

The Factors Governing the Distribution of the Rare Plants
Braya longii and *Braya fernaldii* (Brassicaceae) in Natural Habitats

By
Susan Tilley

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Department of Biology
Memorial University of Newfoundland.

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ABSTRACT

The ability of a species to persist in a given habitat and the capability of that species to disperse and establish new populations in unoccupied suitable habitats is imperative for their long-term survival, especially in conditions of environmental change. The limestone barrens of the Great Northern Peninsula on the island of Newfoundland is a hotspot of plant diversity housing several endemics such as *Salix jejuna*, *Braya longii* and *B. fernaldii* (Brassicaceae). In 1997 and again in 2000, the Committee on the Status of Endangered Wildlife in Canada listed *Braya longii* as endangered, and *B. fernaldii* as threatened. The habitat of these calciphiles has been fragmented through human development making the colonization or re-colonization of habitat difficult. To increase the chances of their long-term survival it is essential to protect all critical habitats, including unoccupied suitable habitat. The protection of critical habitat is also a mandate of the Canadian *Species At Risk* Act and the Newfoundland and Labrador *Endangered Species* Act.

To define the critical habitat of *Braya longii* and *B. fernaldii* (Brassicaceae) the importance of unoccupied habitat was evaluated by determining if unoccupied habitats were capable of supporting *Braya* species, and hence be included within the definition of critical habitat. To test the occupancy hypothesis, both substrate types in occupied and unoccupied habitat patches in naturally disturbed sites were seeded with the site-specific *braya* species and the percent emergence and survival of the seedlings measured. At all sites, in all levels of occupancy and both substrate types, *Braya* seeds emerged and persisted throughout the summer and at least into the fall, indicating that unoccupied sites are capable of supporting *Braya*. There was no substantial loss of seedlings to herbivory

at any site for either species, indicating the long-term persistence in these sites is possible. Therefore, unoccupied sites should be included as critical habitat may be of use in restoration efforts. To test whether dispersal limitation was responsible for the lack of colonization of unoccupied habitat, the size of the soil seed bank, amount of seed rain, and distribution of natural seedling emergence was measured. The soil seed bank and seed rain analysis of *Braya* concluded that the *Braya* seed bank is dispersed and variable. Analysis of the distance of seedlings to adult plants revealed that seeds disperse within 50 cm of the adult plant. This suggests that the distribution of both *Braya* species within a site and between sites is limited by dispersal. As a result, the process of colonization of unoccupied patches may be long; indicating that long-term management plans of critical habitat must be put in place.

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INTRODUCTION

The survival of a plant species depends on the availability of suitable habitat and the ability for the individuals of the species to persist in these habitats (Ehrlén and Eriksson, 2000). The long-term survival of a plant species also includes the capability of that species to disperse and establish new populations in unoccupied suitable habitats, as the distribution of suitable habitats is dynamic and can be expected to vary with climate change and anthropogenic disturbance (Ehrlén and Eriksson, 2000; Primack et al., 1992). All suitable habitats, both occupied and unoccupied by a plant species, can be defined as critical habitat as the species requires them for long-term survival.

The purpose of both the recently enacted federal *Species At Risk Act* (December 2002) and provincial *Endangered Species Act* (December 2001) is to prevent extinction or extirpation of a species as a result of human activity (Government of Newfoundland and Labrador, 2002; Canada's Parliament, 2002). Assurance that a species will survive is in part based on the ability to protect its critical habitat, which the *Endangered Species Act* defines "as the habitat that is critical to the survival of a species" (Government of Newfoundland and Labrador, 2002). However, knowledge of most rare species' critical habitat is lacking (Primack, 2000). Conservation of critical habitat needs to include presently unoccupied suitable habitat within and among established populations to allow metapopulation dynamics to proceed unimpeded (Quintana-Ascencio et al., 1998). Dispersal within the metapopulation, meaning between and among localized populations, allows for re-colonization of an area following extinction (Hanski and Gilpin, 1997). Destruction of critical habitat not only destroys present individuals but also changes the ability of plants to colonize and re-colonize within and among suitable habitats. As a

result, there is a need to define and protect unoccupied suitable habitats that have the potential to be colonized (Quintana-Ascencio et al., 1998). Allowing metapopulation dynamics to proceed increases the probability a species will persist as its habitat changes or is lost. A quantitative description of designated species' critical habitat is integral to providing adequate habitat protection, enforcing legislation, and developing appropriate management plans for rare plants.

Past studies of habitat availability, fragmentation, and destruction indicate that the availability of suitable habitat is the limiting factor in the distribution of plant species (Hanski, 1994; Fahrig and Merriman, 1994). In addition, studies of seed dispersal and patch dynamics in forested and scrubland areas indicate that the ability of plants to disperse to suitable habitats can also limit species distribution (Eriksson, 1996; Ehrlén and Eriksson, 2000; Primack et al., 1992; Quintana-Ascencio et al., 1998; Thiede et al., 1996). However, once established in suitable habitat the distribution of the plant species depends on their potential to survive in that patch (Ehrlén and Eriksson, 2000).

The limestone barrens on the Great Northern Peninsula of the island of Newfoundland is a hotspot of plant diversity housing almost 50% of the island's rare plants, such as the endemics *Salix jejuna*, *Braya longii*, and *B. fernaldii* (Hermanutz et al., 2002). Harvard botanists, Bayard Long and M. L. Fernald, first discovered *Braya longii* in 1924 and *B. fernaldii* in 1925 (Meades, 1996a, b). In 1997 and again in 2000, the Committee on the Status of Endangered Wildlife in Canada listed *Braya longii* as endangered and *B. fernaldii* as threatened (Hermanutz et al., 2002). Both species are taxonomically closely related and have similar life histories and ecology (Hermanutz et

al., 2002). *Braya longii* differs from *B. fernaldii* in having larger petals, smaller sepals, and pubescent siliques (Meades, 1996a, b; Parsons 2002).

Both species of *Braya* have very restricted ranges. *Braya longii* historically and presently has been found within a range of 6 km along the coast of Newfoundland from Yankee Point to Sandy Cove, with a newly discovered site at Anchor Point, 14 km to the south (Figure 1; Hermanutz et al., 2002; Meades, 1996a). Historically, *Braya fernaldii* was found from St. Barbe to Burnt Cape, a 120 km stretch. This range has increased to include a population in Port au Choix, 70 km south of St. Barbe (Figure 2; Hermanutz et al., 2002; Meades, 1996b). The most significant barriers to their long-term survival are habitat loss and fragmentation due to quarrying of limestone, road construction, and community development (Hermanutz et al., 2002; Janes, 1999). *Braya longii* is presently distributed into 5 populations and *B. fernaldii* is distributed into 14 populations (Hermanutz et al., 2002), therefore it is vital to determine the critical habitat that should be protected to ensure the survival of the individual populations and the species.

The arctic like weather of the Great Northern Peninsula has further fragmented each population by creating a landscape with scattered patches of suitable arctic-alpine plant habitat. In particular, these 2 species of *Braya* exploit gaps in the vegetation produced by small-scale disturbances, such as frost action and wind and soil erosion, to survive (Greene, 2002; Noel, 2000). Frost action on the limestone barrens has led to the formation of patterned substrate, such as sorted circles and sorted stripes, a phenomenon that is common in polar, subpolar, and alpine regions (Mann, 2003; Washburn, 1956). Sorted circles are areas of patterned substrate with a sorted appearance due to a border of stones that surround a center of finer soil material (Mann, 2003; Washburn, 1956). Sorted

Figure1

Figure2

stripes are patterned substrate found on slopes that have a stripped appearance due to parallel lines of stones separated by stripes of finer material (Mann, 2003; Washburn, 1956). Unsorted substrate is also affected by frost action, however no visible sorting of the soil material can be seen. *Braya* species grow in both sorted and unsorted substrates (Greene, 2002).

The ability for a seed to disperse depends on factors such as the morphology of the seed, the weight of the seed (Ehrlén and Eriksson, 2000), field conditions, and the height from which the seed disperses (Thiede et al., 1996). Both *Braya* species produce hundreds of seeds per year per plant but *Braya longii* seeds weigh approximately 2.5 times more than *B. fernaldii* seeds (Hermanutz et al., 2002), and the average fruiting stalk height of a *Braya longii* plant in 2002 was 44.17 mm compared with 18.02 mm for *B. fernaldii* plants (Hermanutz, unpublished data). The spatial arrangement of individual seedlings is determined by seed dispersal and subsequent seed shadow (Thiede and Augspurger, 1996). The occupation of a habitat includes temporal as well as spatial elements and therefore some portion of unoccupied suitable habitats may become occupied in the future as a result of either dispersal into the area as seed rain or by seed present in the soil seed bank. Similar species have a long-lived seed bank, however the size and distribution of either *Braya* species seed bank is unknown (Hermanutz et al., 2002).

The ability of plants to persist in a habitat is dependent on the species ecological requirements and its ability to endure herbivory, pathogens, nutrient limitation, and disturbance (Thiede et al., 1996). Habitat that appears suitable may be unoccupied by *Braya* individuals as a result of inability to access the patch due to limited dispersal

ability or because the habitat may in fact be unsuitable for the species to complete its life cycle. The suitability of unoccupied habitats can be evaluated by the addition of seed (Ehrlén and Eriksson, 2000). *Braya* inhabiting disturbed populations are damaged by the insects, *Plutella xylostella* (L) (Diamondback moth) and *Delia platura* (Meigen) (cabbage root maggot), and an unknown fungus pathogen that limit individual's survival (Hermanutz et al., 2002). In other studies, the persistence of plant species has been unsuccessful because of high levels of seed and seedling predators and a decrease in disturbance by hurricanes and fire that create gaps in the vegetation for the plants to exploit (Primack et al., 1992).

In this study the distribution of the rare plants *Braya longii* and *B. fernaldii* are investigated to determine whether unoccupied habitat should be defined as critical habitat for these species. The objectives of this study were to determine: 1) if unoccupied sites are suitable habitats by experimentally adding stratified *Braya* seeds; 2) if dispersal limits colonization of unoccupied sites by quantifying seed rain into those sites and resident soil seed bank size; 3) if the dispersal capabilities of parent plants is limiting seedling distribution; 4) if the level of seedling herbivory limits the ability for seedlings to persist in suitable habitat; and 5) if the type of substrate (sorted or unsorted) differently affects the above parameters.

MATERIAL AND METHODS

SITE SELECTION

To define the critical habitat of *Braya longii* and *B. fernaldii* 3 naturally disturbed study sites were established for each species. Naturally disturbed sites are defined as having no obvious disturbance to the substrate and vegetation due to anthropogenic activity (Greene, 2002). The sites were selected based on a general definition of suitable habitat set by Greene (2002; Table 1). The sites containing suitable habitat were then analyzed with a second set of criteria that defined each site as either an “occupied” or “unoccupied” site (Table 2). These criteria were necessary to partition whether the availability of suitable habitat or the dispersal capabilities of *Braya* species limits their distribution. The purpose of defining detailed criteria for both occupied and unoccupied sites was to keep additional factors that may determine distribution constant through all study sites.

After each site was analyzed with both sets of criteria, 2 occupied sites and 1 unoccupied site for each species was established (Table 3). Many sites did not fit the criteria and therefore were eliminated as possible sites for this study (Table 4). The exception to site inclusion was Sandy Cove, as it was included as an occupied site even though it lacks sorted substrate, as there was no other alternative. *Braya longii* only grows in 3 natural sites: Sandy Cove, the Airstrip, and the Lion’s Club. The Lion’s Club could not be used in this study, as there was no *ex situ* seed bank available to complete the field emergence tests using conditioned seeds (Table 4).

Table 1: The criteria that define suitable habitat for both *Braya* species (after Greene, 2002).

Criteria
Includes non-vegetated areas
Includes non-wetland areas
Presence of exposed substrate
Above the high tide water level

Table 2: The criteria that define an occupied or unoccupied study site for both *Braya* species.

Occupied	Unoccupied
Contains suitable habitat	Contains suitable habitat
Anthropogenically undisturbed	Anthropogenically undisturbed
Contains either <i>Braya longii</i> or <i>B. fernaldii</i> individuals	Absence of both <i>Braya longii</i> and <i>B. fernaldii</i> individuals
Presence of sorted or unsorted substrate	Presence of sorted or unsorted substrate
Less than 1 km from the ocean	Less than 1 km from the ocean
Presence of <i>ex situ</i> seed bank at MUN Botanical Gardens	Found within the natural distribution of <i>Braya longii</i> or <i>B. fernaldii</i>

Table 3: The site name, location and study species, and occupancy of each study site.

Site	Location	Species	Occupancy
Airstrip	Sandy Cove	<i>Braya longii</i>	Occupied
Sandy Cove	Sandy Cove	<i>Braya longii</i>	Occupied
Tuck Site	Sandy Cove	<i>Braya longii</i>	Unoccupied
Anchor Point	Anchor Point	<i>Braya fernaldii</i>	Occupied
Port au Choix	Port au Choix	<i>Braya fernaldii</i>	Occupied
Ice Point	Anchor Point	<i>Braya fernaldii</i>	Unoccupied

Table 4: The reasons occupied or unoccupied sites containing suitable habitat were eliminated from the study.

Location	Number of Possible Study Sites in Area	Occupancy	Reason
Lions' Club	1	Occupied	No <i>ex situ</i> seed bank available
Bear Cove	1	Unoccupied	Too far inland
Anchor Point	6	Unoccupied	Too far inland and/or did not contain both substrate types
Port au Choix	3	Unoccupied	High level of human activity in area

STUDY SITES

All names and locations used for study sites are consistent with *Braya* Recovery Plan (Hermanutz et al., 2002). The Sandy Cove Airstrip was built between 1974 and 1979, but the adjacent substrate contains natural limestone heath, exposed bedrock, patchy vegetation, and patterned substrate (Figure 1; Greene, 2002). Sandy Cove also has natural limestone heath and exposed bedrock but does not have patterned substrate. The Tuck site is less than 1 km from the Airstrip, and is separated from the Airstrip and the ocean by a forested strip (Figure 1). This reflects the proximity of all *Braya longii* sites to each other. All three sites are 13 to 15 m above sea level and a few hundred meters from the ocean (Greene, 2002).

Anchor Point is 1 to 1.5 km farther inland than Sandy Cove is separated from the ocean by a forested area (Greene, 2002). Anchor Point is 15 to 20 m above sea level and contains both patterned substrate, with 0.5 to 1.5 m wide polygons, and unpatterned substrate (Greene, 2002). Port au Choix is part of the Tableland formation, whereas the Anchor Point area is part of the Eddies Cove formation (Figure 2; Greene, 2002). Port au Choix contains patterned substrate but not sorted polygons as with all previous sites. Instead, the substrate at Port au Choix is a stripped pattern. Port au Choix is a Natural Historic Site and thus receives heavy visitation. Ice Point has both sorted polygons and unpatterned substrate and is greater than 1 km from a seed source. This reflects the 190 km range of *Braya fernaldii* on the Great Northern Peninsula (Hermanutz et al., 2002).

OCCUPANCY

Within an occupied site there are two levels of occupancy, “occupied present” and “occupied absent”. The occupied present plots function as a control to observe and measure natural activity of *Braya* adults, seedlings, and seeds. An occupied present area is a 1 m x 1 m plot that contains a flowering adult individual. There were 20 of these studied at each site, 10 in sorted substrate and 10 in unsorted substrate, with the exception of Port au Choix (Table 5). At Port au Choix there are very few plants and thus it was only possible to find 13 occupied present plots, 3 in sorted substrate and 10 in unsorted substrate. The function of the occupied absent plots was to measure small-scale dispersal ability of *Braya* from nearby occupied present plots. An occupied absent area is also a 1 m x 1 m plot, however it contains no *Braya* individuals and is at least 2 m away from a flowering adult individual. In both occupied absent areas and unoccupied sites, as in occupied present areas, there were 20- 1 m x 1 m plots established, 10 in sorted substrate and 10 in unsorted substrate (Table 5). The function of the unoccupied plots was to measure large-scale dispersal ability of *Braya* from nearby occupied sites.

ADDITION OF STRATIFIED SEED TO OCCUPIED AND UNOCCUPIED PLOTS

To determine if unoccupied sites are unoccupied because of inappropriate conditions for germination and emergence, stratified, scarified seeds were added to 50 cm x 50 cm plots in both sorted and unsorted substrate of occupied and unoccupied sites. Each plot in sorted substrate attempted to cover as much of the sorted circle as possible and all plots were mapped for the presence and location of indigenous *Braya* seedlings and adult plants. In occupied present areas each type of substrate had 1 control and 1 seed

Table 5: Summary of the number of each treatment applied to each *Braya longii* and *Braya fernaldii* study site.

Species	Site	Plot	Substrate Type	Treatment			
				Observation Plots	Stratified Seed Addition Plots	Soil Seed Bank Samples	Seed Rain Traps
<i>Braya longii</i>	Airstrip	Occupied Present	Sorted	10	1	25	10
			Unsorted	10	1	25	10
		Occupied Absent	Sorted	10	3	25	10
			Unsorted	10	3	25	10
	Sandy Cove	Occupied Present	Unsorted	10	1	25	10
			Unsorted	10	3	25	10
	Tuck Site	Unoccupied	Sorted	10	3	25	10
			Unsorted	10	3	25	10
<i>Braya fernaldii</i>	Port au Choix	Occupied Present	Sorted	3	1	10	10
			Unsorted	10	1	25	10
		Occupied Absent	Sorted	10	3	25	10
			Unsorted	10	3	25	10
	Anchor Point	Occupied Present	Sorted		1	25	10
			Unsorted	10	1	25	10
		Occupied Absent	Sorted	10	3	25	10
			Unsorted	10	3	25	10
	Ice Point	Unoccupied	Sorted	10	3	25	10
			Unsorted	10	3	25	10

addition plot, for a total of 4 plots in occupied present areas (Table 5). Plots established in occupied absent and unoccupied areas had 1 control and 3 seed addition plots, for a total of 8 plots in each type of substrate. Fewer seeded plots were set up in the occupied present areas where it was evident that there is suitable habitat because plants are naturally present. The occupied present plots were included to determine the natural emergence rate of this year to compare it with the emergence rate in occupied absent and unoccupied plots. Seeds used for the seed addition experiment were dry, cold stratified

after harvest for approximately 2 to 3 months to ensure that they had completed their winter dormancy process. The seed coats of all seeds were then scarified with fine sandpaper to mimic the natural action of seed movement through the soil profile due to frost heave. For many populations, only a minimum quantity of seed from the *ex situ* collection was available. The seeds used for the seed addition experiment were harvested in 2001 from each site in support of the *ex situ* program at MUN Botanical Garden. Only seeds collected from the site were used to seed plots established in that site. Seeds from other populations were not introduced, as it has been shown that each population appears to be a unique genetic unit (Parsons, 2002). In the unoccupied sites, the population of *Braya* closest to the site was used in the seeded plots. At Ice Point, Anchor Point seeds were used and at the Tuck site, Airstrip seeds were used in the seeded plots.

Seeds were added to all sites between June 3 - 6 (2003). Each seed was laid on the soil and patted down gently to ensure it stayed in the soil. A seed was added to each 10 cm x 10 cm block where the grid lines crossed and the position was marked with a toothpick. Plots were mapped in June and surveyed again in July, August, and September to observe seedling emergence and survival as well as any insect damage. Port au Choix could not be surveyed in September due to vandalism of the identification tags, making seedlings unidentifiable. Due to a limited supply of seeds all sites did not have the same number of seeds planted in the seeded plots. At Anchor Point and Ice Point 15 seeds were planted, at the Airstrip and the Tuck Away site 20 seeds were planted, and at Port au Choix and Sandy Cove 25 seeds were planted.

LABORATORY EMERGENCE TESTS

Given that not all seeds are viable, it is imperative that the potential emergence rate is known to be able to predict maximum seedling emergence rate in the field. To determine the emergence rate of each population under controlled conditions, an emergence experiment was initiated. A variable number of seeds per population, determined by availability (120 Port au Choix seeds, 120 Sandy Cove seeds, 45 Airstrip seeds, and 56 Anchor Point seeds), were placed on the surface of the soil in 11 cm x 6cm x 16cm peat flats. As in the seed addition experiment, seeds planted were dry, cold stratified and the seed coats of all seeds were scarified with fine sandpaper. The soil mixture was 15 parts soil sample from the Great Northern Peninsula, 15 parts peat, and 1 part perlite. The average pH of *Braya* substrate is 8.0 (Greene, 2002). To raise the soil mixture's pH level to 8.0, powdered lime was added. The seeds were kept under a temperature regime mimicking spring conditions on the Great Northern Peninsula (16°C day /10° C night, 17 hours light) and allowed to germinate. A maximum of 20 seeds were placed in each peat flat and the flats were placed in a Percival Scientific Environmental Chamber, Series 965 Microprocessor®. A toothpick marked the position of each seed. Seeded flats were moved around every three days too ensure all flats receive the same amount of light. The flats were watered every three days with 150 ml of tap water.

NATURAL SEEDLING RECRUITMENT IN OCCUPIED AND UNOCCUPIED SITES AND LEVEL OF LOSS TO HERBIVORY

To determine the level of natural seedling recruitment within a site and the distance those seedlings were dispersed from the parent plant, the distribution of

seedlings in 1 m x 1 m plots was mapped. In addition to comparing the distribution of natural seedlings in sorted and unsorted substrate and the dispersal distance, these plots were vital for determining if herbivory is an important source of mortality in seedlings, as has been documented in adult plants (Hermanutz and Parsons, 2002; Parsons, 2002).

At each site, 10 plots containing sorted polygons and 10 randomly selected plots of unsorted substrate were sampled for a total of 20 plots at each site (Table 5). Nails in 2 diagonally opposite corners indicated the plot position and tags marked the plot number. The average size frost boils in limestone barrens (including the center and edge) is approximately 50 cm x 50 cm (Noel, 2000). Therefore, each 1 m² plot in sorted substrate usually includes a full frost boil. Each plot was mapped in June and resurveyed in July and August to measure seedling recruitment and the distribution of seedlings and adult plants within the plots. Each seedling was examined for insect damage. In July some plots had to be moved and new plots were set up because *Braya* plants were found in occupied absent plots. This was because the *Braya* were just starting to grow in June and some plants did not have any foliage until July, making them impossible to notice.

SIZE OF SEED BANK

The size of the seed bank was analyzed to determine whether seeds were present in unoccupied sites and the possible distribution of future *Braya* individuals. To compare the size of the seed bank at all sites 5 soil samples were collected from a maximum of 5 unsorted and 5 sorted plots in occupied present, occupied absent, and unoccupied areas for a total of 440 soil samples (Table 5). The plots used to collect soil samples were decided before seedling emergence as to not be biased by the number of seedling per plot.

Each soil sample was 10 cm deep and 3 cm x 3 cm wide. In unsorted substrate, soil samples were taken from the 4 corner positions and 1 from the center of the plot because the seeds may be anywhere in the substrate. In sorted substrate, seedlings and adult plants are concentrated around the edge of the sorted polygons (Noel, 2000). In the sorted polygons 4 soil samples were taken from the edge and 1 was taken from the center. Soil samples were collected before the seeds were dispersed at all sites. All soil samples were taken between August 7 - 8 (2003), with the exception of Port au Choix where soil samples were taken on July 2. Port au Choix plants mature earlier due to the more southerly location of this site.

Soil samples were kept in a refrigerator at 4° C after collection. Particles greater than 1 cm in diameter were removed from each soil sample. The soil samples were weighed and then filtered through 3 sieves with mesh widths of 2.0 mm, 0.6 mm, and 0.15 mm. The number of seeds per sample was determined by visually inspecting each sieved soil sample for *Braya* seeds with a stereomicroscope. The ability of this technique to remove all *Braya* seeds from the soil sample was tested and confirmed by placing a known number of *Braya* seeds into a blank soil sample, processing the sample as above, and removing the seeds. *Braya fernaldii* seeds was used because it is smaller on average than *B. longii* seeds.

SEED RAIN ANALYSIS

The seed rain into and within sites was analyzed to determine if seed dispersal limits *Braya* distribution and whether seeds were able to disperse to unoccupied sites. To determine the level of seed rain into the study areas seed traps were established at each

site. Seed traps consisted of 8.5 cm diameter petri traps containing a piece of sticky paper that covered the entire bottom of the petri plate. The sticky paper was stuck to the bottom of each petri plate with two-sided carpet tape. A drainage hole for water was also drilled into the petri plate. In each site, 5 seed traps were added to 2 unsorted and 2 sorted plots in occupied present, occupied absent, and unoccupied areas for a total of 180 traps (Table 5). The seed traps established in the occupied present areas function as controls, as it is expected that the parent plants have the capacity to disperse seeds within the 1m² plot.

In each plot the seed traps were arranged in the 4 corner positions and 1 in the center. Each seed trap was anchored to the substrate by a nail through the center of the trap. The traps were anchored to the substrate between August 7 - 8 (2003) before the plants dispersed seed, with the exception of Port au Choix where the traps were anchored on July 2. This allowed for a maximum time period to measure seed rain. One trap was lost from each of the Ice Point, Anchor Point, Tuck, and Sandy Cove sites by September. It is suspected that they blew away in the wind. Fifteen traps were lost by high winds from Port au Choix because the substrate is very loose rock, but also because this site receives heavy visitation. Ten of the fifteen traps were missing from an area where other field gear had also been tampered with.

SOIL TEMPERATURE

Soil temperature was an important physical factor to measure as it is known to have a significant affect on the emergence of seedlings and therefore provides information on the suitability of each site. Soil temperature was measured and compared between occupied and unoccupied sites and in sorted and unsorted substrate by Donato

(2002). The soil temperatures were measured daily using StowAway Tidbit Temperature Data Loggers®. These small, water proof, battery operated instruments record the soil temperature at set intervals. Each instrument was placed at a 10 cm depth below natural undisturbed substrate in many of the sites (Table 6).

DATA ANALYSES

Both the 1m x 1m plots used to take observations on the natural distribution of seedlings, and the 50 cm x 50 cm plots to which *Braya* seed was added were mapped with a 1:10 ratio, so that each square on graph paper represented 10 cm³ on the ground. From the maps the number of seedling in occupied present, occupied absent, and unoccupied sites and the average distribution of *Braya* seedling around a parent plant was calculated.

Minitab Statistical Software for Windows, Version 13.32 was used to carry out all statistical tests (eg. ANOVA) performed in this study. For each test residuals were examined for normality, independence, and homogeneity to ensure that the assumptions assumed in statistical test were not violated. *Braya longii* and *B. fernaldii* were analyzed separately in each test. P-values from these tests were used to determine whether differences between data were statistical significant when alpha was 5%. In the laboratory emergence tests one-way ANOVA's were used to determine if percent emergence, days to first emergence, and time to 50% emergence were statistical different due to the population from which the seeds were collected. In situations where the p-value was between 0.02 and 0.07 the data was randomized. In the seed addition experiment

Table 6: The location of soil temperature recorders in each site (Donato, 2002).

Hobo ID	Site	Species	Occupancy	Substrate Type
1	Airstrip	<i>Braya longii</i>	Occupied	Sorted
2	Airstrip	<i>Braya longii</i>	Occupied	Unsorted
3	Sandy Cove	<i>Braya longii</i>	Occupied	Unsorted
4	Tuck Site	<i>Braya longii</i>	Unoccupied	Sorted
5	Anchor Point	<i>Braya fernaldii</i>	Occupied	Sorted
6	Anchor Point	<i>Braya fernaldii</i>	Occupied	Unsorted
7	Port au Choix	<i>Braya fernaldii</i>	Occupied	Sorted
8	Ice Point	<i>Braya fernaldii</i>	Unoccupied	Unsorted

the p-values obtained from the general linear model were used to determine whether differences seen in percent emergence were statistically significant between the population, level of occupancy, or substrate type in which they were found. Before these statistical tests were performed data was standardized to laboratory emergence results because it is known viable seeds do not always germinate (Hermanutz and Parsons, 2002). Within the observational plots, one-way ANOVA's and general linear models were constructed to determine if the number of seedlings differed between occupied present plots because of the population or substrate type in which they were found. The soil temperature data was also analyzed using a general linear model, which determined whether significant differences in soil temperature were a result of the population, substrate type, or month from which the measurements were taken.

Sigma Plot for Windows, Version 8.0 was used to create all graphs and Microsoft Excel 2000 was used to carry out general descriptive statistics.

RESULTS

LABORATORY EMERGENCE TESTS

On average *Braya longii* populations obtained a higher percent emergence and took fewer days to reach first emergence and 50% emergence than *B. fernaldii* (Table 7). The percent emergence and time to reach 50% emergence was significantly affected by the population from which the seeds were collected for *Braya longii* seeds, but not *B. fernaldii* (Table 8). *Braya longii* seeds harvested from the Airstrip site emerged fastest and to the highest level.

ADDITION OF STRATIFIED SEED TO OCCUPIED AND UNOCCUPIED PLOTS

At all sites, in all levels of occupancy, and both substrate types, *Braya* seeds emerged and persisted for the survey period indicating that unoccupied sites are capable of supporting *Braya* growth. The substrate type and the presence or absence of *Braya* in the plots was not found to significantly affect the percent emergence of *Braya longii* or *B. fernaldii* seedlings in the addition plots (Table 9). In contrast, the population identity was found to significantly affect the percent emergence of *Braya longii* and *B. fernaldii* seedlings (Table 9). The Tuck site had the highest percent emergence of all *B. longii*, while Port au Choix and Anchor Point had approximately equal percent emergences of *B. fernaldii* (Figure 3). It could not be determined if substrate type affected *Braya longii* seeds as Sandy Cove only had unsorted substrate and thus there was no information to make a comparison between substrate type.

Table 7: The percent emergence, number of days to first emergence, the number of days to 50% emergence (T_{50}) for each population.

Population	Species	Emergence (%)	Days to First Emergence	T_{50}
Airstrip	<i>Braya longii</i>	94%	11.80	14.80
Sandy Cove	<i>Braya longii</i>	71%	12.50	20.00
Port au Choix	<i>Braya fernaldii</i>	50%	16.00	28.00
Anchor Point	<i>Braya fernaldii</i>	61%	16.75	30.25

Table 8: Comparison of the affect of the population from which seeds were collected on response variables in laboratory emergence tests. F and P-values obtained from one-way ANOVA's.

Response Variables	Species	F value	P value
Percent emergence	<i>Braya longii</i>	11.06	0.009*
	<i>Braya fernaldii</i>	2.68	0.140
Date to first emergence	<i>Braya longii</i>	0.06	0.819
	<i>Braya fernaldii</i>	0.08	0.783
Time to 50% emergence	<i>Braya longii</i>	7.00	0.027*
	<i>Braya fernaldii</i>	0.38	0.565

*Significant result when $p < 0.05$.

Table 9: Comparison of the affect of population, substrate type, and the presence of *Braya* at the time of emergence on percent emergence. F and P-values obtained from a general linear model.

Variable	Species	F value	P value
Population	<i>Braya longii</i>	11.14	0.007*
	<i>Braya fernaldii</i>	5.37	0.016*
Substrate Type	<i>Braya longii</i>	n/a	n/a
	<i>Braya fernaldii</i>	0.01	0.941
Presence of <i>Braya</i>	<i>Braya longii</i>	0.35	0.575
	<i>Braya fernaldii</i>	0.97	0.338

*Significant result when $p < 0.05$.

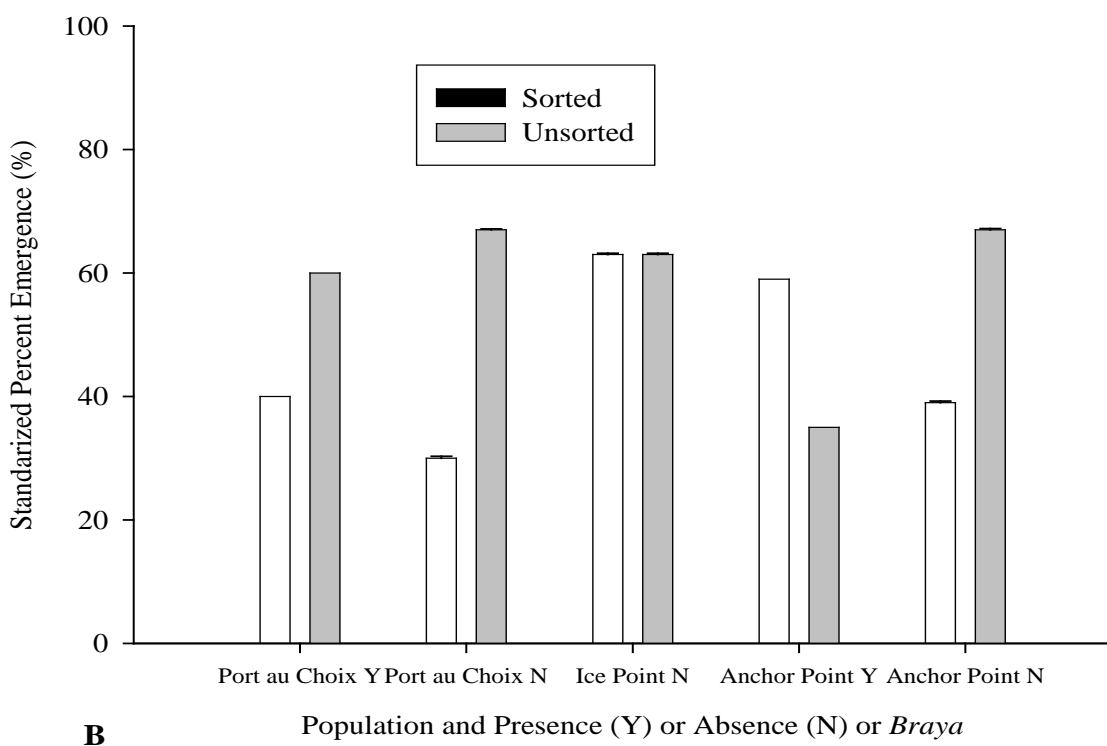
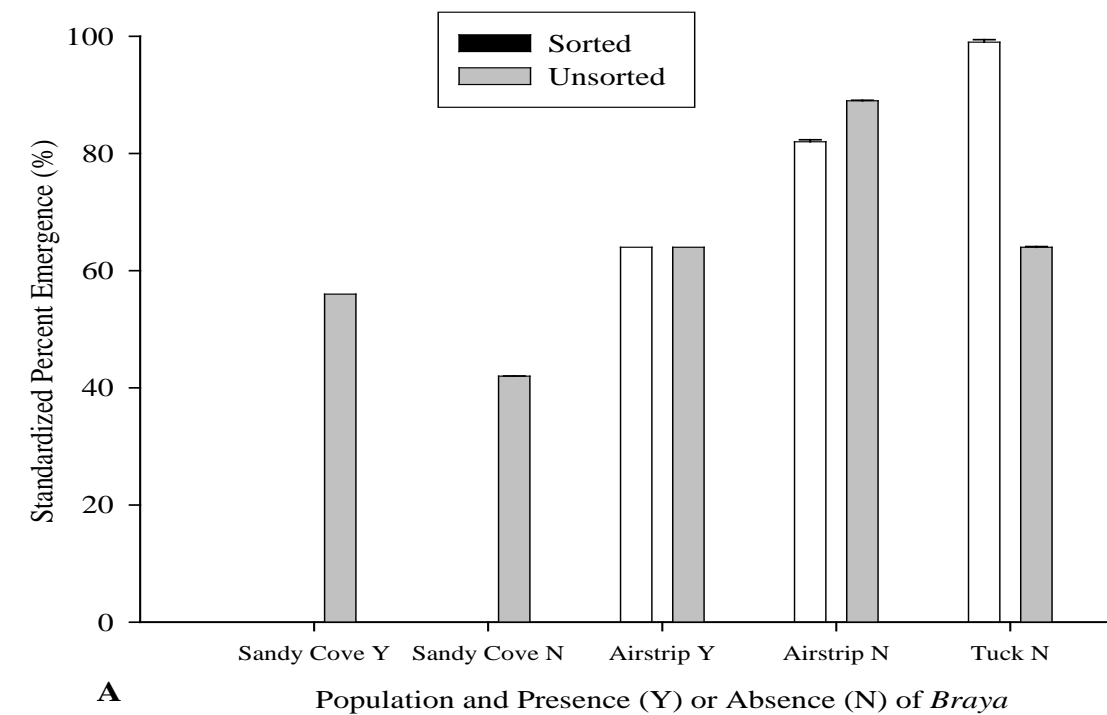


Figure 3: A comparison of the percent emergence (\pm SE) of (A) *Braya longii* and (B) *Braya fernaldii* seeds in sorted or unsorted substrate in each study site. The percent emergence is standardized against the laboratory percent emergence data.

SEED BANK

No seeds were detected in the seed bank for any other sites, either occupied or unoccupied, suggesting seeds are highly dispersed within the soil profile and at very low densities. This was not due to the method by which the seeds were extracted as the control test recovered all seeds added to the blank soil sample.

SEED RAIN ANALYSIS

There were no seeds found on the seed rain traps from any site, unoccupied or occupied, suggesting seeds disperse only short distances from the parent plant, and that no seeds reached unoccupied sites. This was not due to the inability for the seed traps to trap and hold *Braya* seeds because objects such as rocks, insects, and plants with similar sized seeds were caught by the traps and remained stuck to the traps for the survey period.

NATURAL SEEDLING RECRUITMENT IN OCCUPIED AND UNOCCUPIED SITES AND LEVEL OF LOSS TO HERBIVORY

No natural seedlings were found to emerge throughout the summer in occupied absent or unoccupied plots; seedlings were only found in occupied present sites. The number of seedlings that emerged in the occupied present sites varied among months, substrate types, and populations. In general, the month in which most seedlings emerged was July. There was a significant difference between the number of seedlings in sorted and unsorted substrate of *B. fernaldii* populations (Table 10) with sorted substrate having more seedlings than unsorted substrate (Figure 4). The highest number of *Braya fernaldii*

Table 10: Comparison of the affect of population and type on the number of seedlings emerging from each site. F and P-values obtained from a general linear model.

Variable	Species	F value	P value
Population	<i>Braya longii</i>	9.78	0.006*
	<i>Braya fernaldii</i>	2.60	0.118
Substrate Type	<i>Braya longii</i>	n/a	n/a
	<i>Braya fernaldii</i>	7.49	0.010*

*Significant result when $p < 0.05$.

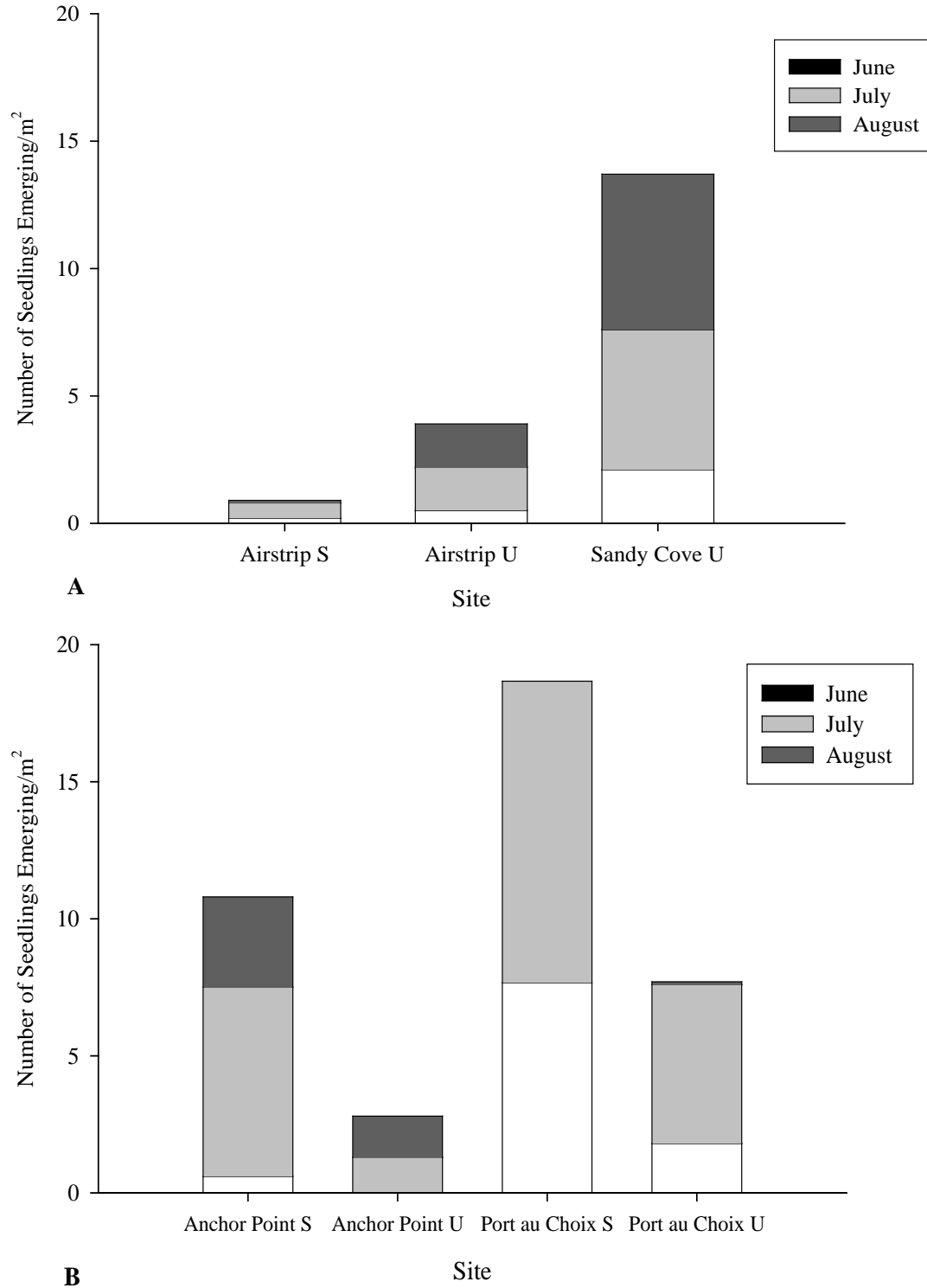


Figure 4: The average number of (A) *Braya longii* and (B) *Braya fernaldii* seedlings emerging per month per occupied present plots (1 m²) of each study site, in both sorted (S) and unsorted (U) substrates.

seedling emerged in Port au Choix, in sorted substrate (Figure 4). The number of seedlings differed significantly between the *B. longii* populations (Table 10) with Sandy Cove having a larger number of emerged seedlings than the Airstrip (Figure 4). In contrast, the total number of germinated *B. fernaldii* seeds did not differ significantly among populations (Table 10).

The density of *Braya* seedlings decreased as the distance from a multiple flowering individual increased (Figure 5). The density of *Braya* seedlings was highest between 0 cm and 20 cm away from a multiple flowering individual and no *Braya* seedling were found 50 cm away from a multiple flowering individual, indicating that the average dispersal distances of a *Braya* seed is less than 50cm (Figure 5). Seeds dispersed further in unsorted substrates than sorted substrates (Figure 5).

There was no substantial loss of seedlings to herbivory at any site for either species. Only one seedling at Ice Point was noted to have portions of the cotyledons removed by herbivory.

SOIL TEMPERATURE

The soil temperature at both *Braya* species sites showed a general increase from June to August and then a decrease in September (Figure 6). Typically, *Braya fernaldii* sites had higher soil temperatures than *B. longii* sites (Figure 6), with Port au Choix having significantly higher average soil temperature in each month than any other *B. fernaldii* population (Table 11). The maximum soil temperatures in *Braya* sites were measured in August and the minimum soil temperatures were measured in June (Figure 6). The differences between soil temperatures recorded in each month were significant

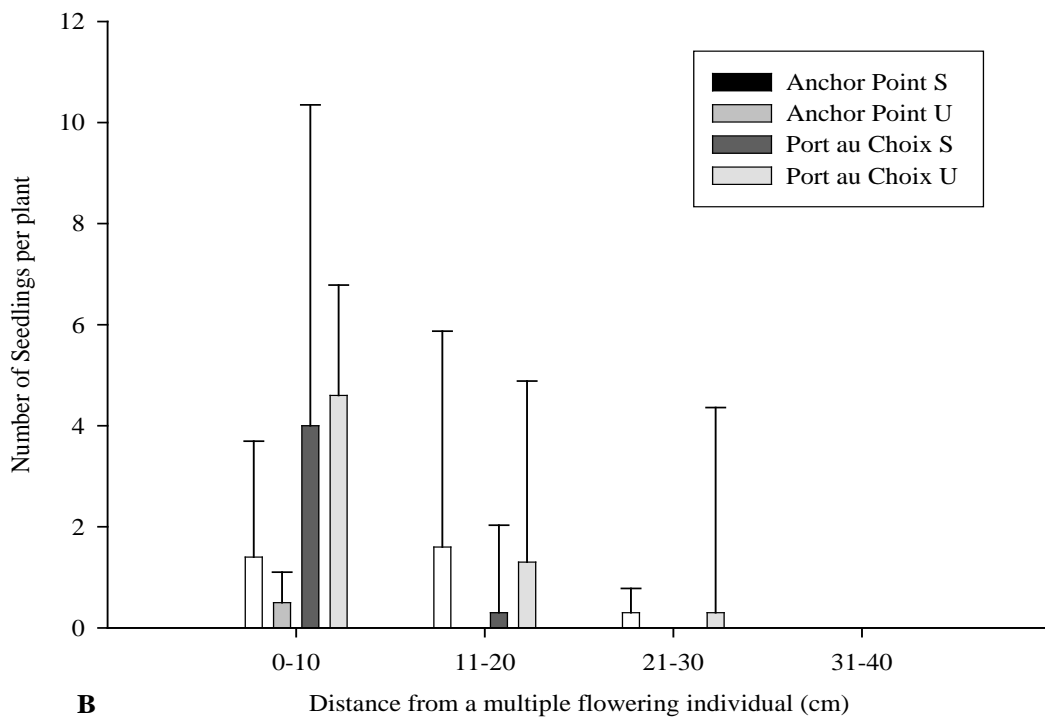
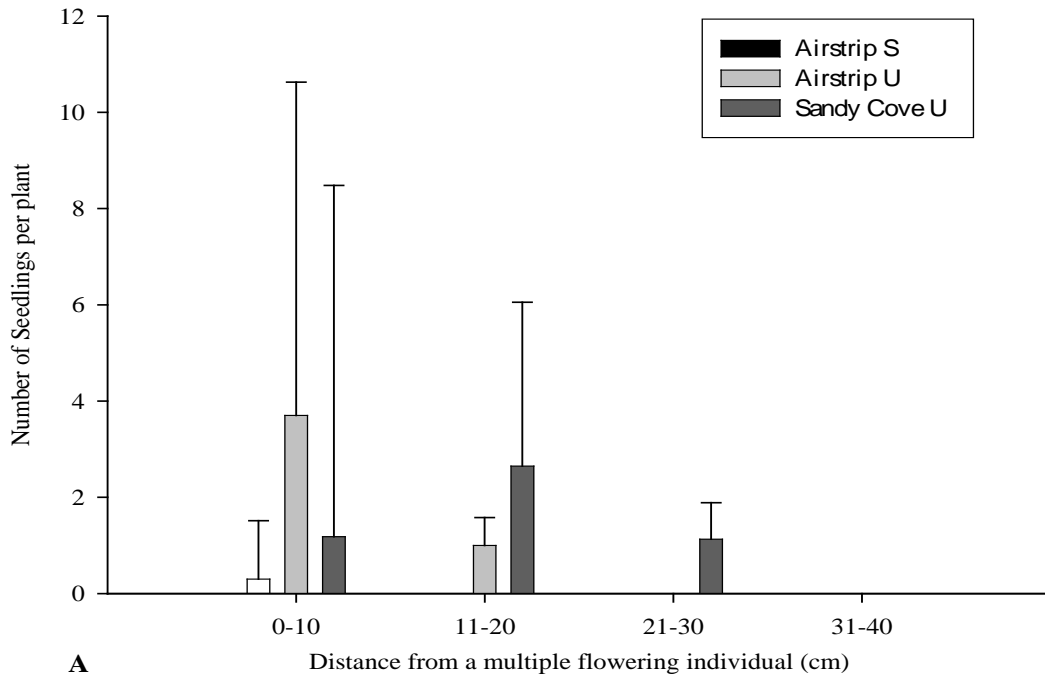


Figure 5: The average change in (A) *Braya longii* and (B) *Braya fernaldii* seedling density (\pm SD) moving away from a multiple flowering individual in either sorted (S) or unsorted (U) substrate of each study site.

Table 11: Comparison of the affect of population, substrate type, and month on the soil temperature. F and P-values obtained from a general linear model.

Variable	Species	F value	P value
Population	<i>Braya longii</i>	3.77	0.065
	<i>Braya fernaldii</i>	5.00	0.035*
Substrate Type	<i>Braya longii</i>	1.42	0.264
	<i>Braya fernaldii</i>	1.90	0.202
Month	<i>Braya longii</i>	33.73	0.000*
	<i>Braya fernaldii</i>	38.84	0.000*

*Significant result when $p < 0.05$.

(Table 11). In contrast, the occupancy and substrate types from which measurements were taken did not significantly affect the soil temperature (Table 11).

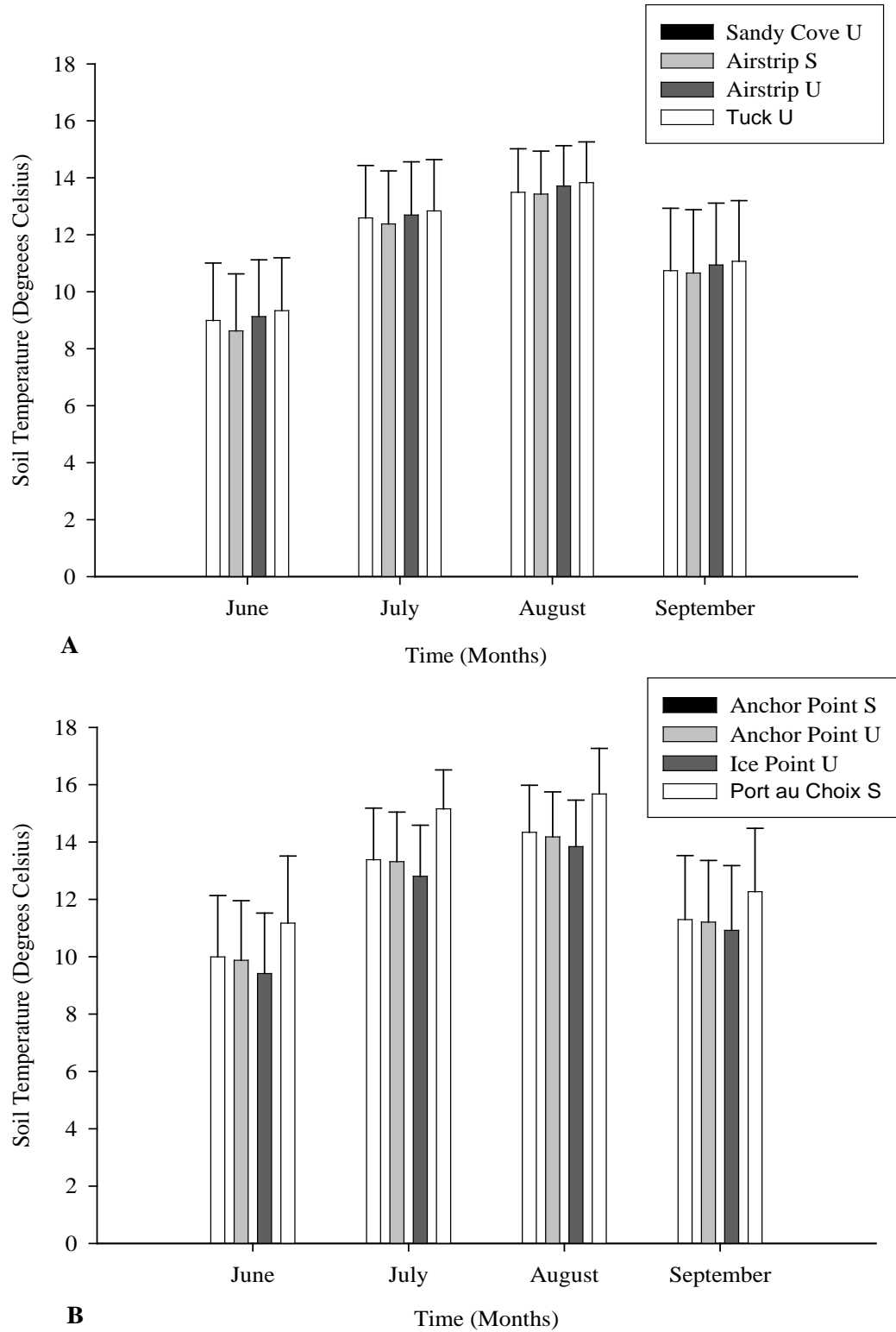


Figure 6: The average soil temperature (\pm SD) per month in either sorted (S) or unsorted (U) substrate of (A) *Braya longii* and (B) *B. fernaldii* study sites.

DISCUSSION

One of the problems in defining critical habitat for the conservation of rare plant species is determining what habitat is vital for the long-term survival of the species. This research illustrates that suitable habitats within the geographic range of *Braya* yet unoccupied by *Braya* represent critical habitat. It is integral for the future preservation of *Braya* to include suitable yet unoccupied habitat in the definition of critical habitat for the maintenance of metapopulation dynamics. Unoccupied habitat must be available for future colonization, as metapopulations of occupied habitats shift to new disturbances as the old forest booms become overgrown and unsuitable. By allowing the metapopulation dynamics to proceed normally *Braya* will have an increased ability to survive environmental changes by colonizing and/or re-colonizing patches of suitable unoccupied habitats. The absence of *Braya* within occupied areas or unoccupied sites cannot be attributed to unsuitable conditions for emergence and early seedling growth. Although habitat loss is one of the greatest threats to the persistence of these *Braya* species, it appears that dispersal is the primary limitation in the colonization of new habitat patches and to the distribution of the rare plants *Braya longii* and *B. fernaldii*.

Limitation of dispersal presents a problem in the conservation of rare plants, especially when the habitat is highly fragmented, as plants may be unable to disperse to suitable substrate at a rate equal to further habitat fragmentation and climate change (Primack and Miao, 1992). The lack of colonization of unoccupied sites due to limited dispersal ability has been suggested as the primary reason for limited distribution of other rare plant species (Primack and Miao, 1992). Dispersal limitation is exacerbated by ongoing fragmentation of suitable habitat on the landscape in both species of *Braya*.

Anthropogenic disturbance has fragmented larger populations of *Braya* into smaller units and frost action on the limestone barrens has created natural fragmentation within each population of *Braya*. When population sizes are small, as with *Braya*, and the rate of dispersal among fragments is low, the extinction rate within each fragment increases (Primack, 2000). To increase the chance of *Braya* species persistence it is important to manage the metapopulation dynamics and ensure as much suitable habitat as possible remains intact, whether or not it is presently occupied.

Additions of seed to previously unoccupied habitat patches indicate that in all plots except Port au Choix, *Braya* seedling of both species emerged and survived until the winter, confirming that these areas are suitable for seedling survival. The natural dispersal of either *Braya* species to these unoccupied sites cannot be expected to occur in the near future, as the average dispersal distances are less than 50 cm. In other studies of plant distribution, seedling recruitment was not found in suitable unoccupied habitats 100 m away from occupied habitats for the 20 years that the study was carried out (Primack and Miao, 1992). Since *Braya* species have been in this area since the 1920's, and they have not yet colonized all possible habitats, we can assume that the colonization or re-colonization of a suitable habitat is a long process, the length of which is increased with habitat fragmentation and loss.

The short dispersal distance of *Braya* seeds may explain why there were no seeds found in either the soil seed bank or the seed traps sampled in occupied absent areas and unoccupied sites. However, it was expected that seeds would be present in occupied present areas as each *Braya* individual in naturally disturbed sites can annually produce on average 150 – 400 seeds per year and the soil seed bank is thought to be long lived

(Hermanutz et al., 2002). One explanation for the lack of seeds may be the locations from where the soil samples were taken and the locations where the seed rain traps were placed. Based on the average dispersal distance, the soil samples and seed traps were too far from the fruiting plants to capture seeds.

Although long distance dispersal and secondary dispersal is possible it is not a common event for many plant species (Fenner, 1985). Morphologies of the seed have been found to affect both the short and long distance dispersal of the seeds (Leishman, 2000). The average seed weight for *Braya* seeds collected in 2000 was 1.1 mg for *Braya longii* and 0.5 mg for *B. fernaldii* (Hermanutz, 2001). In previous studies, seed weights of 0.1 to 5 mg have been shown to be primarily dispersed by forces such as wind and water (Leishman, 2000). As well, architectural attributes of the parent plants, such as fruiting stalk height, have been found to affect the dispersal distance of the seeds (Thiede and Augspurger, 1996; Wilson and Traveset, 2000). The average fruiting stalk height of a *Braya longii* plant in 2002 was 44.17 mm compared with 18.02 mm for *B. fernaldii* plants (Hermanutz, unpublished data). In previous studies, a taller fruiting stalk from which the seed is released has been found to significantly increase the dispersal distance of the seed (Thiede and Augspurger, 1996). In this study the dispersal distance for *Braya longii* was not found to be larger than that of *B. fernaldii* although *B. longii* has a taller fruiting stalk. A difference in dispersal may not have been seen because of the differences in the seed weights of each *Braya* species and the affect of wind at each site. Previous studies have suggested that smaller seeds can disperse farther from the parent plant (Leishman, 2000). Thus although *Braya fernaldii* has a shorter fruiting stalk, which may limit dispersal distances it also has lighter and smaller seeds which typically have farther

dispersal distances. From studies on dispersal distance in laboratory conditions it has been noted that although trends in dispersal distance are seen regarding seed size, architectural attributes of the parent plants, and methods of dispersal, once in the field these trends are dramatically changed by uncontrollable environmental factors (Leishman, 2000).

In situations where water affects the dispersal distance of the seed the morphologies of the seed or parent plant do not play a large role in the dispersal distance. Instead, water dispersal is affected by the physical characteristic of the habitat that determines where the water will flow. Once the seed reaches the ground it can be caught in rocks and vegetation and therefore it is unlikely that the seed will be further dispersed by wind (Fenner, 1985). Since *Braya* species exploit zones of small-scale disturbance surrounded by dense vegetation (Hermanutz et al., 2002), it is very likely that *Braya* seeds get caught in vegetation and as a result their dispersal is limited. Gravel substrate and rocks also impede the dispersal capabilities of *Braya* as their limestone barrens habitat is extremely gravelly with many crevices that can trap seeds. In previous studies, dispersal distance has been found to decrease when dense vegetation surrounds the parent plant by changing wind force and water currents (Thiede and Augspurger, 1996).

The production of seed by *Braya*, as with other arctic-alpine species, is dependent upon environmental factors and therefore is spatially and temporally variable (Chambers, 1995). As a result, the soil seed bank and seed rain into and among sites is also spatially and temporally variable (Chambers, 1995). Alpine and arctic seed banks have been broken into three categories: xeric, mesic, and hyric. The seed bank of *Braya* species fits into the xeric category, as *Braya* habitat is rocky and found on exposed ridges. This type

of seed bank combined with the fact that subarctic/alpine seed banks have previously been found to contain low numbers of seeds (between 0 and 100 seeds/m²) (Chambers, 1995; Fenner, 1985) suggests that lack of seeds found in *Braya* soil seed banks is predictable and not unusual. From this study it is evident that the seed bank of *Braya* is small and dispersed, therefore sampling effort should be more intensive in future studies of the soil seed bank. However, such intensive sampling is not possible with rare species with dwindling habitat.

Population studies by Noel (2000) noted that the areas of sorted circles that experience intermediate levels of disturbance contained higher densities and a higher mean number of individuals than any other natural substrate. This indicates that in natural situations substrate type may play a large role in seedling distribution. However the suitability of the substrate, indicated by the percent emergence, was similar in both sorted and unsorted substrates of both *Braya* species study sites. This illustrates that the differences in densities of *Braya* in each substrate type is not due to a difference in the suitability of the substrate but instead due to the dispersal of seeds within that substrate type or that later life history stages require different conditions than seedlings. This is supported by the analysis of the seed shadow for each species. The analysis revealed that seeds disperse further in unsorted than sorted substrate. As a consequence, *Braya* are more scattered in unsorted than in sorted substrate. Both sorted and unsorted substrates support growth and survival of *Braya* and therefore both substrate type should be included in habitat protection and management. This will not be a difficult task as sorted and unsorted substrates are in close proximity within each site.

In cases like *Braya longii* where the species is at risk of extinction, unoccupied suitable habitat may provide opportunities to restore and reintroduce populations to ensure persistence. From studies that have used unoccupied sites as tools in restoration efforts it has been noted that the establishment of seedlings can be highly effective in colonizing or re-colonizing an area (Primack and Miao, 1992). However, this occurs when the unoccupied site is suitable for not only germination and emergence but long-term persistence, meaning that naturally occurring disturbances should be present and levels of seed or seedling predators should be low (Primack and Miao, 1992). Adult *Braya* in anthropogenically disturbed sites, have suffered high levels of damage by the *Plutella xylostella* (L) (Diamondback moth) and *Delia platura* (Meigen) (cabbage root maggot). There is a concern that these insects will also cause mortality of seedlings (Hermanutz et al, 2002). In this study only one seedling among all sites was affected by herbivory. This indicates that at least in 2002, herbivory did not limit the ability of seedling to persist in unoccupied sites, and probably will not limit the early stages of distribution of *Braya*. However, it should be noted that in 2002 adult plants were also not highly affected by the Diamondback moth because herbivory is often highly spatially and temporally variable (Hermanutz and Parsons, 2003). To determine if seedlings are unaffected by insect herbivores, seedlings need to be monitored for a number of years. These results also suggest that seedlings in natural sites are not at risk of extirpation by the Diamondback moth and therefore are prime habitat for colonizing or re-colonizing an area with *Braya* individuals. However, as anthropogenically disturbed sites have high rate of insect infestation and these sites may not be appropriate for restorations.

These results support the hypothesis that the distribution of both *Braya* species within a site and between sites is limited by dispersal. This is further supported by the lack of seed rain into *Braya* habitat patches and the depauperate seed bank. The limited dispersal of *Braya* species, as indicated by these results, enforces the need for immediate and effective habitat protection of occupied sites. Future observations of the fate of the seed and emergent seedlings in the additional experimental plots will be critical in assessing if the presently unoccupied habitat patches will continue to support *Braya*, and hence if these patches represent truly critical habitat. It is possible that unoccupied areas are unoccupied because of factors that negatively affect juvenile or adult stages of the plant, as opposed to the seedling stage. This research included only studies of seedlings, therefore it is imperative that future research includes studies of adult plants and their long-distance dispersal capabilities to determine the possibility for *Braya* species to colonize unoccupied habitat. This knowledge of critical habitat for *Braya* individuals will assist in the process of determining the optimum locations for habitat protection.

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