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Are Frost Boils Important for the Recruitment of Arctic-Alpine Plants?

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Abstract

To determine if canopy gaps offer “safe sites” for recruitment and persistence of arctic-alpine plants, we compared seedling densities in frost boils and closed vegetation, and examined persistence of *Diapensia lapponica* within frost boils. Seedling density was greater within frost boils, and *D. lapponica* numbers increased in resurveyed frost boils, suggesting persistence. Lower seed bank size combined with higher seedling numbers confirmed that frost boils represent favorable sites for germination.

Introduction

Recent evidence suggests seedling recruitment is a common method of colonizing gap-generating disturbances in arctic-alpine habitats (Chambers et al., 1990; Cooper et al., 2004). In these habitats, frost boils offer “safe sites” for recruitment by reducing competition for space, light, and nutrients, and by providing a gap within the closed vegetation (Barbour and Billings, 1988; Eriksson and Froborg, 1996; Stenstrom, 1999). However, soil upheaval and needle ice formation in frost-disturbed ground causes seedling mortality and upheaval of adults (Anderson and Bliss, 1998). Tundra vegetation and frost boils occur at higher elevations (ca. >950 m) of the Mealy Mountains of Labrador, Canada. The objective of this study is to determine the link between seedling establishment and persistence in frost boil habitats by investigating recruitment patterns of key arctic-alpine plant species, comparing seed bank size between vegetated areas and frost boils, and comparing abiotic aspects of frost boils.

Materials and Methods

The study site (53°38'N, 58°52'W) was approximately 20 km SE of Lake Melville on the south side of an unnamed 1057 m summit in the Mealy Mountains. Local permafrost is indicated by an average air temperature of -4.5°C (2001–2004), consistent with a long-term average of -4 to -7°C interpolated from regional data (Environment Canada, 2003).

In 2001, four study sites were chosen at 995 m a.s.l., comprising ~2000 m², and resurveyed in 2002 and 2004. Two active frost boils in each site, ranging in size from 187 to 1501 cm², were sampled. Vegetation, including seedlings (individuals with cotyledons), and substrate characteristics within each frost boil were mapped using a 1 m² quadrat divided into 10 cm × 10 cm cells. Due to time constraints resurveys included four and seven of the eight frost boils, respectively. For comparison, seedling surveys were conducted within closed canopy in 2002 by randomly locating the quadrat in vegetated substrate adjacent to target frost boils.

Seedlings were mapped within each quadrat cell to determine if there was a gradient in seedling numbers from the center to the edge of each frost boil. The 2001 data from all frost boils were pooled, and cells without seedlings were removed. Numbers of seedlings of unknown and known species (*Diapensia lapponica*, *Minuartia groenlandica*, and *Silene acaulis*) and the numbers of non-seedlings (individuals without cotyledons) of these three species were plotted

against the distance from the center of the frost boil to determine optimal distance for establishment. To determine seedling persistence within frost boils, size categories (small non-flowering, large non-flowering, small flowering, and large flowering) were assigned to the non-seedlings of *D. lapponica*; the only species identified in all classes.

Five 5 × 5 × 10 cm soil cores were collected from each of five active frost boils to determine the relationship between soil seed density to seedling densities in frost boils and adjacent closed vegetation. Cores were taken in vegetation (50 cm upslope and downslope from the frost boil) at the upper and lower frost boil edges and in the center of the frost boil. Each sample was divided into three depth layers (0–2; 2–5; 5–10 cm). Samples were kept cool (~3°C) until seeds were extracted using a modified Malone's Technique (D. Benoit, personal communication, 1999; Malone, 1967).

To measure the soil activity profile, dowels were placed across two frost boils at each site. Two dowel lines (insertion depth of 10 cm and 5 cm at three of the four sites, and 10 cm only at the fourth site) were arranged across the longest length and through the center of each frost boil.

Minitab® (Releases 13 and 14) Statistical Analysis Software for Windows was used for all statistical tests. When the *P*-values approached alpha (0.05) and residuals were not normal, data were randomized (10,000+ times; Manly, 1997). ANOVAs were used to test the differences in seedling recruitment (dependent variables: seedling density), and the number of seeds between frost boil and closed canopy substrates. Within frost boils, seedling locations along the center to edge gradient were determined using regression.

Results

Seedling numbers were consistently higher in frost boil substrate (total number of seedlings: 273 (*n* = 8; survey area = 4615 cm²), 269 (*n* = 4; survey area = 2167 cm²), 383 (*n* = 7; survey area = 3114 cm²)) in 2001, 2002, and 2004, respectively, compared to closed canopy areas (total number of seedlings: 10 (*n* = 5; total area = 490 cm²)) (Sutton, 2002). Three species, *D. lapponica*, *S. acaulis*, and *M. groenlandica* were identified in 2001, (23%, 9%, and 25%, respectively, of that year's total seedling recruitment in frost boils), and patterns of occurrence were similar in subsequent years (24%, absent, and 50% for 2002; 13%, <1%, and 17% for 2004). All other seedlings were grouped into an “unidentifiable” category (43%, 26%, and 28.5% of total seedlings recorded in frost boils in 2001, 2002, and 2004, respectively).

Within frost boils, the density of seedlings was similar in all years, and significantly greater than the 2002 closed vegetation densities

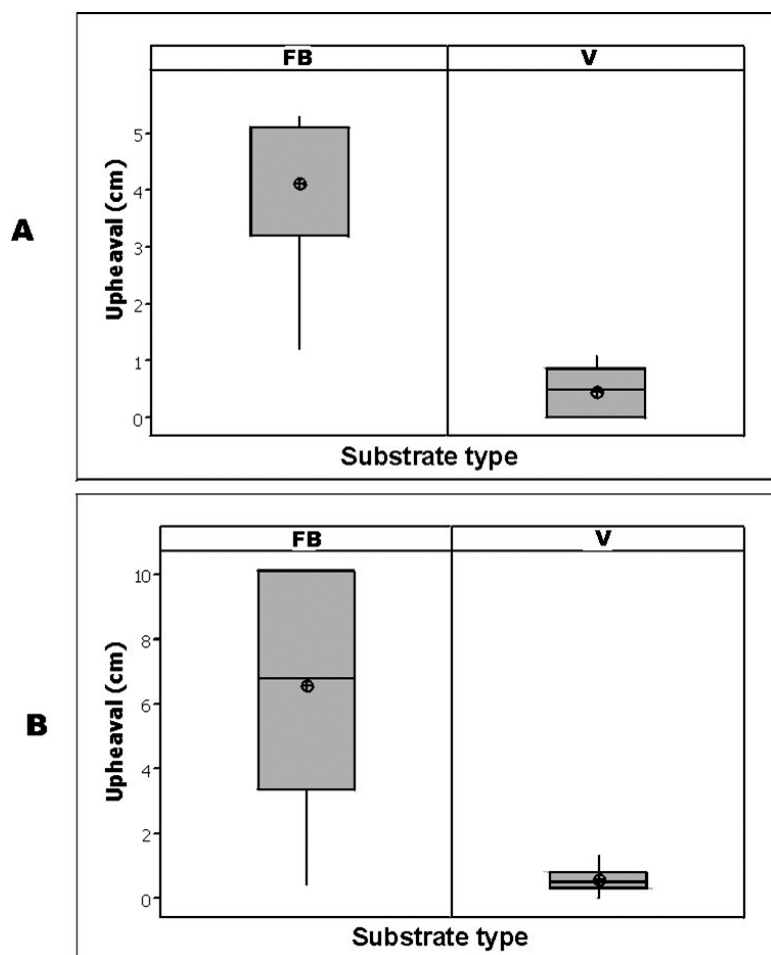


FIGURE 1. Interquartile Range Box plots showing level of soil upheaval with substrate type; (A) 5 cm depths, and (B) 10 cm depths. Circles indicate mean values, the bottom box represents the 25th percentile, and the top box the 75th percentile. FB = frost boil; V = closed vegetation.

($F = 7.55_{[1,7]}$, $P = 0.029$; randomization did not change P -value significance). Overall *D. lapponica* seedling densities in frost boils were consistent within years (Sutton, 2002), while the numbers of small non-flowering individuals of *D. lapponica* increased from 2001 to 2002 (with a range of 28% to 327%; Sutton, 2002). The highest mortality of *D. lapponica* occurred during the transition from the juvenile to the flowering. Other species (*M. groenlandica*, *Cardamine bellidiflora*, *Luzula confusa*) also showed this affinity to frost boils, rather than closed vegetation (Sutton, 2002).

Within frost boils, seedling numbers increased from the center toward the edge ($F = 5.89_{[1,118]}$, $P = 0.017$; number of cells containing seedlings = 119; Sutton, 2002); both seedlings and non-seedlings had a similar distribution. Numbers of small and/or non-flowering individuals were generally greater than the numbers of larger, flowering individuals.

A total of 85 seeds were extracted from 71 soil samples and were found in all substrate categories. Seed numbers differed significantly ($F = 3.69_{[2,67]}$, $P = 0.030$), with the vegetated substrate containing the greatest number of seeds.

Frost boils displayed variable levels of upheaval that were significantly greater than within closed vegetation ($F = 88.74_{[1,39]}$, $P < 0.001$ for 5 cm dowels; $F = 36.93_{[1,65]}$, $P < 0.001$ for 10 cm dowels; Fig. 1). All dowels that were totally displaced were located in frost boil substrate, and significantly greater upheaval occurred in the center compared to near the edges of frost boils ($F = 8.54_{[1,65]}$, $P = 0.005$ for 10 cm dowels).

Discussion

In the Mealy Mountains of Labrador, frost boils represent safe sites for germination, with higher seedling numbers than closed canopy areas. Consistently higher seedling densities, along with persistence of

juvenile and adult plants, particularly *D. lapponica*, indicated that frost boils are important sites for recruitment in arctic-alpine habitats. By providing sites for seedlings as well as mature individuals of species that are apparently unable to persist within the closed vegetation, frost boils play an integral role in community structure by maintaining genetic diversity, facilitating variation in age-class structure, and maintaining biodiversity. However, further studies are needed to confirm long-term persistence within frost boils. In Alaska, even characteristically barren frost boils contain various plant species (Walker et al., 2004).

Within frost boils, higher numbers of seedlings and juveniles compared to adults, along with a similar distribution of all age classes from the center to the edges of the frost boils indicates that mortality continues over time and that all individuals are affected by conditions within the disturbances.

Higher seed numbers in vegetated substrate compared to frost boil substrate suggest a higher germination potential within closed vegetation. However, significantly more seedlings were observed growing in frost boils. Furthermore, significantly warmer (by 3–4°C) summer soil temperatures within frost boils (Sutton, 2002) may allow seeds to germinate earlier and benefit from a longer growing season.

While results of seedling distribution across frost boils could not be directly compared to the results of upheaval (because separate frost boils were used for these analyses), regressions indicate that the optimal location for establishment is at the frost boil's edge, and seedlings decreased near the center where the level of disturbance is at a maximum. Individuals that had experienced at least one year of heave (non-seedlings) also exhibited this pattern. Walker et al. (2004) described heave levels ranging from 3 to 5 cm within vegetated inter-boil areas, but notes that heave levels were 3 to 8.5 times greater in frost boils compared to inter-boil substrate.

Conclusion

In our study area frost boils represent a significant area of disturbance (average of 0.73 frost boils m^{-2} in an area of $\sim 2000 \text{ m}^2$ (Sutton and Hermanutz, unpublished data, 2004), with an average diameter of $>0.5 \text{ m}$). With increased concern over long-term effects of global climate change at higher latitudes, it becomes critical to understand how seedling recruitment of arctic-alpine plants responds to cold soil processes, and what impacts climate change will have on frost boils. Frost boil responses to climate change are predicted to be variable across bioclimates (Walker et al., 2004). Our climate data indicate that the frequency of freeze-thaw cycles in the near-surface soil layer is high (5–6 cycles) (Sutton, 2002); continued monitoring of these cycles and the resulting impacts on seedling recruitment is crucial. Our research indicates that changes in the dynamics of frost boils due to climatic warming would have drastic effects on seedling recruitment, and hence arctic-alpine biodiversity, if habitats critical to successful germination and persistence of key plant species are altered.

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