Repros, Jodhpur.
- Brown, J. S. & Venable, D. L. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Nat.* 127: 31–47.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Bio.* 12: 119–129.
- Cohen, D. 1967. Optimizing reproduction in randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent conditions. *J. Theor. Bio.* 16: 1–14.
- Cook, R. E. 1980. Germination and size-dependent mortality in *Viola blanda*. *Oecologia* 47: 115–117.
- Evenari, M. 1985. The desert environment. Pp. 1–19. In: Evenari, M., Noy-Meir, I. & Goodall, D. W. (eds), *Ecosystem of the World Vol. 12A*. Elsevier Science, New York.
- Gutterman, Y., Witztum A., & Evenari, M. 1967. Seed dispersal and germination in *Blepharis persica* (Burm.) Kuntze. *Isr. J. Bot.* 16: 213–234.
- Harper, J. L. 1977. *The population biology of plants*. Academic Press, London.
- Inouye, R. S. 1980. Density-dependent germination response by seeds of desert annuals. *Oecologia* 46: 235–238.
- Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *J. Ecol.* 83: 253–262.
- Lacey, E. P. 1982. Timing of seed dispersal in *Daucus carota*. *Oikos* 39: 83–91.
- Lee, J. M. & Hamrick, J. L. 1978. The effect of time of germination on the demographic characteristics of musk thistle population. *Bull. Ecol. Soc. Am.* 59: 51.
- Leon, J. A. 1985. Germination strategies. Pp. 129–143. In: Greenwood, P. J., Harvey, P. H. & Slatkin, M. (eds), *Evolution: Essays in honour of John Maynard Smith*. Cambridge University Press, London.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York.
- Miller, T. E. 1987. The effects of emergence time on survival and growth in an early old-field plant community. *Oecologia* 72: 272–278.

- Pantastico-Caldas, M. & Venable, D. L. 1993. Competition in two species of desert annuals along a topographic gradient. *Ecology* 74: 2192–2203.
- Philippi, T. & Seger, J. 1989. Hedge one's bets, revisited. *Trends Ecol. Evol.* 4: 41–43.
- Philippi, T. 1993a. Bet-hedging germination of desert annuals: beyond the first year. *Am. Nat.* 142: 474–487.
- Philippi, T. 1993b. Bet-hedging germination of desert annuals: Variation among population and maternal effects in *Lepidium lasiocarpum*. *Am. Nat.* 142: 488–507.
- Rees, M. & Long, M. J. 1992. Germination biology and the ecology of annual plants. *Am. Nat.* 139: 484–508.
- Rees, M. 1994. Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *Am. Nat.* 144: 43–64.
- Roach, D. A. 1986. Timing of seed production and dispersal in *Geranium carolinianum*: effects on fitness. *Ecology* 67: 572–576.
- Ross, M. A. & Harper, J. L. 1972. Occupation of biological space during seedling establishment. *J. Ecol.* 60, 77–88.
- Ruhren, S. & Dudash, M. R. 1996. Consequences of the timing of seed release of *Erythronium americanum* (Liliaceae), a deciduous forest myrmecochore. *Am. J. Bot.* 85: 633–640.
- Samson, D. A. & Werk, K. S. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *Am. Nat.* 127: 667–680.
- Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55: 291–303.
- Shanker, V. 1983. Depleted vegetation of the desertic habitat: Study on its natural regeneration. *CAZRI Monograph* 21: 1–30.
- Tremlett, M., Silvertown, J. W., & Tucker, C. 1984. An analysis of spatial and temporal variation in seedling survival of a monocarpic perennial, *Conium maculatum*. *Oikos* 43: 41–45.
- Venable, D. L. 1985. The evolutionary ecology of seed heteromorphism. *Am. Nat.* 126: 577–595.
- Venable, D. L. 1989. Modelling the evolutionary ecology of seed banks. Pp. 67–87 In: Leck, M. A., Parker, V. T. & Simpson, R. L. (eds), *Ecology of soil seed banks*. Academic Press, San Diego.
- Venable, D. L. & Lawlor, L. 1980. Delayed germination and dispersal in desert annual: escape from space and time. *Oecologia* 46: 272–282.
- Wada, N., Narita, K., Kumar, S. & Furukawa, A. 1995. Impact of overgrazing on seed predation by rodents in the Thar Desert, northwestern India. *Ecol. Res.* 10: 217–221.
- Weaver, S. N. & Cavers, P. B. 1979. The effects of date of emergence and emergence order on seedling survival rates in *Rumex crispus* and *R. obtusifolius*. *Can. J. Bot.* 57: 730–738.