

InfoNorth

Ecological and Evolutionary Consequences of Experimental Warming in a High Arctic Tundra Ecosystem

by Anne D. Bjorkman

INTRODUCTION

OVER THE PAST 100 YEARS, GLOBAL TEMPERATURES have risen by an average of 0.85°C (IPCC, 2013). This trend is especially pronounced in the Arctic, where temperatures have risen by 2°C over the past 50 years alone and are expected to rise an additional 2°–5°C by the end of this century (ACIA, 2005). This rapid increase in temperature is expected to have wide-ranging implications for Arctic ecosystems, including changes in biodiversity, ecosystem functioning, and nutrient cycles. The future of Arctic ecosystems will depend on three factors: the extent to which individuals can adjust to warmer temperatures through phenotypic plasticity, the rate of immigration of species from southern latitudes, and the rate at which evolutionary adaptation at the species level can take place in a rapidly changing environment (Aitken et al., 2008; Gienapp et al., 2008). In essence, if species cannot adjust to warmer temperatures in situ (phenotypic plasticity), they must move, adapt, or die.

Widespread changes in the Arctic are already underway. Recent syntheses of plant community composition data have shown that some functional groups, particularly shrubs and graminoids, have responded positively to warming, while others, including lichens, have declined (Elmendorf et al., 2012). This “shrubification” of the Arctic is likely to have important consequences for the herbivore community and to alter snow distribution, duration, and albedo effects (Myers-Smith et al., 2011). Individual species have also shown changes in response to warming. Plants in areas of rapid warming often respond by flowering and senescing earlier, although responses vary substantially by location and growth form (Oberbauer et al., 2013).

Despite a growing body of evidence that plants are changing in response to warming temperatures, little is known about the mechanisms behind these changes. Classical studies of Arctic species have demonstrated that although individual populations show a high degree of phenotypic plasticity, adaptation to local conditions was also widespread (Mooney and Billings, 1961). This genetic diversity within the species as a whole could become important as environmental conditions change. If plastic responses are not sufficient to keep up with the rapid rise in

temperatures, adaptation within the population or through the migration of seeds or pollen northward may become necessary to maintain Arctic species.

Rapid adaptation to environmental change has already been described in some species. The critical photoperiod of northern populations of pitcher plant mosquitoes (*Wyeomyia smithii*) has shifted towards that of more southern populations, thus lengthening the breeding season for these populations (Bradshaw and Holzapfel, 2001). In the Yukon, evolutionary adaptation accounted for 13% of an observed shift in parturition date for red squirrels (*Tamiasciurus hudsonicus*) (62% was a result of phenotypic plasticity) (Reale et al., 2003; Berteaux et al., 2004). In plants, evolution in response to increased drought was detected in a population of *Brassica rapa* after only a few generations (Franks et al., 2007). However, the vast majority of studies describing observed trait shifts in response to climate change provide no evidence of whether these shifts are plastic or adaptive (Parmesan and Yohe, 2003; Gienapp et al., 2008).

Migration in response to warming temperatures has also been widely documented. In the United Kingdom, 63% of evaluated butterfly species have experienced northward range shifts over the past century (Parmesan et al., 1999). Similarly, British bird species have experienced an average northward range shift of 18.9 km (Thomas and Lennon, 1999). In the Arctic, a majority of surveyed sites show evidence of northward tree line advancement (Harsch et al., 2009). In a meta-analysis of data from 1700 plant and animal species worldwide, Parmesan and Yohe (2003) described an average northward range shift of 6.1 km (or 6.1 m upward in elevation) per decade across all species.

Although migration is perhaps the most widely discussed of the three climate-change responses, it is far from certain that species will be able to track their optimal climate northward as the climate warms. Predicted rates of future climate change are much greater than those of historical changes; species will therefore be required to track changes in climate at speeds 100 times those of historical migrations (Davis, 1989; Aitken et al., 2008). In addition, potential migration pathways have been considerably fragmented by human land use, especially agriculture and residential settlement (McCarty, 2001). These obstacles represent a further barrier to species dispersal and migration. Finally,

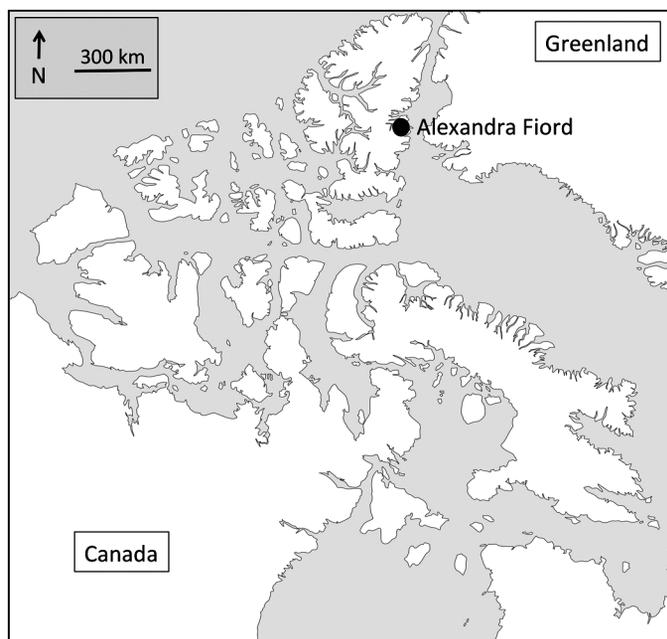


FIG. 1. Map of the eastern Canadian Arctic showing the location of Alexandra Fiord, Ellesmere Island.

even if dispersal is not limited, a variety of local factors can prevent the successful establishment of propagules in a new environment (Davis and Shaw, 2001). A lack of adaptation to photoperiod, soil type, moisture regime, or biotic interactions could slow or inhibit species migrations.

While there is substantial evidence that plasticity, adaptation, and migration will all play a role in how species respond to climate change, the relative importance of each process is not known. The goal of my project is to investigate all three of these processes in a High Arctic tundra ecosystem.

STUDY SITE

In 1992, an ITEX (International Tundra EXperiment) site was established at Alexandra Fiord on Ellesmere Island (79° N) to study the effects of experimental warming on tundra plants (Fig. 1). The ITEX protocol includes open-top, clear-sided chambers (OTCs) that warm the air inside by 1.5°–3°C, thus mimicking the effect of projected climate warming (Henry and Molau, 1997). Phenological and phenotypic trait data on a suite of species have been collected annually in the OTCs and control plots since 1993 (except in 1999 and 2006), along with dates of snowmelt (Fig. 2). Information on temperature and precipitation at the site is available for all years since 1993. Combined, these data provide a unique and detailed picture of the effects of warming on tundra vegetation, both within the experimental framework and also over time.



FIG. 2. ITEX open-top chambers and control plots at Alexandra Fiord, Ellesmere Island.

EXPERIMENTS

My study will address three major questions: 1) how have Arctic plant species responded to 20 years of experimental ITEX warming? 2) Has adaptation to warming occurred over the 20 years of the experiment? and 3) Does warming facilitate the survival and growth of southern populations at northern latitudes?

The first question will be answered using the phenological and phenotypic trait data collected between 1992 and 2013 for a number of forb, graminoid, and shrub species in at least two different habitat types (one dry, one mesic) to determine the direction and magnitude of the effect that experimental warming has had over the past 20 years. Because these data have been collected in nearly every year since 1993, I am also able to determine whether the magnitude of the observed response to warming has increased, decreased, or remained constant over time. Finally, I will use local temperature and snowmelt data to elucidate the mechanisms behind these changes.

In order to determine whether the differences between treatments (warm/control) and habitat types observed in the previous experiment are due to phenotypic plasticity or evolutionary adaptation, I performed a reciprocal transplant experiment with three species that are abundant in the ITEX plots (forbs *Oxyria digyna* and *Papaver radicum*, and grass *Arctagrostis latifolia*). Seeds or ramets collected from the OTCs were planted into control plots and vice versa, as well as from each plot back into itself (as a control). This design was replicated in two different habitat types, one dry with early snowmelt and one mesic with later snowmelt. Seeds from control plots were also reciprocally transplanted between the two different habitat types to look for adaptation to local environmental conditions.

During the summer of 2011, I planted more than 3000 seedlings into these three reciprocal transplant experiments. I also recorded germination rates, timing of germination, timing of first mature leaf, and survival for each seedling planted (Fig. 3). In 2012 and 2013 I measured



FIG. 3. Anne Bjorkman at Alexandra Fiord in 2011 (photo by Breanne Johnson).

survivorship, phenology (timing of leaf-out and first mature leaf), and total leaf area for each individual at peak growing season and at the end of the growing season.

The third question concerns the role of immigration in Arctic ecosystems under warming temperatures. Specifically, I ask whether populations from southern latitudes have an adaptive advantage over “native” populations under anticipated climate change scenarios (i.e., $\sim 2^{\circ}\text{C}$ warmer) despite a lack of adaptation to local environmental conditions such as soil type or moisture regime.

In order to answer this question, I collected seeds from southern populations (e.g., southern Nunavut, Alaska, and Sweden) of the same three species mentioned above. I then planted seedlings from both northern (“native”) and southern (“immigrant”) populations into experimentally warmed and control plots during the summer of 2011 (a total of ~ 2000 plants). I also collected information about timing and success of germination, timing of first mature leaf, total leaf area, and survival for each individual in 2011, 2012, and 2013. If southern populations perform better than the native population when experimentally warmed, it would indicate that warming will facilitate the northward migration of populations and species despite their lack of adaptation to local environmental conditions.

PRELIMINARY RESULTS

Preliminary analyses indicate that there are significant differences in phenology and other traits between the warmed and control plots, and that these differences are largely driven by the timing of snowmelt rather than by temperature. Although temperature has increased substantially ($\sim 2^{\circ}\text{C}$) over the past 20 years at Alexandra Fiord, the mean date of snowmelt has not changed, and therefore the mean flowering date has also remained relatively stable.

When phenological differences are analyzed across different sites, the differences between habitat types (dry vs. mesic and early vs. late snowmelt) are often as large or

larger than the differences between warmed and control plots within a habitat type. This result indicates that there is substantial local variation in these traits, and it raises the question of whether this variation is purely plastic or whether there are also genetic differences between populations over small spatial scales. The results of the between-habitat reciprocal transplant experiments will help to clarify this.

Survival of seedlings in the within-ITEX transplant experiments was remarkably high ($> 90\%$ for all three species). Because of the uniformly high survival, there were no significant differences in survival between treatments (i.e., seeds planted in warmed or control plots) or between source treatments (i.e., seeds collected from warmed or control plots). There were, however, significant differences in timing of leaf maturity and in growth for some species.

Seedling survival in the migration experiment was also high (70%–90%), but populations did differ significantly in their survival. Populations from the two southernmost latitudes (Alaska and Sweden) had significantly lower survival than more northern populations. Phenological and growth variables also differed by population and by treatment.

SIGNIFICANCE OF RESEARCH

The results of these experiments have potentially important implications for our understanding of the future of Arctic ecosystems. While several previous studies have found evidence of species “adapting” to climate change, few studies have even attempted to determine whether this “adaptation” is evolutionary adaptation or merely phenotypic plasticity (Gienapp et al., 2008). The capacity of species to respond to environmental changes through phenotypic plasticity is limited (DeWitt et al., 1998), and if the results of my research confirm that observed shifts among Arctic species are found to be attributable to phenotypic plasticity only, it could indicate the inability of Arctic species to adapt to projected changes in climate, which could lead to extirpation of species, widespread shifts in community composition, and changes in ecosystem processes. Likewise, limitations to dispersal and the importance of local adaptations will play a decisive role in predicted northward migrations of species. Changes in the plant community will undeniably have widespread effects, including impacts on animal species that use vegetation for food and cover and on aboriginal communities in the Arctic that traditionally depend on these plant and animal species. Better understanding the ecological and evolutionary processes at work in Arctic plant communities can help us to better predict, and possibly even influence, the future of ecosystems in the Arctic and around the world.

ACKNOWLEDGEMENTS

I am extremely honored to have received the Jennifer Robinson Memorial Scholarship for 2013. Additional funding and logistical support were provided by the Natural Sciences and Engineering Research Council of Canada, the Polar Continental Shelf Program, and the University of British Columbia. I owe a huge debt of gratitude to five amazing summer field crews, without whom this project would not have been possible.

REFERENCES

- ACIA. 2005. Arctic climate impact assessment: Scientific report. New York: Cambridge University Press. 1042 p.
- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., and Curtis-McLane, S. 2008. Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications* 1(1):95–111.
- Berteaux, D., Réale, D., McAdam, A.G., and Boutin, S. 2004. Keeping pace with fast climate change: Can Arctic life count on evolution? *Integrative & Comparative Biology* 44(2):140–151.
- Bradshaw, W.E., and Holzapfel, C.M. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences* 98(25):14509–14511.
- Davis, M.B. 1989. Lags in vegetation response to greenhouse warming. *Climatic Change* 15:75–82.
- Davis, M.B., and Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292(5517):673–679.
- DeWitt, T.J., Sih, A., and Wilson, D.S. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution* 13(2):77–81.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., et al. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453–457.
- Franks, S.J., Sim, S., and Weis, A.E. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences* 104(4):1278–1282.
- Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., and Merilä, J. 2008. Climate change and evolution: Disentangling environmental and genetic responses. *Molecular Ecology* 17(1):167–178.
- Harsch, M.A., Hulme, P.E., McGlone, M.S., and Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12(10):1040–1049.
- Henry, G.H.R., and Molau, U. 1997. Tundra plants and climate change: The International Tundra Experiment (ITEX). *Global Change Biology* 3(S1):1–9.
- IPCC (Intergovernmental Panel on Climate Change). 2013. Climate change 2013: The physical science basis. Working Group I Contribution to the Fifth Assessment Report of the IPCC.
- McCarty, J.P. 2001. Ecological consequences of recent climate change (Review). *Conservation Biology* 15(2):320–331.
- Mooney, H.A., and Billings, W.D. 1961. Comparative physiological ecology of Arctic and alpine populations of *Oxyria digyna*. *Ecological Monographs* 31(1):1–29.
- Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., et al. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* 6(4):045509, doi:10.1088/1748-9326/6/4/045509.
- Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., Dawes, M.A., et al. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Philosophical Transactions of the Royal Society B* 368, 20120481.
- Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Reale, D., Berteaux, D., McAdam, A.G., and Boutin, S. 2003. Lifetime selection on heritable life-history traits in a natural population of red squirrels. *Evolution* 57(10):2416–2423.
- Thomas, C.D., and Lennon, J.J. 1999. Birds extend their ranges northwards. *Nature* 399:213.

Anne Bjorkman is the 2013 recipient of the Jennifer Robinson Memorial Scholarship. She is currently a doctoral student in the Department of Geography and the Biodiversity Research Centre at the University of British Columbia, Vancouver. E-mail: annebj@gmail.com