Pathogens, herbivores, and phenotypic plasticity of boreal *Vaccinium vitis-idaea* experiencing climate change

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**Abstract.** Climate warming is occurring at a rapid rate in the boreal forest; mean winter temperature has increased about 4°C in Alaska over the last 40 years and about the same increase is predicted over the next 40 years. Warming temperatures tend to increase the number and kinds of herbivores and pathogens. How will boreal plants to respond to these abiotic and biotic changes? To address these questions we used common gardens and reciprocal transplants of *Vaccinium vitis-idaea* at sites with contrasting abiotic conditions near Fairbanks, Alaska. Plant morphology, chemistry, resistance to pathogens and herbivores, and survival were all strongly influenced by the destination environment (planting site and block within site), and less by the site of origin for the seed. Overall, seedlings survived significantly better at the summer cold site, which was buffered from drought as a result of its northern aspect, presence of sphagnum moss and permafrost (86.4% survival versus 48.5%). However, this cool damp site had more stem-killing consumers, the pathogens *Phomopsis columnaris* and *Exobasidium vaccinii* and mammalian browse, all of which became more common over the three years of the study as the plants became larger. Taken together, these results suggest that the seedling stage is likely to be vulnerable to droughts, except at sites with thick moss cover, which results in greater duration of summer moisture. Thus, as the climate warms, seedling growth will be restricted to those sites where the adult stages will later suffer from more stem-killing pathogen attack and mammalian browse.

**Key words:** Alaska; climate change; *Exobasidium vaccinii*; global warming; herbivory; local adaptation; lingonberry; phenolic; *Phomopsis columnaris*; plasticity; reciprocal transplant; *Vaccinium vitis-idaea*.

**INTRODUCTION**

The boreal forest biome, the second largest on the planet, covers a vast area including most of Canada, Alaska, Scandinavia and Siberia (Hultén 1968, Johnson et al. 1995, Moen 1999). The boreal biome is currently undergoing very rapid climate change. For example, in the last 50 years (1954–2003), Alaska has seen an increase between 1°C and 2°C averaged across the year, with a 3–4°C increase in winter (Corell et al. 2004). As a result, growing season length (defined as temperatures >0°C) in Fairbanks has increased by 45–50% in the last 100 years (Wendler and Shulski 2009). Projections for the future are for 4–7°C increase by 2100 (Corell et al. 2004). How is this warming likely to affect plant species living in the boreal forest? One prediction is that cold-adapted plant species are likely to experience drought stress as the climate warms due to increased transpiration (Barber et al. 2000, Lloyd and Fastie 2002). Another prediction is that with warming, plant
Table 1. Environmental data for all study sites and for the common gardens.

| Variable                        | All sites Mean | Range      | Vaccinium sites Mean | Range      | BNZ5N Mean | Range      | JEN1F Mean | Range  |
|--------------------------------|----------------|------------|----------------------|------------|------------|------------|------------|--------|
| Geographic                      |                |            |                      |            |            |            |            |        |
| Latitude (°N)                   | 293            | 140 - 750  | 293                  | 140 - 750  | 303        | 140 - 750  | 360        | 140    |
| Longitude (°W)                  | 147°27'33" - 148°22'38" | 147°27'33" - 148°22'38" | 148°16'54" - 149°50'00" | 148°16'54" - 149°50'00" |
| "Northness" (cosine (aspect))   | -0.13          | -1 to 0.92 | -0.07                | -0.99 to 0.92 | 0.73       | 0          |            |        |
| "Eastness" (sin(aspect))       | 0.03           | -1 to 0.98 | 0.03                 | -1 to 0.98  | -0.68      | 0          |            |        |
| Slope (category)               | 1.6            | 0 to 4     | 1.6                  | 0 to 4     | 4          | 0          |            |        |
| Elevation (m asl)              | 293            | 140 - 750  | 293                  | 140 - 750  | 303        | 140 - 750  | 360        | 140    |
| Environmental                   |                |            |                      |            |            |            |            |        |
| August                          |                |            |                      |            |            |            |            |        |
| Soil temp (°C)                 | 7.9            | 4.2 - 11.8 | 6.9                  | 4.2 - 10.0 | 4.2        | 10.0       | 4.2        | 10.0   |
| Soil moisture (%)              | 7              | 4 - 13     | 7                    | 4 - 13     | 13         | 7          |            |        |
| Summer                          |                |            |                      |            |            |            |            |        |
| Air temp (°C)                  | 0              | -2.1 to 0.7| -0.1                 | -2.1 to 0.7| -0.15      | 0.7        |            |        |
| Absolute humidity (g m⁻³)      | 0              | -10.3 to 9.3| -0.9                | -10.3 to 3.0| -2.3       | -10.3      | -2.3       | -10.3  |
| RH (%)                         | 0              | -1.3 to 1.3| 0.5                  | -1.3 to 2.1| -0.3       | -1.3       | -0.3       | -1.3   |
| Winter air temp (°C)           | 0              | -3.9 to 2.8| -0.9                 | -3.9 to 2.8| 1.35       | -0.96      | 1.35       | -0.96  |
| Mean below-snow temp (°C)      | 0              | -6.3 to 10.9| -1.1                | -6.3 to 1.7| 1.4        | -0.7       | 1.4        | -0.7   |
| Min below-snow temp (°C)       | -12.9          | -31.3 to -1.6| -15.9               | -31.3 to -7.1| -12.1     | -12.8      | -12.1     | -12.8  |
| Date of snowmelt (Julian date) | 143            | 136 to 162 | 143                  | 136 to 162 | 156        | 138        | 156        | 138    |
| Thaw depth (cm)                | 77             | 29 to 100  | 57                   | 30 to 100  | 30.37      | 100        |            |        |
| Vegetation                      |                |            |                      |            |            |            |            |        |
| Moss depth (cm)                | 6              | 0 to 35    | 11                   | 0 to 35    | 35.23      | 1          |            |        |
| Litter depth (cm)              | 3              | 0 to 6     | 2                    | 0 to 6     | 0          | 5.5        |            |        |
| % ground cover                 | 2              | 0 to 5     | 3                    | 0 to 5     | 5          | 2          |            |        |
| % vegetation cover             | 3              | 1 to 5     | 3                    | 2 to 5     | 2.58       | 4.25       |            |        |
| % canopy cover                 | 64             | 0 to 94    | 48                   | 0 to 91    | 39.41      | 56.2       |            |        |

Notes: Vaccinium sites are those at which V. vitis-idaea was present. Because dates for which data were available varied by site as a result of equipment failure, all temperature and humidity values are mean deviations from the daily across-site means. Abbreviations are: asl, above sea level; temp, temperature; RH, relative humidity; min, minimum.

Herbivores and pathogens will increase in both species richness and in the amount of damage they cause (Ayres 1993, Lonsdale and Gibbs 1996, Coakley et al. 1999, Ayres and Lombardero 2000, Malmström and Raffa 2000), leading to decreases in plant fitness, and potentially to even more rapid changes in vegetation. In this paper we explore the relationships between the abiotic environment, plants, and their pathogens and herbivores. Throughout the text we refer to the collection of plant pathogens and herbivores as “consumers” because they remove leaf tissue from photosynthesis. Consumers is a more neutral term than “enemies”, “pests”, or “parasites” and we prefer it because plant damage does not always result in fitness loss (Strauss and Agrawal 1999, Roy and Kirchner 2000).

To address questions concerning the relationships between temperature, damage by consumers, and potential changes in plant communities, we took advantage of the presence of large environmental differences at small scales in northern regions (Okland et al. 1990, Okland 1994, Gould and Walker 1999, Armbruster et al. 2007). For example, differences in vegetation between the north and south sides of hills become more exaggerated as one travels northwards (Moen 1999). These environmental and vegetative differences are set up, in part, by the combination of short summers, low angle sun, and variation in aspect and slope that lead to differences in solar energy absorption (Moen 1999, Armbruster et al. 2007). Complex interactions between vegetation, fire (Chambers and Chapin 2002, Amiro et al. 2006, Johnstone and Chapin 2006) and permafrost (Bonan 1991, Shur and Jorgenson 2007) add to the environmental variation. Despite the high environmental heterogeneity and the resultant small-scale beta-diversity (Okland et al. 1990, Rae et al. 2006), the species richness (alpha diversity) of plants and insects of the boreal forest is low, probably because few species can tolerate the extremely cold winters (Bale et al. 2002).

We set up common gardens at two sites differing in environmental characteristics, including temperature (Table 1, Fig. 1), to ask how differences in the abiotic environment affect...
plants and the organisms that consume them. To address these questions, we measured plant morphology, chemistry, survival, and damage by consumers in our common gardens. We were particularly interested in whether there was evidence of local adaptation to the sites. Local adaptation has been measured in two ways: by the relative fitness of local genotypes versus non-local, “foreign” transplants within the same site and by whether or not a genotype has higher fitness at its site of origin, when at “home” versus away (Kawecki and Ebert 2004).

Another possibility besides local adaptation, given the large environmental variation at small scale in the Arctic, is that selection has favored phenotypic plasticity such that seedlings can grow and thrive in many environments. Theory suggests that species such as V. vitis-idaea that encounter variable environments, and have high gene flow due to insect pollination, obligate outcrossing and animal dispersal, are likely to be phenotypically plastic instead of being locally adapted (de Jong 1995, Sultan 1995, Gandon 2002). In addition to morphological responses to the abiotic environment, we were interested in the responses of plants to their local biotic environment. Do the transplant sites have similar consumers, and does the origin of the plants affect damage by consumers?

**METHODS**

**The plants**

*Vaccinium vitis-idaea* L. (lingonberry or lowbush cranberry, Ericaceae) is circumpolar in distribution, and is found across a wide range of environments within the boreal forest and tussock tundra (Hultén 1968, Viereck and Little 1986). *V. vitis-idaea* is an important food plant for many animals (Ericson 1977, Norment and Fuller 1997, Kapel 1999, Rode and Robbins 2000) including humans (Rennick 1996, Saastamoinen et al. 2000). This species is insect pollinated (Froburg 1996) and apparently they are nearly obligate outcrossers since they suffer from a drastic reduction of fertility when self-fertilized (Froburg 1996, Guillaume and Jacquemart 1999). *V. vitis-idaea* also has high capacity for vegetative reproduction (Hautala et al. 2001, Persson and Gustavsson 2001); nonetheless, genetic analyses show high within-population diversity (89.2%; Persson and Gustavsson 2001), suggesting that sexual reproduction is more common than asexual reproduction. Ecological studies of re-
recruitment indicate that seedling establishment takes place after disturbance generates an open-
ing (Hautala et al. 2001, Eriksson 2002).

Environmental variable data collection
The environmental data described in here are part of a larger study of plant consumers in response to climate initiated in 2002 (Mulder et al. 2008; C. P. H. Mulder and B. A. Roy, unpublished manuscript). For the larger study, 21 sites within 60 km of Fairbanks, Alaska were selected to maximize differences in summer temperature and moisture regimes (by selecting sites with different slopes and aspects), and in winter temperature regimes (by varying elevation, which is positively correlated with winter temperature due to temperature inversions).

To characterize the sites, both with respect to each other and within the context of potential sites available in interior Alaska, we measured a number of abiotic and biotic variables. Means and ranges for all sites as well as for sites where *V. vitis-idaea* was present are provided in Table 1. Since our focus was on inter-site comparisons, we used data that were available for all sites for the same time periods. Different types of measurements were made during different seasons, but at the same time periods across sites. Temperature and relative humidity of the air were measured every 30 min using a HOBO-Pro data logger (Onset Computer, Cape Cod, Massachusetts, USA). Winter temperature below-snow (at ground-level, between soil and snow) was measured every 1.5 hour using a HOBO temperature data logger. Summer mean temperatures and relative humidity are based on data from August 2003, June–August 2004, and June–July 2005. Winter mean air temperatures are based on December 2003–February 2004 and December 2004–February 2005 values. Date of snowmelt was estimated based on below-snow temperature data (defined as the first day on which the temperature was \( >1^\circ\text{C} \)). Summer mean soil temperatures are means of measurements taken on 18–23 August 2003 and 8–16 August 2004 (10 measurements per site taken with a Hanna HI 145 temperature probe at 10 cm depth [Hanna Instruments, Woonsocket, Rhode Island, USA]). Depth of thaw was measured in cm on 19–24 July 2003 and entered as ‘100’ if \( >1\text{ m} \). We measured moss depth and litter depth and visually estimated percent ground cover (percentage of ground covered by lichens and bryophytes), and understory cover (percentage of ground covered by vegetation up to 1 m in height) in 20 1-m\(^2\) quadrats per site. Canopy cover was estimated in five locations per site using a convex spherical crown densiometer (Model A; Forest Densimeters, Bartlesville, Oklahoma, USA).

To compare the sites used in this study to other locations at which *V. vitis-idaea* was present and to those where it was not found, we used principle components analysis (PCA) to reduce the many strongly correlated variables to a few axes. The first two axes explained 31\% and 18\%, respectively, of the variation among sites. The first axis (PC1) can best be described as a summer soil temperature gradient: sites that score high on this axis tend to have a southern aspect, early snowmelt, deep thaw depths and warm soils, and a thin moss layer but a thick understory, overstory, and litter layers (Fig. 1). The second axis (PC2) represents a winter temperature gradient: sites that score high have high winter temperature both above and below the snow, and because they occur at higher elevations they also have cool summer temperatures and late snowmelt dates (since the temperature inversions that are responsible for the warmer winter temperatures at higher elevations reverse prior to snowmelt).

Seed collection and common garden sites
*V. vitis-idaea* was restricted to the colder sites (Fig. 1, Table 1). Berries were collected in the fall of 2003 from the 10 sites at which it was present. Three collection sites were located in the Bonanza Creek LTER (BNZ1S, BNZ5N and BNZ7N), four were in the Caribou-Poker Creek Research Water Shed (CPC12S, CPC13S, CPC15S and CPC5N), one site was on private land east of Fairbanks (JEN1F), one was from Murphy Dome (MUD8N) and one was on the campus of the University of Alaska, Fairbanks (UAF3F). At four of the sites (BNZ5N, BNZ7N, CPC5N, MUD8N) the Vaccinium parent plants were rooted in *Sphagnum* moss, at two sites (BNZ1S and JEN1F) they were rooted in soil, and at the rest of the sites they were rooted in some combination of moss (not necessarily *Sphagnum*) and soil.

The plants were started in a greenhouse, where they grew for 5 months until they were trans-
planted into three common garden sites: JEN1F, BNZ5N and CPC13S (Fig. 1). Unfortunately, the intermediate site CPC13S (Fig. 1) burned in a forest fire shortly after transplanting. The two remaining common gardens were BNZ5N, located within the Bonanza Creek LTER and JEN1F, which was located on private land. These two sites differed by every characteristic we measured (Table 1). The Bonanza Creek site was on a steep, north-facing slope with a high percent cover of Sphagnum, cool summer temperatures and warm winter temperatures. The JEN1F site had small-scale ups and downs but no dominant slope direction, it had less moss cover and warmer summer temperatures, but colder winter temperatures than BNZ5N.

Greenhouse methods
Seeds were removed from the berries and were soaked in 2000 ppm gibberellic acid (GA) prior to being placed in petri dishes on 2 February 2004 for germination. The first seedlings germinated on 20 February 2004; all seedlings were transplanted on 26 March to 200 cm³ conetainers (D-40 cells, Stuewe and Sons, Corvallis, Oregon, USA) filled with a 50:50 mix of coconut coir and vermiculite, and placed in a greenhouse. Seedlings were watered as needed with a one-quarter-strength nutrient solution (approximately 70 ppm N). Prior to transplanting we counted the number of leaves and measured the height and longest leaf length of each seedling. Plants were placed outside the greenhouse to acclimate for four days prior to transplanting to the field on 12–13 July 2004.

Experimental design
Because different numbers of berries were found at the sites, and different numbers of seeds germinated, we did not have equal numbers of seedlings to transplant from each site of origin. Instead, we divided seedlings evenly among the three destination sites (66 seedlings per site), and randomized their placement within sites. At each site, seedlings were transplanted in July 2004 into two blocks consisting of five rows, with 1 m between rows. We transplanted 33 seedlings per block into four rows of 7 and one row of 5. Within the rows, the seedlings were 0.5 m from each other. The planting area was not disturbed except for the small spot where the seedling was placed.

Measurements of morphology and consumers
We measured the height of the longest stem each year in August (2004, 2005 and 2006), we counted the number of living stems and the number of leaves on each plant in two years (2005 and 2006). At the end of the experiment in 2006 we collected dry weight measures of the aboveground tissue and the roots.

Plants were assessed annually in August 2004–2006 for damage by herbivores and pathogens. We estimated the area removed (percent damage) by each kind of consumer on two leaves per plant, and counted the number of kinds of consumers present on each plant. However, stem damage was not reflected in the random sample of two living leaves/plant and three consumers removed entire stems (browse, dieback and Exobasidium). Since removal of whole stems is more likely than leaf damage to reduce host fitness, and stem damage was captured in the whole plant data, we focused the analysis on whole plant measures (presence of each type of damage and number of kinds of damage/plant).

Plant chemistry
Plant phenolic chemistry can respond to both the physical environment, such as light and temperature (Kuokkanen et al. 2001, Semerdjieva et al. 2003, Nybakken et al. 2012), and to pathogens and herbivores (Mayer 2004, Nagle et al. 2011). To minimize variation caused by changing environmental conditions (Appel et al. 2001), all the samples were collected on the same day in August 2006. To measure total phenolics, we used the Folin-Ciocalteu Assay, following Singleton and Rossi (1965). Briefly, the leaves were freeze-dried, ground, and extracted with 50:50 methanol : water and total phenolics were measured colorimetrically with a spectrophotometer (Model 2100; Unico, Dayton, New Jersey, USA).

Statistical analyses
To examine morphological, chemical and enemy responses we used factorial ANOVA, ANCOVA and repeated-measures ANCOVA. The explanatory terms in the models were: origin (random), destination (fixed), destination × origin (random), block nested in destination (ran-
We measured height and number of leaves before transplanting and used these initial greenhouse measurements as covariates. We included the initial size covariates because they could carry over into the field and plants that are bigger are often better competitors (e.g., de Wit and van den Bergh 1965, Grace and Tilman 1991, Stanton et al. 2004) and may also be bigger targets for consumers (Burdon 1987).

Analyses of the field data were complicated by an unbalanced data set resulting from variation in seed germination and the loss of one site to a forest fire. To determine origin versus destination effects, we used the five origins that were replicated (>1 individual per block). This reduced the overall data set by 18 individuals, and also reduced the number of origins from ten to five. However, we were more confident that the data set was robust for statistical analysis because for each origin there was replication within the destination sites and blocks.

Survival analysis requires special analysis due to having unusual distributions (exponential, in our case) and bias (Allison 1995). The bias is referred to as censoring, and results from the individuals that are left at the end of the study that would have kept living if the experiment had continued (i.e., a plant that was found dead at the end of the experiment would have the same death date as one that was terminated on that day). We therefore modeled survival with a parametric survival model, using the exponential distribution (Bekkaoui et al. 2003) and the number of days to death as the dependent variable. Plants that were still alive at the end were designated as “censored” and the model statistically adjusted for them.

To test for local adaptation, it is necessary for the performance of a genotype to depend on where it is planted, that is it is necessary for there to be origin by destination interactions in which the home or local genotype has higher fitness. When these interactions were significant we used specific contrasts that test for home site advantage across sites (for the reciprocally transplanted genotypes) and within sites (all genotypes) to test for whether local plants have higher fitness than foreign ones: Contrast 1 = Home versus away, BNZ5N@BNZ5N vs. BNZ5N@JEN1F; Contrast 2 = Home versus away, JEN1F@JEN1F vs. JEN1F@BNZ5N; Contrast 3 = Local versus foreign, BNZ5N@BNZ5N vs. all four other genotypes at BNZ5N; Contrast 4 = Local versus foreign, JEN1F@JEN1F vs. all four other genotypes at JEN1F.

Damage by pathogens and herbivores was measured as present or absent on each plant for each kind, and was analyzed with logistic regression. The number of kinds of damage was analyzed with repeated measures ANCOVA since we measured damage on the same plants each year. The explanatory variables were the same as the other models (see Table 2).

We used SAS version 9.1 for all statistical analyses, except for the survival analysis, which we performed in JMP Pro 9.0.2 (SAS Institute, Cary, North Carolina, USA). Variables were transformed when necessary to meet normality and heterogeneity assumptions.

**Results**

**Morphology in the common gardens**

The planting environment (=destination) significantly influenced all the traits measured (Table 2, Fig. 2), indicating phenotypic plasticity. At BNZ5N, where the plants were rooted in Sphagnum and experienced cool summers, but relatively warm winters, plants were generally shorter (7.92 ± 0.43 cm vs. 12.5 ± 0.77), with more leaves (31.44 ± 2.91 vs. 17.93 ± 3.06), more living stems (3.62 ± 0.19 vs. 2.74 ± 0.39), and bigger roots (0.21 ± 0.02 g vs. 0.17 ± 0.03) than at JEN1F, where summer temperatures were relatively warm, winter temperatures were cold and they were rooted in soil.

Morphology was influenced by a combination of the genotype’s origin and the site it was planted in (origin × destination interactions) for two traits, height and dry weight (Table 2, Fig. 2), and the number of live stems was also nearly significant (P = 0.08). Closer analysis, however, revealed little evidence for local adaptation. To test for local adaptation it is necessary to decompose the significant origin × destination interactions with specific contrasts to determine whether there is a home site advantage or whether the local genotype performs better than foreign genotypes at the same site (Table 2). JEN1F genotypes had taller stems when planted at home than away, but BNZ5N genotypes were taller away than at home, and were even taller.
though not significantly so) than JEN1F plants at their home site (Fig. 2A). Neither of the local versus foreign contrasts (Contrasts 3 and 4; Table 2) for stem height were significant. For the root dry weight origin × destination interaction (Fig. 2D) none of the local adaptation contrasts were significant, though there was a tendency ($P = 0.075$) for the local genotype at BNZ5N to be larger than all other genotypes at that site (Fig. 2D).

**Survival in the common gardens**

Overall, the death of plants from different origins depended on the destination environment (Fig. 3). Survival was best at the transplant destination BNZ5N where 86% (57/66) survived, versus 48% survival (34/66) at JEN1F. Looking at the five origins with replication (Fig. 3), there were no significant origin by destination effects ($\chi^2_{4,13} = 4.88, P = 0.2999$). However, site of origin ($\chi^2_{4,13} = 11.18, P = 0.0246$), destination ($\chi^2_{1,13} = 27.84, P < 0.0001$), and block ($\chi^2_{2,13} = 9.06, P = 0.0108$) were all statistically significant (Fig. 3).

**Consumers in the natural common gardens**

All the kinds of consumer damage occurred at both sites (Fig. 4), with the exception of *Ophiognomonia*, which only occurred at the

### Table 2. ANCOVA of morphology and chemistry in the common gardens.

| Variable               | Source     | df num | SS   | $F$   | $Pr > F$   | Dir. | Error df | Model $R^2$ |
|------------------------|------------|--------|------|-------|------------|------|----------|-------------|
| Height                 | GH height  | 1      | 235.93 | 28.67 | <0.0001    | +    | 63       | 0.58        |
| GH no. leaves          | 1          | 18.03  | 2.19  | 0.1439|            |      |          |             |
| Origin                 | 4          | 7.19   | 0.87  | 0.485 |            |      |          |             |
| Dest                   | 1          | 320.91 | 39.00 | <0.0001|            |      |          |             |
| Origin × Dest          | 4          | 20.22  | 2.59  | 0.0448|            |      |          |             |
| Block(Dest)            | 2          | 6.38   | 0.77  | 0.4651|            |      |          |             |
| Contrast 1             | 1          | 104.9  | 12.75 | 0.0007|            |      |          |             |
| Contrast 2             | 1          | 106.7  | 12.97 | 0.0006|            |      |          |             |
| Contrast 3             | 1          | 2.39   | 0.2904| 0.5919|            |      |          |             |
| Contrast 4             | 1          | 0.041  | 0.0050| 0.9441|            |      |          |             |
| No. leaves             | GH height  | 1      | 1970.96 | 8.73  | 0.0044    | +    | 62       | 0.53        |
| GH no. leaves          | 1          | 4080.67 | 18.07 | <0.0001|            |      |          |             |
| Origin                 | 4          | 146.47 | 0.65  | 0.6301|            |      |          |             |
| Dest                   | 1          | 5046.49 | 22.34 | <0.0001|            |      |          |             |
| Origin × Dest          | 4          | 164.98 | 0.94  | 0.5746|            |      |          |             |
| Block(Dest)            | 2          | 1642.03 | 6.95  | 0.0015|            |      |          |             |
| No. live stems         | GH height  | 1      | 6.99   | 3.70  | 0.059      |      | 63       | 0.43        |
| GH no. leaves          | 1          | 29.25  | 15.46 | 0.0002|            |      |          |             |
| Origin                 | 4          | 2.44   | 1.29  | 0.284 |            |      |          |             |
| Dest                   | 1          | 23.85  | 12.61 | 0.0007|            |      |          |             |
| Origin × Dest          | 4          | 4.05   | 2.14  | 0.086 |            |      |          |             |
| Block(Dest)            | 2          | 2.62   | 1.40  | 0.2683|            |      |          |             |
| Root dry weight        | GH height  | 1      | 0.1    | 6.30  | 0.0138     | +    | 63       | 0.37        |
| GH no. leaves          | 1          | 0.11   | 6.89  | 0.0106|            |      |          |             |
| Origin                 | 4          | 0.02   | 1.51  | 0.1788|            |      |          |             |
| Destin                 | 1          | 0.07   | 4.39  | 0.0443|            |      |          |             |
| Origin × Dest          | 4          | 0.04   | 2.48  | 0.0528|            |      |          |             |
| Block(Dest)            | 2          | 0.02   | 1.22  | 0.303 |            |      |          |             |
| Contrast 1             | 1          | 0.007  | 0.4496| 0.5050|            |      |          |             |
| Contrast 2             | 1          | 0.015  | 0.9435| 0.3351|            |      |          |             |
| Contrast 3             | 1          | 0.052  | 3.26  | 0.0756|            |      |          |             |
| Contrast 4             | 1          | 0.027  | 1.71  | 0.1958|            |      |          |             |
| Total phenolics        | GH height  | 1      | 6336.04 | 4.50  | 0.0379    | +    | 63       | 0.49        |
| GH no. leaves          | 1          | 46.21  | 0.03  | 0.8569|            |      |          |             |
| Origin                 | 4          | 1954.69 | 1.39  | 0.3487|            |      |          |             |
| Destin                 | 1          | 54329.8 | 38.55 | <0.0001|            |      |          |             |
| Origin × Dest          | 4          | 322.13 | 0.23  | 0.9214|            |      |          |             |
| Block(Dest)            | 2          | 8389.52 | 5.95  | 0.0043|            |      |          |             |

Notes: This dataset was from the last census in 2006, and used the five origins for which there was replication within destinations. Type I SS were used in the ANCOVAS to factor out the covariates. Abbreviations are: Dest, destination; Dir, direction; df, degrees of freedom; GH, greenhouse; SS, sum of squares. The following contrasts were run to examine local adaptation when there was a significant origin by destination interaction: Contrast 1 = Home versus away, BNZ5N@BNZ5N vs. BNZ5N@JEN1F; Contrast 2 = Home versus away, JEN1F@JEN1F vs. JEN1F@BNZ5N; Contrast 3 = Local versus foreign, BNZ5N@BNZ5N vs. all four other genotypes at BNZ5N; Contrast 4 = Local versus foreign, JEN1F@JEN1F vs. all four other genotypes at JEN1F.
summer warm, winter cold JEN1F site. While the kinds of consumers were similar among sites, the incidence of damage (percent of plants attacked) varied significantly among the sites (Fig. 4). Most of the kinds of damage observed are illustrated in Fig. 5. Leaf thickening, cupping, an increase in red anthocyanins and eventual leaf and stem death were caused by the fungus *Exobasidium vaccinii* (Fuckel) Woronin (Fig. 5A). This pathogen occurs throughout the European and North American ranges of *Vaccinium* (Pehkonen et al. 2008, Farr and Rossman 2012). Another kind of stem death, “dieback”, was particularly common at the summer cold, winter warm site BNZ5N (Fig. 4). These stems and leaves became brown or black, but without the characteristic thickening of *Exobasidium*. This dieback may have had a variety of causes, since both physical damage (Bokhorst et al. 2010) and pathogens (Farr et al. 2002) can lead to stem death. However, we cultured the fungus *Phomopsis columnaris* D. F. Farr & Castlebury (Fig. 5B) from every sample we examined (*N* = 10), suggesting that this recently described pathogen (Farr et al. 2002) was the major cause of stem death at the transplant sites. A “mildewed or sooty” appearance on leaves was caused by *Ophiognomonia alni viridis* (Podlahova & Svrček) Sogonov (not illustrated here). While *Alnus viridis* is the most typical host for this fungus, it is also found on plants that co-occur with *A. viridis*, such as *Vaccinium* and *Betula* (Sogonov et al. 2008). The
reddish blushing symptom (Fig. 5C) indicates high levels of anthocyanins, which can be caused by either abiotic or biotic stressors (Semerdjieva et al. 2003, Ek et al. 2006, Hansen et al. 2006, Pehkonen et al. 2008). There were three major kinds of herbivory: mammalian browse damage, insect mining and chewing (Fig. 4). There were two kinds of leaf miners; one was a blotch miner that removed tissue between veins, leaving the upper epidermis intact (Fig. 5D, E), the second miner species left long narrow tracks that tended to be straight when in the center of the leaf (Fig. 5F) or curved if on the edge of the leaf. The blotch miner damage (Fig. 5D, E) is consistent with that of the casebearer moths Coleophora murinella Tengstrom or Coleophora glitzella Hofmann, neither of which have been reported from Alaska (Ferris et al. 2012). The most likely of the two is C. glitzella, which is native in the neighboring Yukon Territory, whereas C. murinella is known only from Nova Scotia and Newfoundland (J.-F. Landry, personal communication). The “asco + mine” symptom (Fig. 4) resulted from a combination of the blotch miner and fungal damage. The miner left behind a thin piece of upper epidermis, on which an unidentified ascomycete fungus sometimes sporulated. Since we were unable to isolate fungi from three kinds of spots (pink, yellow and black), insects probably caused them. Our observations suggested that most, if not all of these unidentified spots were caused by leaf miners that had aborted or were young and had not yet grown (Fig. 5E).

Consumer damage depended on destination.
environment (Figs. 4 and 6). Damage was more frequent at BNZ5N for all types (Fig. 4), except for *Ophiognomonia*, which only occurred in 2 of 3 years at JEN1F. BNZ5N had significantly more plants exhibiting chewing damage in all three years, and in 2 of 3 years significantly more plants were browsed, mined and died back at BNZ5N.

We summed the number of kinds of herbivores and pathogens on each plant for each year (Fig. 6) and examined these data in repeated measures analysis. Destination mattered; there were more pathogens at the summer cool, winter warm site, BNZ5N (Fig. 6A–C). The number of kinds of pathogens present on a plant depended on where the plant originated from at each destination (significant origin by destination interaction, $F_{4,61} = 2.57$, $P = 0.0467$; Fig. 6A, C, E). There were fewer kinds of pathogen damage at JEN1F than BNZ5N for three origins (BNZ5N, JEN1F, BNZ7N), about the same number for UAF3F, and a lot more for CPC13S (Fig. 6). There was little variation in pathogen resistance until the third year (Fig. 6). While the repeated measures analysis showed a significant origin by destination interaction, this disappeared in the univariate tests (not shown).

The number of kinds of herbivores present depended on the site; there were more kinds on average at BNZ5N (significant destination effect, $F_{1,61} = 37.91$, $P < 0.0001$, Fig. 6B, D, F), and there was also significant variation among blocks within sites ($F_{2,61} = 2.57$, $P = 0.0005$). Taller plants at the time of transplanting had more kinds of both herbivores and pathogens (positive effects of the covariate height $F_{2,61} = 9.56$, $P = 0.0030$ for herbivores, $F_{2,61} = 10.01$, $P = 0.0024$ for pathogens). Unlike pathogens, there was no origin × destination interaction for the number of kinds of herbivores. There was no association between the number of pre-transplanting leaves in the greenhouse and the numbers of kinds of damage (no effect of the number of leaves

(continuation of Fig. 4 legend)

all origins. Each plant was searched for presence and absence of each damage type. (A) 2004, (B) 2005, (C) 2006. $P$ values were derived from logistic regression (likelihood ratio $\chi^2$ tests);* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Blk = black, Yell = yellow.
Fig. 5. Symptoms and casual agents for some of the kinds of damage found on Vaccinium vitis-idaea. (A) Symptoms caused by the fungus *Exobasidium vaccinii* (Fuckel) Woronin (Ustilaginomycetes, Exobasidiales). (B) Close-up of the conidiomata of the fungus *Phomopsis columnaris* D. F. Farr & Castlebury (Diaporthales, Ascomycetes), which causes stem dieback. (C) Pink blushing on leaves, cause unknown. (D) Fresh blotch mines, and at arrow, the circular wound characteristic of casebearer moths (*Coleophora* sp.) when the case detaches. (E) Older blotch mines. (F) Linear mine on a detached leaf. A larva from an unknown insect (likely moth or fly) causes this symptom. Note also the pink spots on the lower edge of the leaf. We called these “pink spots” and they were often associated with mines. These may be very young mines that have not grown yet, or they may be aborted (dead) mines.
covariate in any of the models).

The number of kinds of consumers present depended on consumer type and census year (Figs. 4 and 6). The number of kinds of damage by pathogens increased over each of the three years (Fig. 6A, C, E), whereas the number of kinds of herbivore damage decreased in the second year, but went back up in the third (Fig. 6B, D, F; census by destination interactions for both herbivores; Wilks’ lambda $F_{2,61} = 12.90, P < 0.0001$ and pathogens Wilks’ lambda $F_{2,61} = 4.62, P = 0.0136$). Similar to the variation in consumer

Fig. 6. Number of kinds of pathogens and herbivores for each year of the study. (A) Number of kinds of pathogens 2004. (B) Number of kinds of herbivores 2004. (C) Number of kinds of pathogens 2005. (D) Number of kinds of herbivores 2005. (E) Number of kinds of pathogens 2006. (C) Number of kinds of herbivores 2006.
kinds depending on year for the destinations, this was also true for the blocks within sites for herbivores (census by block interaction Wilks’ lambda $F_{4,122} = 4.92$, $P = 0.0010$), but not for pathogens.

**Plant chemistry**

Several factors significantly influenced the concentrations of plant phenolics, including the destination garden, block (Table 2) and potentially, herbivory. *Vaccinium* planted at BNZ5N had consistently higher concentrations than those at JEN1F, even though there were also within-site block effects. There were no detectable effects of origin on phenolics. Phenolic concentration was significantly positively correlated with the number of kinds of herbivore damage on plants ($r = 0.44$, $P < 0.0001$), but not with the number of kinds of pathogen damage ($r = -0.09$, $P = 0.4650$).

**DISCUSSION**

**Phenotypic plasticity**

The plants showed a large degree of morphological phenotypic plasticity in response to the environmental differences between sites (Fig. 2). For example, the numbers of leaves ranged from nearly 0 to about 50 and height varied between 4.5 cm to greater than 14 cm. Nonetheless, all genotypes survived best at the one site, BNZ5N. This site is thick with sphagnum and very wet, which buffered the seedlings from the 2004 drought that led to the fire that burned our third site. The 2004 fire season was the worst on record for the state with more than 2.7 million ha burned (NOAA National Climatic Center, State of the Climate Wildfires). We can put the superior survival of seedlings at BNZ5N into context by examining Fig. 1, where we have graphed the distribution of all 21 of our sites based on site characteristics, *V. vitis-idaea* is found mostly at sites with colder summer soil temperatures, small depth of thaw, high moss cover and low canopy cover. The summer of drought suggests that seedlings will be most vulnerable in the sites with warm summer soils (right half of Fig. 1; sites indicated with squares do not have *V. vitis-idaea*).

For every measurement except height, the plants at JEN1F were, on average, smaller (Fig. 2). These changes are consistent with the kinds of morphological changes observed by Chapin and Shaver (1996) in their long-term (1981–1989) manipulation of temperature, nutrients and light on *Vaccinium vitis-idaea*. Relative to controls at the end of the experiment higher temperatures increased biomass, whereas biomass was decreased by several factors, including: N addition, nutrients plus increased temperature, and shade. Our JEN1F garden was warmer in the summer but colder in the winter with more canopy cover (a measure of shading) than the BNZ5N garden (Table 1). The combination of elongated stems and small belowground biomass at this site are consistent with shade effects being larger than the warmer summer temperatures.

The small-scale environmental variation within sites was reflected in the block effects for some traits (phenolics, leaf number, herbivory, Table 2). The variation in percent plant cover and soil temperature within sites, especially within BNZ5N, help to explain these block effects. There was more variation within BNZ5N than JEN1F in terms of both August 2003 soil temperatures (BNZ5N range = 0.2–9°C vs. JEN1F = 9.6–10.6°C, $N = 20$) and densiometer readings (BNZ5N range = 19-63 vs. JEN1F = 46-61, $N = 16$).

**Local adaptation?**

While there was strong evidence of phenotypic plasticity and differentiation in morphology among sites, there was much less evidence for local adaptation. We used two different measures of local adaptation, the between site comparison of home versus away and the within site local versus foreign comparison. If we assume that plant size is a reliable fitness proxy, which is reasonable given the many species for which this is true (reviewed by Weiner et al. 2009), then there was a little evidence of local adaptation: for stem length in plants originating from JEN1F (Fig. 2A) via the home versus away comparison, and for the local versus foreign comparison for root size at BNZ5N (Fig. 2D). The within site local versus foreign comparisons more effectively isolate the genetic effects of adaptation, whereas the home site advantage between environment comparisons include the contribution of response to the environment (Nuismer and Gandon 2008), including maternal effects (Kawecki and Ebert 2004).

Low mortality and the resultant small sample
sizes at the summer cool, winter warm BNZ5N site may explain why there was no origin by destination interaction for survival. We expect that with more time, survival would have shown significant origin by destination interactions, given the data. For example, for the reciprocally transplanted genotypes (BNZ5N and JEN1F), when planted away from their home site average days to death was 659 ± 36 days, whereas when planted at their home sites, it was almost 30 days longer, at 687 ± 32 days. In just three years, these differences are close to significant. For long-lived species, such as *V. vitis-idaea*, that are living in environments with short growing seasons it can take many years to see phenotypic and fitness differences (Bennington et al. 2012). For *Eriophorum vaginatum*, local adaptation was not evident until after 17 years had passed, indicating that long time periods may sometimes be necessary for estimating local adaptation in long-lived species (Bennington et al. 2012).

**Response to pathogens and herbivores**

Both the number of kinds and the population sizes of plant consumers typically increase with warming temperatures (Desprez-Loustau et al. 2007, Robinet and Roques 2010), though there can be species-specific responses downwards as well (Roy et al. 2004, Burdon et al. 2006). Climate warming also increases the risk of arrival of novel consumer species or genotypes (Pautasso et al. 2010), but whether the warming happens in the summer or winter can be important. We found more kinds of both pathogens and herbivores at the summer cold but winter warm BNZ5N site than at JEN1F, which is summer warm but winter cold (Fig. 4). These results are in agreement with reviews showing that it is often winter temperatures that control the distributions of many organisms, including pathogens and herbivores (Coakley et al. 1999, Harvell et al. 2002, Desprez-Loustau et al. 2007, Robinet and Roques 2010).

What were the fitness consequences of attack by plant consumers? We did not census frequently enough to associate specific kinds of attack with death. However, mammalian browsing and two of the pathogens, *Exobasidium* and the *Phomopsis*, kill or reduce the production of stems (Wolfe and Rissler 1999, Farr et al. 2002). Both the stem pathogens were uncommon but becoming more common over time (Fig. 4A–C), and in 2 of 3 years were more common at BNZ5N than at JEN1F. This is consistent with information from a prior study on *Exobasidium*, which found that it occurs most often at summer cool localities (Pehkonen and Tolvanen 2008). In our last census (2006) about 10% of all stems at both sites were succumbing to *Phomopsis*. The most common type of herbivory was chewing damage, with 80% or more of plants exhibiting signs of it (Fig. 5), and with higher frequency at BNZ5N. However, the percent of leaf area removed by chewers was small (<2%) on a per leaf basis (Fig. 7).
If the Vaccinium plants are adapted to their local consumers, the reciprocally transplanted ones should have higher resistance (=fewer kinds of damage) at their home site, and less resistance at novel away sites, and within sites the locals should more resistance than the foreigners. We found no statistical evidence that there was local adaptation by the plants to their consumers, although the differences among the genotypes were increasing over time (Fig. 7). It is very tricky to assess adaptation to pathogens given that hosts vary in resistance and pathogens vary in virulence (Thrall et al. 2002). To disentangle these associations, it is necessary to examine variation in both hosts and pathogens simultaneously. A good approach for the future would be to use cross inoculation studies with multiple host genotypes and pathogen strains known to differ in virulence.

Secondary chemistry

In our field transplant experiment the planting environment (destination and block within destination) was strongly associated with total phenolic content of the leaves (Table 2). A number of environmental factors have been experimentally shown to induce phenolics in Vaccinium vitis-idaea: UV-B (Semerdjieva et al. 2003), but also shade (Hansen et al. 2006), and increased temperature and nutrients (Hansen et al. 2006). Our site with the highest concentrations was BNZ5N, which was on a north slope and received less direct light, but it also had less canopy cover and was thus less “shady” in the canopy sense, than the other common garden, JEN1F. However, several characteristics of the site are not consistent with published literature on what increases phenolic concentrations in this species: BNZ5N had colder soil and air temperatures during the growing season (Table 1) and nutrient availability was also likely to be lower than JEN1F because the plants were rooted in sphagnum, rather than in soil. All these factors are more likely to cause reduced, not elevated levels (Hansen et al. 2006).

Induction by insects may better explain the elevated levels of phenolics than the physical environment does. Across sites and individuals, we found that the number of kinds of herbivores was significantly \( r = 0.44, \ P < 0.0001 \) positively correlated with phenolic concentrations of individual plants, and there were more kinds of herbivores present at the site with the highest phenolic concentrations (BNZ5N). These data suggest that either the insects are attracted by high phenolic concentrations (or something correlated with them), or that the plants have increased their phenolic concentrations in response to the insects. Several studies have shown that phenolics can be induced by herbivores (e.g., Boege 2004, Stevens and Lindroth 2005, Kaplan et al. 2008, Pascual-Alvarado et al. 2008). In the future it would be useful to determine whether phenolics are induced in V. v.idaea by performing an insect removal experiment such as the one Young et al. (2010) did with aspen and leaf miners.

Seedlings versus adults

An important question is whether adult plants and seedlings face the same selective environment. Resistance to consumers can depend on ontogeny (Singh and Rajaram 1992, Steffenson et al. 1996, Boege and Marquis 2005), and the kinds or abundances of consumers may also depend on plant size (Gilbert et al. 2007). We had data from 20 adult plants from the same years at these sites as well (C. P. H. Mulder and B. A. Roy, unpublished manuscript); to facilitate comparison between the data sets, we graphed them in Fig. 7. The amount of leaf tissue removed by herbivory was similar between adults and seedlings, but seedlings had more leaf area removed by pathogens and more kinds of damage than adults did, particularly at the summer cold, winter warm BNZ5N site (Fig. 7). Note that the two pathogens that caused stem death (Phomopsis columnaris and Exobasidium vaccinii) are not reflected in the percent leaf area removed data shown in Fig. 7, because percent leaf damage was measured only on living leaves. These two deadly pathogens were most common at BNZ5N and become more common as the study progressed (Fig. 4), suggesting that as the plants aged, they were more likely to be attacked by these pathogens.

While survival of the seedlings was lowest at the drier JEN1F, adult survival at this site was high relative to all the other sites of origin when we collected seeds in both 2003 and 2004 (B. A. Roy and C. P. H. Mulder, unpublished data). Furthermore, adult plants at JEN1F had the
highest reproduction of any of the sites. In other words, what is bad for seedlings may not necessarily be bad for established plants.

Conclusions

_Vaccinium vitis-idaea_ exhibits a range of plastic responses to differing abiotic and biotic environments. The natural populations of this species are not continuous in the boreal forest, but can be better thought of as metapopulations separated by abiotic factors and connected by animal-mediated gene flow, favoring phenotypic plasticity but not local adaptation. The majority of the mortality in our experiment occurred the year following a major drought and was primarily at the site with warm summer temperatures, where the plants were rooted in soil. This suggests the seedling stage is vulnerable to droughts unless they are at sites with thick moss cover and the resulting longer duration of summer moisture, and is consistent with work in Sweden that found recruitment at only a subset of sites, the damp ones (Eriksson and Froborg 1996). Thus, if droughts increase in duration or frequency with climate change, seedling growth will be increasingly restricted to mossy sites, which have more stem killing consumers and are worse for adult growth and reproduction.

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