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Expansion dynamics and performance of the dwarf shrub *Empetrum hermaphroditum* (Ericaceae) on a subarctic sand dune system, Nunavik (Canada)

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A B S T R A C T

Many tundra plant species rely more heavily on clonal propagation than on sexual reproduction. However, if reproduction bottlenecks are alleviated, shifts in the balance between these strategies can occur. To better understand the colonization and expansion dynamics of clonal dwarf shrubs in a rapidly changing environment, we monitored a crowberry population (*Empetrum hermaphroditum*) on a sand dune system in subarctic Québec. Our objectives were to quantify survival, recruitment, and growth and to determine whether performance varied across a topographic and successional gradient. In 2012, we resurveyed a 6-ha plot where all individuals had been counted in 2007. Along the successional gradient, we measured vegetation cover, soil characteristics, shoot elongation, and seed germination. Over the 2007–2012 period, the population continued to experience abundant recruitment, fast growth, and low mortality, resulting in a 40% increase in population size and a 244 m² increase in cover. Performance patterns did not match the dune successional gradient; instead, individuals at intermediate positions showed better growth and produced more viable seeds. The ability of crowberry to successfully establish from seed might have been enhanced by the regional warming observed since the 1990s and seems to be part of a dual strategy allowing crowberry to fill gaps while continuing to spread efficiently on the dune system via clonal growth.

INTRODUCTION

Over the last half-century, many shrub species have been expanding in northern ecosystems in response to recent climate change (reviewed by Myers-Smith et al., 2011). Shrub expansion, associated mostly with erect shrub species such as *Betula* spp. and *Salix* spp., can occur via infilling of pre-established stands, increases in canopy height, and establishment on sites previously not colonized by shrub species (Myers-Smith et al., 2011). Although population infilling can be associated with

both clonal growth and recruitment of new individuals (Ropars and Boudreau, 2012; Tremblay et al., 2012; Formica et al., 2014), the colonization of new sites should rely solely on successful establishment from seed (Eriksson, 1989).

The success of sexual reproduction in tundra plant communities is, however, highly unpredictable and has long been considered to be low (Bliss, 1971; Billings, 1987). Instead, many arctic and subarctic species tend to propagate clonally (Billings and Mooney, 1968; Bliss, 1971), a comparatively more cost-efficient and reliable

strategy that allows plants to “forage” for resources in patchy, stressful environments and to recycle and share nutrients between ramets (Jónsdóttir et al., 1996). This strategy promotes long-term population persistence (Eriksson, 1992; Jónsdóttir et al., 1996), even during extended unfavorable periods when seed set or seedling establishment fail (Wookey et al., 1995).

Successful sexual reproduction may nevertheless occur in favorable years (McGraw and Shaver, 1982; Sonesson and Callaghan, 1991) and is of particular importance in promoting colonization of new sites following seed dispersal (Eriksson, 1989) and in maintaining (or increasing) genetic diversity within populations (de Witte et al., 2012). The latter might help adaptation in a changing environment and could explain why most clonal species invest continually in sexual reproduction despite low chances of success (Wookey et al., 1995). Seedling establishment, growth, and survival, however infrequent, have therefore major implications for arctic and subarctic plant communities, affecting their structure, dynamics and evolution.

This balance between reproductive strategies is expected to shift toward increased sexual reproduction under current and future climate change, with longer, warmer summers promoting increased flowering (Alatalo and Totland, 1997; Aerts et al., 2006), germination (Baskin et al., 2002), and seedling survival and growth (Formica et al., 2014). In fact, recent research suggests that sexual reproduction in so-called clonal species is much more frequent and widespread than once believed, with evidence of repeated recruitment observed in many populations (Gabrielsen and Brochmann, 1998; Szmídt et al., 2002; Venn and Morgan, 2009; Boudreau et al., 2010; Douhovnikoff et al., 2010; de Witte et al., 2012). It is therefore timely and essential to understand the relative importance of sexual and clonal reproduction for shrub maintenance and expansion in rapidly changing arctic and subarctic environments.

To better understand how dwarf shrub communities might respond to environmental change, we explored the recent dynamics of an expanding population of crowberry (*Empetrum nigrum* L. subsp. *hermaphroditum* (Hagerup) Böcher; hereafter *E. hermaphroditum*) on a subarctic coastal dune system near Whapmagoostui-Kuujuarapik (Nunavik, subarctic Québec). Our study builds upon a previous census of this population where all individuals within a 6-ha plot were mapped and measured in 2007 (Boudreau et al., 2010), providing a unique opportunity to investigate the demographics of the population. Our first objective was to quantify the recent dynamics (2007–2012) of the population in terms of survival, recruitment, and cover increase. We hypothesized that survival and recruitment would be

greater than mortality, leading to an increase in the species' cover on the coastal dune system. Our second objective was to determine whether performance (growth and reproduction) varied spatially in response to soil properties and intraspecific competition. The location of our study site on a dune system provides a successional gradient (from foredune to fixed dunes) with variations in the physical and biotic environment that can affect performance. We expected shoot elongation and seed viability to be highest toward the end of the gradient (older dunes), where soil moisture and nutrient content are typically higher (Tackett and Craft, 2010) and wind exposure and salt spray are less severe (Wilson and Sykes, 1999). Alternatively, intraspecific competition arising from higher crowberry densities in late-succession zones could lead to reduced performance at the very end of the gradient.

MATERIAL AND METHODS

Study Species

Crowberry is an evergreen ericaceous dwarf shrub with a widespread distribution ranging from temperate to arctic zones. It has a prostrate to hemi-prostrate growth habit, its straggling stems often developing adventitious roots where they touch the ground. In addition to its clonal growth form, crowberry can produce an abundant berry and seed crop, although germination is often low (Bell and Tallis, 1973; Milbau et al., 2009; Graae et al., 2011). It can be a dominant species of the shrub layer in many ecosystems and is often found as dense mats in boreal forests or in heathlands (Tybirk et al., 2000).

Study Area and Study Site

The study took place on the eastern coast of Hudson Bay in subarctic Québec, Canada, southwest of the villages of Whapmagoostui-Kuujuarapik. The area is experiencing rapid warming: mean annual temperatures have increased from -4.3°C (1960–2000) to -2.6°C (2001–2010), and temperature anomalies have become increasingly positive since the mid-1990s (Bhiry et al., 2011). Using the same data (Environment Canada, 2013), we calculated the mean summer (June, July, August) and winter (December, January, February) temperatures for the periods 1971–1994 and 1995–2011. Mean summer temperatures have increased from 9.3°C to 10.9°C ($t_{(37)} = 4.56$, $p < 0.001$), and mean winter temperatures have increased from -21.4°C to -18.3°C ($t_{(37)} = 5.08$, $p < 0.001$). Yearly precipitation averages 660 mm, 38% of which falls as snow. The area is still undergoing rapid

postglacial isostatic rebound which, combined with the large amount of sediments brought in by Great Whale River, results in the seaward advance of the beach (Ruz and Allard, 1994). Dune crests have an elevation gradient ranging from 1 to 4 m, the foredune being the highest (Ruz and Allard, 1994).

The study site was selected in 2007 as a representative and relatively undisturbed part of a 3.5-km-long dune system (Boudreau et al., 2010). Based on evidence from aerial photographs (1959–present), the site has not been heavily impacted by human activity or experienced other disturbance (Desormeaux, 2005), except infrequent all-terrain vehicle circulation restricted to paths. We set up a 200 m × 300 m plot (longest side perpendicular to the ridges) that stretched from the upper beach (vegetation line) to the fixed dunes. The plot was subdivided into seven zones based on topography and vegetation characteristics (Fig. 1, part A). Zone 1 (Z1) encompassed the foredune and was subdivided into (a) upper beach, (b) front of the foredune, and (c) back of the foredune. Zone 2 (Z2) corresponded to the beginning of the first trough up to a well-delimited all-terrain vehicle trail (parallel to the trough) and contained the most seaward *E. hermaphroditum* individuals. Zone 3 (Z3) comprised the remainder of the first trough. Zones 4 and 5 (Z4–Z5) corresponded to the front and back of the second dune, respectively. Zones 6 and 7 (Z6–Z7) comprised the second trough, the latter zone containing extensive *E. hermaphroditum* clonal clusters. Beyond the plot, older fixed dunes support an almost continuous cover of *E. hermaphroditum*. This part of the dune system does not support a forest ecosystem, although white spruce stands can be found on older dunes north of the village.

Empetrum hermaphroditum Population Dynamics

In May 2007, Boudreau et al. (2010) mapped and measured every *E. hermaphroditum* individual inside the study plot. We remapped the same plot five years later, in May 2012. In our study site, genetically distinct individuals (i.e., established from seed) are easy to identify as they have a near-perfect circular form, although in some instances intertwined individuals can be mistaken for a single one (ca. 7% of the individuals; Boudreau et al., 2010). For this study, we considered every near-circular patch of up to 3 m in diameter to be a single individual, while larger, irregular patches were classified as “clonal clusters” made up of an unknown number of intertwined individuals. When two or more distinct individuals recorded in 2007 had coalesced together to form a single patch in 2012, they were also classified as clonal clusters.

As in 2007, we divided the plot into 10 m × 10 m cells to facilitate the detection of both previously mapped and newly established individuals. Each cell was thoroughly searched, and every individual was measured along two perpendicular diameters. The surface area of the large, irregularly shaped clonal clusters was estimated once in 2013. We mapped the population with a total station (Leica Flexline TS06, Leica Geosystems, Norcross, Georgia, U.S.A.), using the center of each individual to record its position. Data from 2007 and 2012 were integrated in ArcGIS 10 (ESRI, Redlands, California, U.S.A.).

By comparing the data sets from 2007 and 2012, we were able to calculate demographic parameters for the population. The mortality rate corresponded to the percentage of individuals recorded in 2007 that could not be found again in 2012 (i.e., that were not at their marked location and did not appear to have coalesced with other individuals nearby). Recruitment was defined as the number of individuals recorded for the first time in 2012, i.e. seedlings ≤5 yrs old. We also quantified the increase in crowberry cover on the dune system as the difference between the sum of all individual leaf crown areas in 2012 and in 2007.

In June 2013 and 2014, all individuals established after 2007 were revisited to assess annual survival and growth rates for this particular age class (≤5 yrs old). We measured the seedlings along two perpendicular axes and noted any signs of disturbance or desiccation.

Performance along the Dune Gradient

Growth

In June 2013, we measured annual stem elongation on 15–20 randomly selected individuals with a diameter ≥20 cm for each of the zones along the successional gradient (total $n = 113$). Stem elongation in *E. hermaphroditum* is measured as the distance between two consecutive sets of lateral shoots (Shevtsova et al., 1997). We measured the distance between the nodes for the sections corresponding to the years 2007 to 2012. Measurements were taken to the nearest millimeter with a ruler on four stems (pointing in the four main cardinal directions) and averaged per individual.

Reproduction

In each zone, we selected between 5 and 33 fruit-bearing individuals on which we harvested 10 fruits to conduct germination trials. Interzone variability in the number of sampled individuals reflects the variability in the abundance of seed-bearing individuals. Seeds were extracted and kept at 4 °C until further analyses. For

each sampled individual ($n = 107$), we used 70 seeds for germination trials (7 lots of 10 seeds placed on filter paper in small Petri dishes) to look for differences in seed viability between zones. Seeds were soaked for 30 seconds in ethanol (70% v/v) and rinsed with distilled water to limit fungal or bacterial infection. Filter papers were soaked with distilled water and the dishes were Parafilm-sealed. As the majority of *E. hermaphroditum* seeds have physiological dormancy, seeds were warm- and cold-stratified (Baskin et al., 2002). Warm stratification took place in an environmental growth chamber with a temperature regime of 25/15 °C (day/night) and a photoperiod of 14 h for 14 weeks. Seeds were then cold-stratified in darkness at 4 °C for 12 weeks.

The germination trial took place in an environmental growth chamber at 25/15 °C (day/night) and with a photoperiod of 16 h. Germination was monitored every other day during the first 8 weeks, then once a week until no further seeds germinated. Distilled water was added as needed to keep the filter paper wet and seedlings were periodically removed. Final germination data was pooled at the zone level to test for differences in seed viability along the gradient.

Biotic and Abiotic Variations along the Gradient

Vegetation Composition along the Successional Gradient

In order to evaluate if the performance of *E. hermaphroditum* was associated with changes in the plant community along the successional gradient, we measured the cover of the main vegetation functional groups (lichens, mosses, herbs, and forbs) along five linear transects spanning the length of the plot (300 m) and set 40 m apart. This sampling design allowed us to capture the variability in the plant functional group abundance between the different zones. The percent cover of each group was visually assessed in a 1-m² quadrat every meter along the five transects, for a total surveyed area of 1500 m². The following cover classes were used: 0–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–90%, and 90–100%.

Empetrum hermaphroditum Abundance

We tested whether high densities of *E. hermaphroditum* had a negative impact on performance due to intraspecific competition. For all the individuals selected for elongation and reproduction measures, we computed the number of *E. hermaphroditum* individuals within a 10-m radius circular plot (centered on the selected individuals) and used this metric as a proxy for competition intensity.

Soil Properties

To assess whether differences in performance along the gradient (if any) were linked to succession-related soil properties, we collected 10-cm-deep soil cores (diameter 2.2 cm) to determine soil moisture and organic matter content. All samples were collected on the same day, 48 h after it rained. Samples were taken at the center (i.e. median distance from upper beach) of each (sub)zone along the five vegetation transects, for a total of 45 samples. The cores were kept in sealed plastic bags, weighed upon collection and stored at 4 °C until further analyses.

To determine soil moisture, the samples were dried at 60 °C for 48 h. Given their sandy nature, this oven time was sufficient to allow the full drying of the samples. The difference between wet and dry mass was then transformed into a percentage of water content.

Organic matter (OM) content was determined by loss on ignition. For this, a dried, pre-weighed, homogenized subsample of each core was burned at 550 °C for 5 h. After allowing the samples to cool in the oven overnight, we weighed them again. The loss in mass is attributable to the combustion of OM (Schumacher, 2002).

Statistical Analyses

To assess whether soil moisture, soil OM content, shoot elongation, and seed germination varied across the plot, we performed interzone comparisons using analyses of variance (ANOVA) or a nonparametric substitute, the Kruskal-Wallis test, when assumptions of normality could not be met. Where there were significant differences between zones, we performed multiple comparisons using Tukey's post-hoc test.

Because of the hierarchical nature of the data (individuals within zones), with performance measured at the individual level and biotic and abiotic factors measured at the zone level, we conducted linear mixed-effects models to determine whether performance was linked to variations along the successional gradient. We used elongation or germination as the response variable, soil moisture or the cover of various plant functional groups (lichens, mosses, herbs, and forbs) as a fixed effect, and zone as a random effect.

To determine whether intraspecific competition affected growth or seed viability, we performed linear mixed-effects models using elongation or germination as the response variable, the number of *E. hermaphroditum* neighbors in a 10-m radius from sampled individuals as the explanatory variable, and zone as a random effect, and compared them to null models (no fixed effects) using Akaike's information criterion (AIC).

All tests were conducted in R version 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria).

We ran all mixed-effects models using the package ‘lme4’ version 1.1.9. We computed pseudo- R^2 (marginal R^2) to evaluate the goodness of fit of mixed-effects models according to Nakagawa and Schielzeth (2013) using the package ‘MuMIn’ version 1.15.1.

RESULTS

Population Dynamics: Survival, Recruitment, and Cover Increase

In the 2007 census, Boudreau et al. (2010) recorded 1154 individuals and 43 clonal clusters (although the latter were not classified as such at the time). In 2012, we found 998 (86.5%) of the 1154 individuals recorded in 2007. Out of the 156 individuals that were not found, 67 individuals (5.8%) had coalesced with either other isolated individuals (in Z2, Z3, and Z5) or with large clonal clusters (in Z6 and Z7), preventing individual measurements. Additionally, the remnants of 31 individuals (2.7%) were found in three recently disturbed, localized areas in Z7 (Fig. 1, part A). As only small fragments were found, it was not possible to reassign them based on the 2007 map. These individuals were rejected from subsequent analyses. Finally, 58 individuals (5.0%) were not found at their 2007 location, suggesting that they died between 2007 and 2012 (Fig. 1, parts A and B). Most of the dead individuals were rather small, 50 out of the 58 individuals having a diameter <20 cm in 2007. Mortality seems to have been caused mainly by trampling, as we often found signs of snowmobile or all-terrain vehicle disturbance where the missing individuals should have been.

We found 461 individuals that had not been recorded in 2007, presumably seedlings that became established between the two surveys (or else small, young individuals missed in 2007). The majority of these seedlings (75%) were recruited in the second trough (Z6–Z7), at the fixed-dune end of the plot (Fig. 1, parts A and C). No seedlings colonized the dune ridges or the foredune, so that the population is not progressing toward the beach but only infilling (Fig. 1, part A). This abundant recruitment resulted in a population size distribution skewed toward small sizes (Fig. 1, part D): individuals having a diameter <50 cm represented 67% of the population in 2012. In contrast with 2007, however, the greatest number of individuals was found in the 10–20 cm and the 20–30 cm size classes rather than in the 0–10 cm size class. Of these 461 newly recruited individuals, only five (1.1%) died between June 2012 and June 2013, and an additional 14 seedlings (3.3%) died the following year (June 2014). About 10% of the surviving seedlings exhibited signs of disturbance or desiccation (reddish-brown leaves, dead stems).

As in 2007, *E. hermaphroditum* cover in 2012 varied greatly between zones, being higher in Z7 (1729.3 m²) than in all the other zones (0.0–225.7 m²). This difference is explained by the presence of 47 large clonal clusters in Z7. For Z2 to Z5, zones in which no clonal clusters were found in 2007, the increase in cover from 2007 to 2012 (+124.9 m²) was almost entirely associated with the horizontal spread of pre-established individuals (+121.8 m²) rather than with the recruitment of new individuals (+3.1 m²), while the loss of cover through mortality was low (–1.3 m²). The cover increase appears greater in Z3 than in the other zones (Fig. 1, part E). For Z6 and Z7, the total cover increase over the 2007–2012 period cannot be calculated because the large clonal clusters were not measured in 2007. The 2012 cover of these clusters was 114.4 m² and 1479.6 m², respectively. Isolated individuals already established in 2007 and remeasured in 2012 increased their total cover from 73.4 m² to 106.2 m² (+32.8 m²) and from 184.5 m² to 245.4 m² (+60.9 m²) in Z6 and Z7, respectively. Newly recruited individuals (Z6: +5.0 m²; Z7: +4.2 m²) and mortality (Z6: –14.5 m²; Z7: –0.8 m²) had little effect on total *E. hermaphroditum* cover in these zones.

Spatial Variations in Performance

Mean stem elongation during the study period ranged from 3 to 8 cm yr^{–1} across individuals and varied significantly between zones (ANOVA: $F_{5,107} = 11.81$, $P < 0.001$; Fig. 2, part A). Growth in Z3 was significantly higher than in Z2, Z5, Z6, and Z7, whereas growth in Z5 was significantly lower than in Z2, Z3, and Z4. The position along the gradient explained 33% of the variation in growth.

Barely any germination occurred during warm stratification (ca. 2%). After warm and cold stratification, germination started rapidly (3–6 days) and continued steadily until approximately day 50. It then slowed and stopped almost completely after ca. 100 days. Final germination rates differed between zones (ANOVA: $F_{5,100} = 4.09$, $P = 0.002$), being significantly higher in Z3 and Z4 than in Z6 (Fig. 2, part B), but inter-individual variability was high. Only 13% of the variance in germination was explained by the spatial position along the gradient.

Abiotic and Biotic Determinants of Performance

Soil moisture and OM content were very low throughout the study plot (Table 1) and were significantly correlated (Pearson coefficient: 0.92, $P < 0.001$). Both parameters varied along the successional gradient (Kruskal–Wallis for moisture: $H = 23.30$, $df = 8$, $P = 0.003$; for OM: $H = 24.74$, $df = 8$, $P = 0.002$), with the upper beach (Z1a)

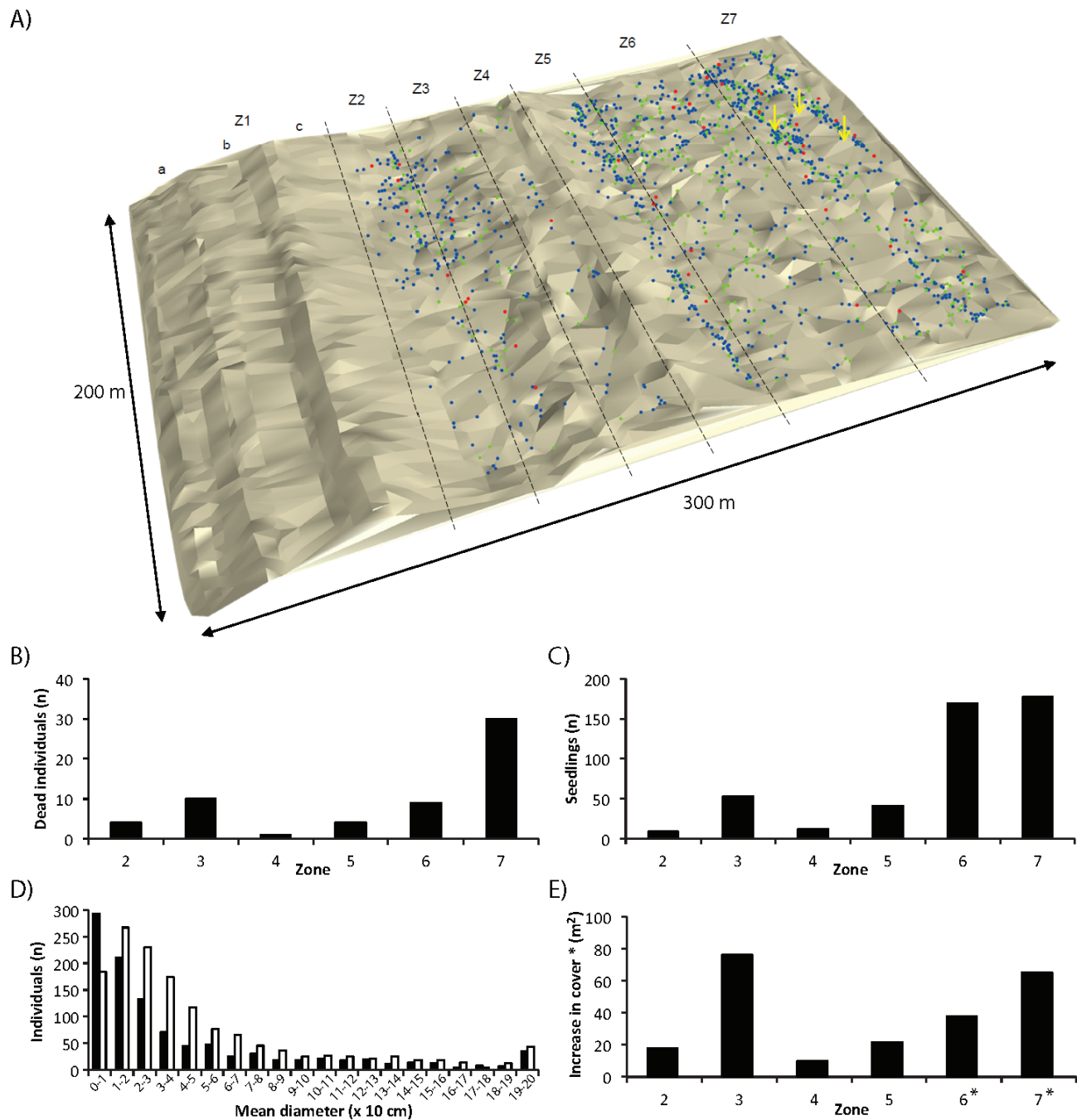


FIGURE 1. The demographics of this *Empetrum hermaphroditum* population suggest rapid expansion on the dune system. (A) Population map on a digital terrain model (TIN structure; 4:1 vertical exaggeration) of the study plot. Blue dots: individuals recorded in 2007 and found again in 2012; red dots: individuals that died since the 2007 survey; green dots: seedlings established since 2007. Yellow arrows indicate three localized disturbed areas where only fragments of individuals were found. Clonal clusters are not represented. Zones are delineated with dotted lines and are as follow: Z1: upper beach (a), front (b), and back (c) of foredune; Z2 and Z3: first trough; Z4 and Z5: front and back of second dune, respectively; Z6 and Z7: second trough. (B) Low mortality and (C) abundant recruitment led to (D) a size distribution skewed toward small classes. Black bars: 2007 distribution; white bars: 2012 distribution. (E) Fast growth and recruitment resulted in important increases in cover; asterisks indicate that the growth of clonal clusters between 2007 and 2012 was not considered.

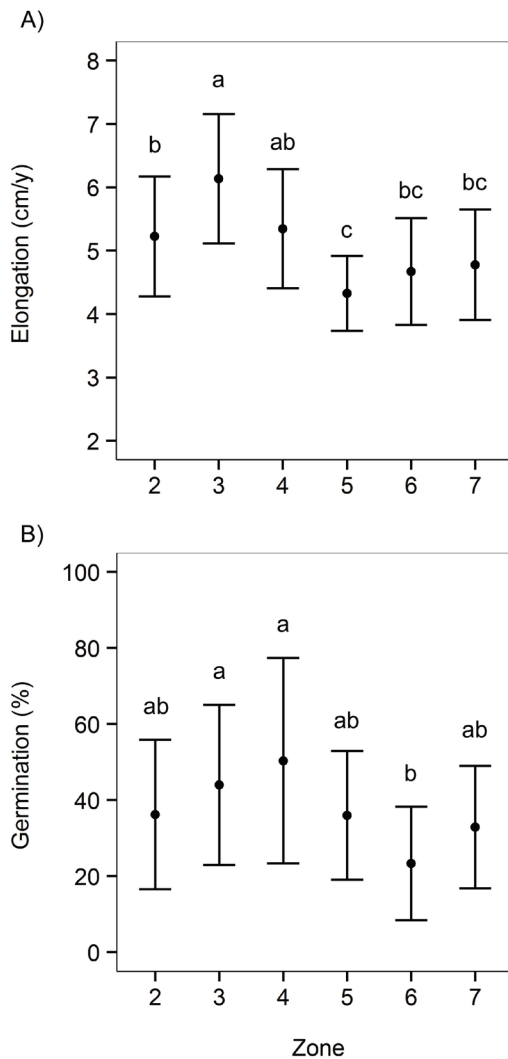


FIGURE 2. Variations in (A) mean annual shoot elongation and (B) seed germination along the dune gradient. Letters indicate significant differences between zones. See Figure 1 for description of zones. Error bars: ± 1 SD.

being drier and having less OM than the other zones. Vegetation exhibited a typical succession pattern along the dune gradient, with a dominance of pioneer plants on the foredune and a mixture of mosses, lichens, herbs, and forbs on the fixed dunes (Z2–Z7; Table 2).

Model comparison of the mixed-effects models revealed that neither soil parameters nor plant functional groups explained shoot elongation better than a null model ($\Delta\text{AIC} < 2$). However, viable seed production was negatively associated with lichen cover ($\Delta\text{AIC} = 3.3$) and positively associated with mosses ($\Delta\text{AIC} = 2.1$), although the variation explained by these models was low (marginal $R^2 = 0.07$ and 0.10 , respectively).

Intraspecific competition did not seem to affect the performance of *E. hermaphroditum* individuals. The

TABLE 1

Soil moisture and organic matter content (\pm SD) in 10-cm cores along the dune gradient (5 cores/zone). Letters indicate significant differences between zones (Kruskal-Wallis, $p < 0.01$); see Figure 1, part a, for description of zones.

Zone	Moisture (%)	Organic matter (%)
Z1a	4.2 ± 2.2^b	0.2 ± 0.0^b
Z1b	8.6 ± 2.3^a	1.0 ± 0.3^a
Z1c	10.3 ± 1.0^a	1.3 ± 0.3^a
Z2	9.8 ± 1.1^a	1.3 ± 0.3^a
Z3	8.6 ± 1.5^a	1.0 ± 0.1^a
Z4	11.7 ± 0.9^a	1.5 ± 0.2^a
Z5	9.1 ± 1.0^a	1.4 ± 0.1^a
Z6	9.1 ± 2.4^a	1.4 ± 0.2^a
Z7	9.6 ± 1.6^a	1.5 ± 0.3^a

number of neighbors in a 10-m radius had no effect on shoot elongation or on seed viability (marginal $R^2 = 0.024$ and 0.001 , respectively; $\Delta\text{AIC} < 2$ in both cases).

DISCUSSION

In this study, we provide evidence of abundant seedling establishment and rapid lateral growth of already established *E. hermaphroditum* individuals. These two processes are together responsible for the rapid infilling of a subarctic sand dune system by a species best known for propagating clonally. By performing a repeated survey, we were able to demonstrate that the population is growing rapidly as a result of abundant recruitment and low mortality. Relative to 2007, the population size in 2012 had increased by 40% and cover, excluding the growth of the clonal clusters, had increased by 244.4 m^2 (a 37% relative increase). However, contrary to our predictions, we found that growth and reproduction were greater at intermediate positions along the gradient and could not be conclusively linked to soil properties (moisture, OM content) or to the intensity of intraspecific competition.

Population Dynamics

We found that the infilling trend described by Boudreau et al. (2010) continued from 2007 to 2012 due to abundant recruitment and low overall mortality. However, the lower number of individuals in the 0–10 cm size class suggests that either recruitment decreased

TABLE 2

Vegetation cover across the dune gradient (see Fig. 1 for description of zones). Cover does not total 100% because we used the medians of the cover classes (e.g., 37.5% for the class 25%–50%) to calculate mean cover in each zone.

Cover type	Z1a	Z1b	Z1c	Z2	Z3	Z4	Z5	Z6	Z7
Sand / bare soil	31.2	1.7	0.2	3.2	3.4	—	0.3	0.2	2.0
<i>Honckenya peploides</i>	3.8	0.4	—	—	—	—	—	—	—
<i>Lathyrus japonicus</i>	38.2	19.1	10.9	4.3	3.0	2.9	1.4	1.1	2.1
<i>Leymus mollis</i>	22.0	27.0	2.9	0.9	0.2	0.4	0.6	0.2	0.1
Herbs and forbs	0.3	29.1	60.8	44.1	27.5	27.8	24.0	21.1	14.5
Mosses	—	1.0	0.7	35.4	34.2	55.5	43.5	21.9	16.3
Lichens	—	—	—	4.8	15.2	9.9	19.4	35.9	28.1
<i>E. hermaphroditum</i>	—	—	—	2.6	3.0	0.5	0.5	1.7	21.6
<i>Vaccinium vitis-idaea</i>	—	—	—	—	0.1	—	0.3	1.0	2.7

slightly during the 2007–2012 period, or new recruits grew faster than before, reaching larger size classes more rapidly. The latter hypothesis is supported by the rapid warming observed in the region over the past decade (Bhury et al., 2011) and the high mean annual elongation we recorded. It is also in accordance with dendrochronological analyses from the same site that revealed a positive relationship between radial growth at the root collar and the sum of growing-degree days during the summer (S. Angers-Blondin, unpublished data).

This abundance of new *E. hermaphroditum* recruits, although opposed to the long-standing paradigm that sexual reproduction is a rare event in stressful northern ecosystems (Billings and Mooney, 1968), is in accordance with findings of low levels of clonality in young populations of this species (Szmids et al., 2002). In another coastal population, sexual reproduction has also been shown to occur, although regeneration in that case was limited by the availability of safe sites for seedling survival (Hill et al., 2012). Similar observations have been made in other “clonal” species such as *Saxifraga cernua* L. (Gabrielsen and Brochmann, 1998), *Carex curvula* All., *Dryas octopetala* L., *Vaccinium uliginosum* L. (de Witte et al., 2012), and *Salix* spp. (Stamati et al., 2007; Douhovnikoff et al., 2010; de Witte et al., 2012), suggesting that sexual reproduction occurs frequently in arctic and subarctic plant populations and can be an important mode of species propagation and expansion.

Spatial Variations in Performance

Contrary to our hypothesis that late-succession habitats would favor *E. hermaphroditum* performance, individuals appeared to grow better and produce more viable seeds in the middle of the successional and topographic

gradient than at the end. Mean annual shoot elongation was greater on average by ca. 1.2 cm in Z3 and Z4 than in Z6 and Z7. However, we were not able to identify the edaphic or ecological drivers of such growth differences along the gradient. The soil properties we measured did not vary significantly across zones colonized by *E. hermaphroditum*, although the small sample size (five cores per zone, once in the summer) may have prevented us from identifying finer-scale spatial or temporal variations that could affect performance. It is possible that other factors that were not measured, such as soil salinity or pH, had an effect on *E. hermaphroditum* performance. However, soil salinity on this dune system is relatively low due to the persistence of sea ice late into the growing season, and decreases from the upper beach to the foredune once sea ice has gone (Imbert and Houle, 2000). The further linear decrease in salinity expected from foredune to fixed dunes could therefore not explain the observed pattern in performance (i.e., peaking in the middle zones). Soil pH generally decreases along the dune succession gradient (Imbert and Houle, 2000; Isermann, 2005) but can vary even at meter-scale between vegetated and non-vegetated ground (Isermann, 2005). As *Empetrum* grows well on acidic soils (Bell and Tallis, 1973) and has been shown to have a stabilizing effect on soil pH on sand dunes (Isermann, 2005), it is unlikely that variations in pH alone could explain the observed patterns in performance.

Although viable seeds were not significantly associated with soil moisture or OM content along the gradient, seeds collected in the zone where soil moisture was maximal (Z4) germinated to a greater extent. Moreover, the observed negative relationship between germination rate and lichen cover suggests that water availability might be of importance even though we were not able

to identify its effect with our soil humidity measurements.

An alternative hypothesis was that intraspecific competition could limit *E. hermaphroditum* performance toward the end of the succession gradient; however, this does not seem to be a constraint at current densities given that the number of competitors around an individual had no effect on stem elongation or the production of viable seeds. In fact, Boudreau et al. (2010) found that the colonization of the dune system had proceeded in an increasingly clustered manner. Such a relationship could suggest that either dispersal is limited and/or individuals are aggregated in “richer” microsites favorable to survival and growth. Although a fraction of the berries is likely carried away by animals, there is visual evidence that many of the fruits remain on the mother plant. The only fruit consumers observed were white-crowned sparrows (personal observations by S. Angers-Blondin and S. Boudreau). Dispersal limitations would also explain the great number of seedlings in zones 6 and 7: even though each individual produces on average fewer viable seeds, there are more individuals producing berries, which then fall within their vicinity.

Colonization and Expansion in a Warming System

Rapid warming of the study area in the past two decades (a 1.6 °C increase in summer temperatures) has likely contributed to the expansion of the population by lifting bottlenecks in the regeneration cycle. Higher temperatures have the potential to promote seed viability and germination in northern plants (Meunier et al., 2007; Milbau et al., 2009). Most *E. hermaphroditum* seeds possess physiological dormancy that requires warm (late summer) and cold (winter) stratification. As a longer warm stratification period increases germination success (Baskin et al., 2002), recent warming in Whapmagoosui-Kuujuarapik might be promoting seed germination. In our study, overall germination was 35%, which is consistent with the results of Hill et al. (2012), who found that 33% of seeds having overwintered in berries subsequently germinated in a greenhouse experiment. Although we acknowledge that germination in the field is probably much lower than under controlled lab conditions, the abundance of seeds produced ensures that a number of seedlings can establish every year.

Warmer temperatures can also increase seedling survival (Weih and Karlsson, 1999). Seedlings in northern ecosystems often experience high mortality: Wager (1938) estimated an annual decrease of 40–60% for individuals aged 5 yrs old or less. In a recent study involving 14 tundra species, Graae et al. (2011) found

similar results, with only ca. 50% of the seedlings surviving their first winter. In cotton grass tussock tundra in Alaska, the annual mortality rate for young *Empetrum nigrum* individuals was 43% (McGraw and Shaver, 1982). In contrast, our 2-yr monitoring of *E. hermaphroditum* seedlings in a similar age class (≤ 5 yrs old) revealed that annual survival is very high ($>95\%$). The continuous, dependable recruitment highlighted by our study seems to predict further population growth, at least until suitable space for seedling establishment becomes limiting (Moulton and Gough, 2011). Our results suggest that dwarf shrubs can efficiently use a dual strategy, filling gaps by establishing from seed and then spreading clonally to monopolize space and resources.

CONCLUSION

We show evidence for rapid infilling in a coastal, subarctic *E. hermaphroditum* population by means of high recruitment, low mortality and fast growth. At current densities, there is no indication of intraspecific competition limiting performance, and the population is expected to continue its expansion through a dual strategy combining sexual reproduction and clonal growth. Sexual reproduction in tundra plants is likely to increase in the future as warmer temperatures alleviate reproductive bottlenecks (Wookey et al., 1995; Klady et al., 2011; Moulton and Gough, 2011). The slow-growing, evergreen dwarf shrub communities that, as of yet, have not been very responsive to climate change (Elmendorf et al., 2012) therefore deserve further attention, as they could experience shifts in reproduction strategies that could greatly alter tundra vegetation.

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