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The timing of seed fall, innate dormancy, and ambient temperature in *Lythrum salicaria*

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Abstract

The timing of seed fall and the innate germinability of newly shed seeds may jointly or separately determine whether they germinate immediately upon landing on a suitable substrate or rather are dormant until a subsequent growing season. In 2 years studies, most seed fall of *Lythrum salicaria* occurred during a 6–8 week period beginning about early November. The seeds were released when daily average temperatures were generally $<15\,^{\circ}C$, the reported threshold temperature for germination. Seeds sampled during autumn and winter exhibited enhancement of germination by storage under cold moist conditions, and this effect was most pronounced for seeds gathered early in the seed dispersal period. Seeds gathered late in the season had a fairly high immediate germinability, apparently through enhancement by winter weather. Since either dissemination phenology or innate dormancy would prevent premature seed germination in this population, the prolonged retention of loosestrife seeds on the maternal plant most likely serves primarily to effect temporally staggered dispersal.

Keywords: Seed dormancy; Seed fall; Loosestrife; *Lythrum salicaria*

1. Introduction

There is a lack of comprehensive information on seed dispersal by purple loosestrife, *Lythrum salicaria* L. (Lythraceae), despite its notoriety in North America as a destructive wetland weed spreading mainly by its seeds. Seed dispersal studies often focus on spatial patterning, but the timing of dispersal is also important (Ervin and Wetzel, 2001). Timing

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helps to determine whether or not newly shed seeds will germinate immediately, or rather be dormant until a subsequent growing season. If germination occurs immediately after seed fall, timing determines the length of time available for growth and establishment before winter dormancy conditions occur. Protracted dispersal, by exposing a given year's seed crop to a greater variability of the speed and direction of abiotic dispersal agents, wind and water, may increase the overall dispersal range of seeds. The timing of seed fall is a function both of the time it takes for fruits to mature and the length of time that seeds are retained on the mother plant.

To be effective in reproduction, seeds must be released onto "safe sites," where conditions are appropriate for their germination and subsequent development (Harper, 1977). Germination in early autumn, while possible, would be maladaptive because the winter weather that shortly follows would kill the plants, hence there are no safe sites at this time. In many species, seed germination is delayed by innate dormancy that serves to stagger germination or delay it until a favorable time (Hartman et al., 1990).

McCaughey and Stephenson (2000) found that, for purple loosestrife plants in an Ont., Canada wetland, the first appearance of germinable seed in freshly harvested inflorescences occurred in early August. That developmental event, occurring approximately 27 days after anthesis, was set forth as a safe cut-off point for effective cutting as a control measure. Even in species that ripen seed quickly, however, dispersal may be spread over a long time (Harper, 1977). As the parent plant may retain germinable seed for an additional period of time, the cutoff date for mechanical removal may be delayed somewhat without missing substantial amounts of natural seed fall. To examine this possibility and discern the likely adaptive value of protracted dispersal, we monitored the number of seeds falling near the bases of naturally occurring plants at 2-week intervals and simultaneously determined the extent to which the seeds were characterized by innate dormancy throughout the dispersal period. These findings are examined in relation to daily ambient temperatures with reference to the reported threshold temperature for loosestrife seed germination of 15 °C (Shamsi and Whitehead, 1974). In addition to yielding basic information about seed ecology, our data may help marsh managers schedule mechanical removal of plants before a population releases its seeds.

Of Eurasian origin, loosestrife is generally acknowledged to be disruptive to North American marshland ecology because it displaces other species and is rarely used by wildlife for food, nesting, or cover (Thompson et al., 1987; Mullin, 1998; but see Farnsworth and Ellis, 2001). Unlike many marsh perennials, which are capable of vegetative propagation, loosestrife is non-clonal and reproduction occurs almost solely by sexually produced seed (Thompson et al., 1987). The species bears two-locular seed capsules that dehisce along the septum separating the locules. At maturity, the capsules are surrounded by the persistent hypanthium. The upper portion of the hypanthium consists of comparatively small calyx segments alternating with longer appendages, situated immediately over the apex of the capsule (Gleason and Cronquist, 1991). It appears that this portion of the hypanthium and also the withered remains of stamens effectively screen much of the space immediately over the mouth of the capsule and apparently deters the loss of seeds during early autumn, at which time capsules are open but shaking of an inverted fruiting spike causes very little seed loss (personal observation). Natural seed departure from the capsules evidently results when the seeds are sifted out of the capsules by the action of wind bending and shaking plants. Weathering of the infructescence appears to contribute to seed dispersal.

2. Methods

2.1. Study site

Seed fall monitoring and seed collection for the germinability assay took place during the seed dispersal season of 1987–1988, and a second seed fall monitoring session took place during 1988–1989, at the Tillman Road Wildlife Management Area in Clarence, Erie County, New York, USA, an approximately 29 ha marsh dominated by *Typha latifolia* L. and other herbs. Water levels varied seasonally and between years. The entire marsh area as well as the low-lying portion of an adjacent swamp forest is typically inundated during spring high water. During summer through winter of 1987, the water receded leaving a muddy substrate, but during 1988, a beaver dam across the outlet stream kept the water level at roughly 20 cm throughout the study period.

2.2. Experimental design

To monitor the release of seeds, 10 seed traps were placed 1 m apart along a line transect through a particularly dense stand of loosestrife. The traps consisted of open-topped square wooden boxes (14 cm × 14 cm × 3 cm high), with a base of plastic window screen reinforced with coarse wire mesh. Each trap was half-filled with perlite, an inorganic planting medium that allowed the passage of rainwater but retained seeds. The traps were replaced at 2-week intervals throughout the seed dispersal seasons. Immediately after retrieval, traps were placed for 2 weeks in a growth chamber set at 22 °C and 12 h light/dark cycles, and then transferred to a greenhouse maintained at 22 °C with ambient lighting, conditions favorable for seed germination and early seedling growth (Shamsi and Whitehead, 1974). After this period, a fraction of the trapped seeds had developed into approximately 0.5 cm tall seedlings that were readily counted. Because seasonal variations in the germinability of seeds altered the proportion of trapped seeds that sprouted and thus were counted, we sampled seeds and determined their germinability at each trap removal session. This consisted of gathering and pooling single individual fruiting spikes from 20 haphazardly selected plants, shaking from them an excess of seeds, and placing a 100 seed sample on moist filter under conditions identical to the seed traps. Seed germination, scored after 21 days, served as a correction factor to account for non-germinated, and therefore uncounted, seeds in the traps. In the first season, an assessment of innate dormancy was undertaken using a duplicate set of 100 seeds during each trap retrieval period and subjecting it to dark cold temperature stratification to overcome any innate dormancy. Stratification consisted of placing the seeds on moist filter paper in a petri dish, covering it with foil, and storing them moist at 4 °C for 100–128 days. After storage, each stratified seed sample was tested for germinability in identical fashion to the freshly harvested seeds. Temperature data were obtained from the National Oceanic and Atmospheric Administration weather station located at the Greater Buffalo International Airport, approximately 4.6 km from the study area.

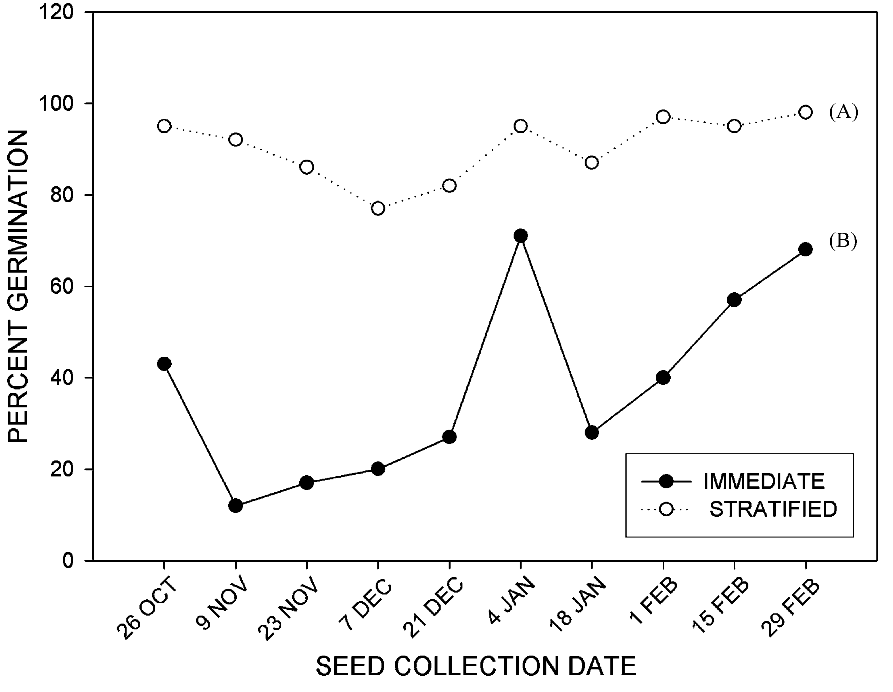

Fig. 1. (A) 1987–1988 and (B) 1988–1989 *L. salicaria* seed fall (connected points) and daily average temperature (unconnected points). Seed fall is mean ± S.E. of square-root transformed counts from 10 traps representing sequential 2-week trapping periods. Temperature data are from nearby airport records; reference line at 15 °C represents reported seed germination threshold (Shamsi and Whitehead, 1974).

3. Results

The first seed fall monitoring season included 10 2-week trapping periods over which a total estimated seed fall of 40,078 seeds m^{-2} was recorded from the mean of 10 traps. The study commenced with a period centered around 19 October during which there was a minor amount of seed fall, comprising approximately 5% of the total recorded for the season (Fig. 1). The following trapping period of the season had the highest seed fall comprising approximately 42% of the total. The remainder of November and the first 3 weeks of December included two periods of substantial, and one of minor, seed fall. About the end of December, there were only trace amounts and the trapping was terminated late in February when seed fall had apparently ended. The second season included monitoring 13 periods during which a total of 2552 seeds m^{-2} was recorded (Fig. 1). This second season was essentially identical to the first in timing, but of much lesser magnitude, probably owing to stress caused by the beaver-induced flooding. All of the seed samples from the 1987–1988 season exhibited enhancement of germination by cool moist storage (Fig. 2). This effect was more pronounced for the seeds gathered during the first half of the seed dissemination period.

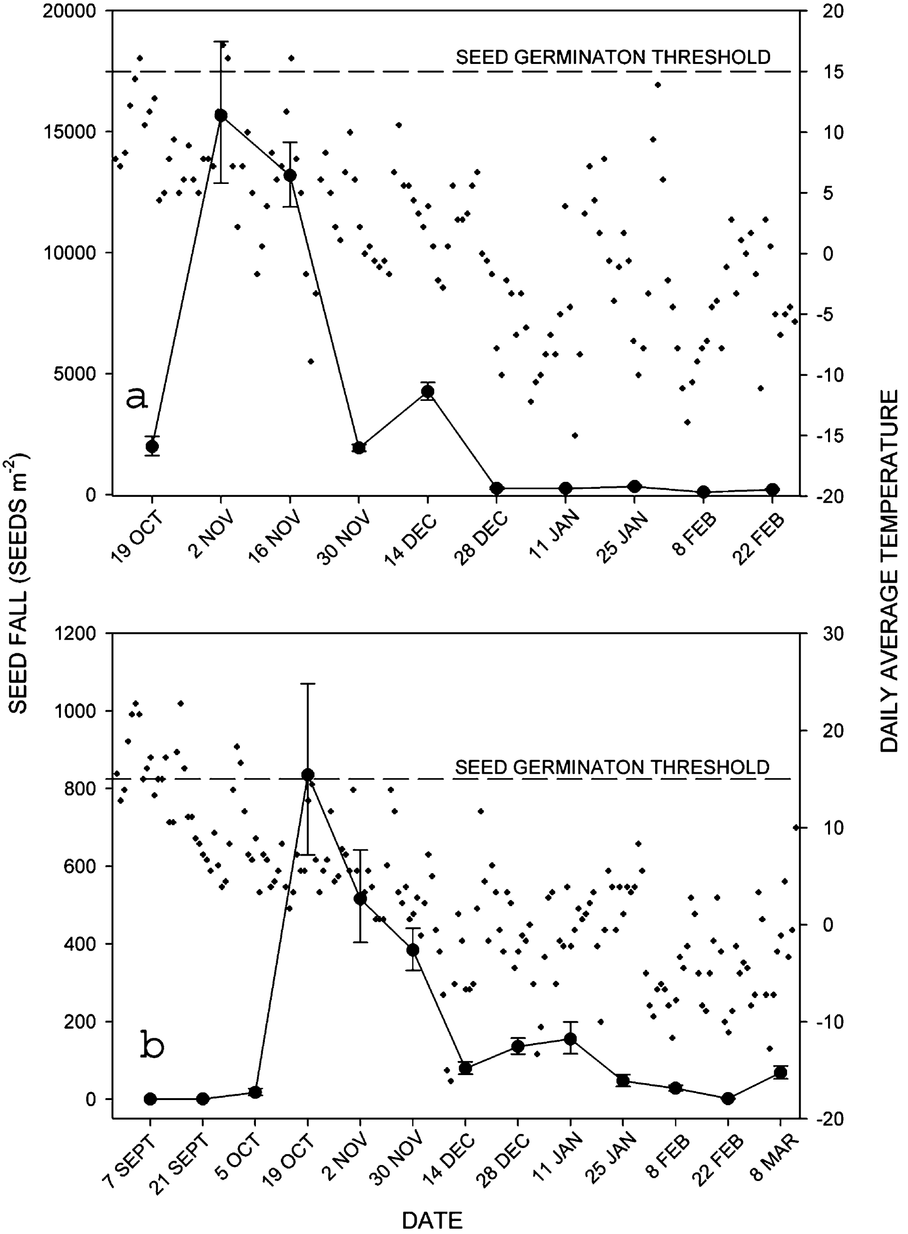

Fig. 2. *L. salicaria* seed germination percentages during 1987–1988 seed fall monitoring period tested in 100-seed lots immediately after collection, and after 100–128 days of cold-moist stratification.

4. Discussion

Under constant temperature conditions, loosestrife reportedly attains greater than 50% seed germination within 5 days at 20 °C, and approximately 90% within 10 days. However, at 15 °C germination is sharply inhibited, with only a trace amount of germination occurring at all, beginning around day 20 (Shamsi and Whitehead, 1974). Young and Clements (2001) reported that alternating temperatures, some of which included a period of low temperatures at levels <15 °C underwent substantial levels of germination. Since temperature fluctuates diurnally there conceivably could be germination in the field even when the daily average temperature is <15 °C. However, the temperature of the saturated soil probably stays fairly constant relative to the ambient air temperature. Lacking precise soil surface temperature data, the present results are interpreted in terms of the constant temperature threshold given by Shamsi and Whitehead (1974), with the understanding that it is only an approximate cut-off point. In this population, there is a 6–8 week period in November and December during which most seeds are released. During each of the two seed fall periods we monitored, only six unseasonably warm days occurred during which the average temperature surpassed 15 °C. These were distributed among three (1987) and four (1988) 2-week seed trapping periods, and no more than three such warm days ever took place sequentially. Moreover, they tended to occur during the early portions of the season when only a slight amount of seed fall was detected. Therefore, it appears that low temperatures during dissemination prevent seedlings from become established by the seed crop of a current year. The finding that *L. salicaria* seeds are characterized by innate dormancy is intriguing. Inasmuch as dispersal occurs during winter, the dormancy may not be of ecological importance in this setting, and delayed seed maturation may be a physiological constraint rather than an adaptive trait. Innate dormancy appears to be common among wetland plants, being found in five of seven marsh species tested by Galinato and van der Valk (1986). Alternatively, it could be of greater importance in its home range, where milder winters may be the norm (e.g. the British Isles).

These results demonstrate that dissemination phenology and innate dormancy both have the potential to prevent autumn germination in this North American population of the introduced wetland weed purple loosestrife. Because the seeds are not immediately germinable, the retention of seeds for a protracted period appears to be more important in staggering dispersal than in preventing premature germination. Marsh managers can probably effectively remove pioneer invading loosestrife plants at any time until the end of the flowering period, and possibly a few weeks after. The mechanism of the fruit dehiscence process, especially as it appears to be related to weather, might explain dispersal phenology. If freeze/thaw fracturing of the capsule causes the release of seeds from the maternal plants, this mechanical component of dissemination could be a contributing factor in the generally northerly distribution of North American purple loosestrife.

References

Ervin, G.N., Wetzel, R.G., 2001. Seed fall and field germination of needlerush, *Juncus effusus* L. Aquat. Bot. 71, 233–237.

Farnsworth, E.J., Ellis, D.R., 2001. Is purple loosestrife (*Lythrum salicaria*) an invasive threat to freshwater wetlands? Conflicting evidence from several ecological metrics. Wetlands 21, 199–209.

Galinato, M.I., van der Valk, A.G., 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Man., Canada. Aquat. Bot. 26, 89–102.

Gleason, H.A., Cronquist, A., 1991. Manual of vascular plants of Northeastern United States and adjacent Canada. 2d ed. New York Botanical Garden, Bronx, NY, lxxv + 910 pp.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London, England, p. 892.

Hartman, H.T., Kester, D., Davies, F.T., 1990. Plant Propagation: Principles and Practices. 5th ed. Prentice-Hall, Englewood Cliffs, p. 559.

McCaughey, T.L., Stephenson, G.R., 2000. Time from flowering to seed viability in purple loosestrife (*Lyhtrum salicaria*). Aquat. Bot. 66, 57–68.

Mullin, B.H., 1998. The biology and management of purple loosestrife (*Lythrum salicaria*). Weed Technol. 12, 397–401.

Shamsi, S.R.A., Whitehead, F.H., 1974. Comparative eco-physiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. 1. General biology, distribution and germination, distribution and germination. J. Ecol. 62, 279–290.

Thompson, D.Q., Stuckey, R.L., Thompson, E.B., 1987. Spread, impact and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. Department of the Interior, United States Fish and Wildlife Service, Fish and Wildlife Research 2.

Young, J.A., Clements, C.D., 2001. Purple loosestrife (*Lythrum salicaria*) seed germination. Weed Technol. 15, 337–342.