Hardiness Zones and Bioclimatic Modelling of Plant Species Distributions in North America©

Daniel W. McKenney[1], John H. Pedlar[2], Kevin Lawrence[3], Pia Papadopol[4] and Kathy Campbell[5]
Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, 1219 Queen Street E. Sault Ste. Marie, Ontario P6A 2E5, Canada
[1]Email: Dan.McKenney@nrcan-rncan.gc.ca
[2]Email: John.Pedlar@nrcan-rncan.gc.ca
[3]Email: Kevin.Lawrence@nrcan-rncan.gc.ca
[4]Email: Pia.Papadopol@nrcan-rncan.gc.ca
[5]Email: Kathy.Campbell@nrcan-rncan.gc.ca

INTRODUCTION

The subject of potential species distributions has long been of interest to ecologists (e.g., Elton, 1927; Scott et al., 2002), but the subject is also important to agriculturalists, horticulturalists, and gardeners as it relates to plant hardiness. Plant hardiness is often thought of as the mortality or dieback of plants caused by temperature stress (mostly cold but also heat). In practical terms, hardiness zones are intended to help define the potential distribution of perennial plant species. The United States Department of Agriculture (USDA) extreme minimum temperature model (and related map) has been a useful surrogate for plant hardiness and is widely used throughout North America (<http://planthardiness.ars.usda.gov/PHZMWeb/>; see also <http://www.ars.usda.gov/Main/docs.htm?docid=15616> for a heat stress model).

In Canada, a plant hardiness map has also been developed (Oulette and Sherk, 1967a, b, c), and has become a standard and familiar source for Canadians. This model employed seven climatic parameters, and was thought to better represent the plant hardiness situation in Canada, where long winters and snow cover can dramatically affect plant survival and performance. McKenney et al. (2001, 2014) updated Canada's hardiness zone maps using recent climate data and modern, mathematically sophisticated climate interpolation techniques. The advent of intensive computer processing techniques and the digitization of plant observation data have opened the door to a shift away from traditional hardiness zones in favour of species-specific potential distribution models. Indeed, there has been a proliferation of species distribution models globally in recent decades (Booth et al., 2014). Any climate-based plant distribution model can be interpreted as a customized hardiness map for that species — a connection that has not been widely recognized. Here we briefly summarize some of the major changes in hardiness zones that have occurred in Canada as the climate has evolved over the last 50 years. We also briefly describe a plant hardiness project for North America that involves the collation and bioclimatic analysis of plant observation data (McKenney et al., 2007a). We illustrate the relationship between the most recent hardiness zones and species distribution models using two representative woody species and show examples of projecting species' range shifts under a changing climate.

CANADA'S HARDINESS ZONES

Hardiness zones are widely known and used around the world to help identify what plants can grow where (Widrlechner et al., 2012). In Canada there are two hardiness zone systems, a made-in-Canada approach based on seven climate variables and the USDA extreme minimum temperature model. The Canadian plant hardiness system was originally developed by Agriculture Canada in the early 1960s using 1930-1960 climate data and involved field-based assessments of woody plant species responses to Canadian climate (Oulette and Sherk, 1967a, b, c). In the original work, survival data for 174 woody plant and shrub species and cultivars were gathered at 108 test stations across the country. A hardiness index was generated at each test location according to performance and survival rates of the various species under study. The hardiness index was ultimately modeled as a function of seven climate variables that influence plant survival and growth in temperate regions:

- Mean minimum temperature of the coldest month
- Frost free period in days
- Rainfall June through November
- Mean maximum temperature of the warmest month
- Rainfall in January
- Mean maximum snow depth
- Maximum wind gust in 30 years.

The original plant hardiness zone map was produced by calculating the hardiness index at 640 climate stations and then hand-interpolating these values onto separate maps of eastern and western Canada (Ouellet and Sherk, 1967c). Raw hardiness values (which ranged from 0 to 92) were classified into 10, 10-unit zones (labelled 0 to 9), and each zone was further divided into two, 5-unit subzones (indicated by the letters a and b). It is these zones that are commonly known to gardeners and other users.

As noted, the USDA hardiness zone map, which is based solely on annual extreme minimum temperature, is also used to guide planting decisions in Canada. The original version of this map was produced in the 1960s (Skinner, 1962) using annual extreme minimum temperature values over the 1899-1952 time period. Ten zones were defined (1-10) based on 5.6°C temperature intervals. This model was recently updated and is available at an 800 m resolution for the United States (including Alaska and Hawaii) and Puerto Rico for the 1976-2005 period (Daly et al., 2012). This updated map has eleven 5.6°C zones (1-11) within the continental United States which are further subdivided into 2.8°C half zones (e.g., 1a, 1b, 2a, etc).

Both the Canadian (Fig. 1) and USDA (Fig. 2) plant hardiness maps have been updated for the Canadian land base using recent and improved climate data and modern climate interpolation methods (McKenney et al., 2001, 2014). High resolution versions of these maps are available at: <http://planthardiness.gc.ca>, which include fine-scaled insets for several regions of the country. Note that the Canadian and USDA zones do not overlap in a simple fashion (McKenney et al., 2006 for a detailed comparison of the two systems); this is to be expected given the very different approaches used to generate the two products.

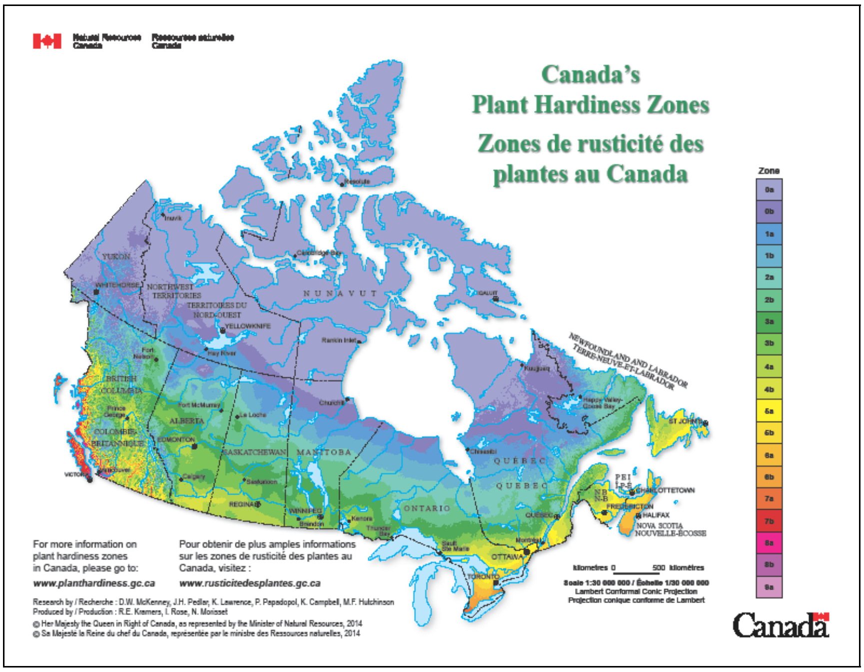

Fig. 1. Canadian plant hardiness zone map for 1981-2010 .

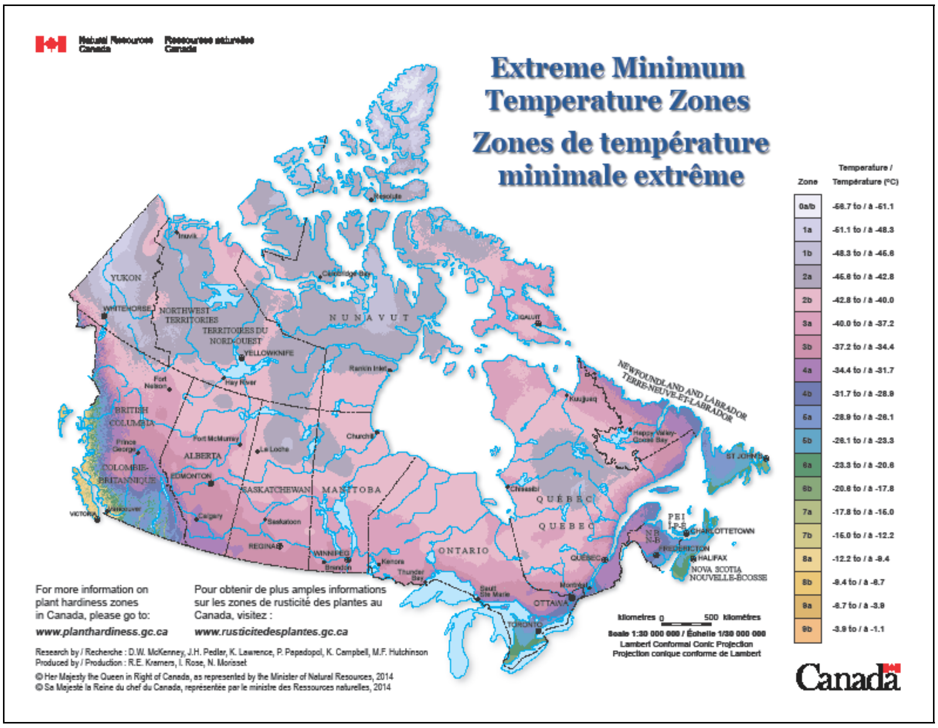

Fig. 2. Extreme minimum temperature plant hardiness zone map for 1981-2010 (follows United States Department of Agriculture approach for hardiness zones).

CLIMATE ENVELOPE MODELS AS HARDINESS MAPS FOR INDIVIDUAL SPECIES

The Canadian and USDA hardiness zone maps summarize gradients in climate variables that, in a general and intuitive way, influence the survival and growth of woody and other perennial plants. Plants are generally assigned to hardiness zones given the experience and expectations of growers and not through exhaustive survival and performance tests (but see <http://prairietrees.ca/prairie.htm> for an example involving shade trees being tested at four nursery locations in the Canadian Prairies). As noted, an emerging alternative is the use of individual species distribution models (also known as climate envelope models), which offer a robust approach for mapping the range limits (or hardiness zone) of a plant species. For this approach, all that is needed are spatial climate models (e.g., McKenney et al., 2013) and longitude and latitude coordinates where the species is known to occur in an enduring manner; experience suggests that as few as 30 reasonably well distributed observations can produce robust models. Importantly, the approach lends itself to rapid updates as new data become available.

In support of this approach, plant distribution data from across North America have been gathered through ongoing citizen science and data sharing agreements with government and non-government organizations (see McKenney et al., 2007a for details). These data, which comprise approximately 3 million plant occurrence observations, have been used to generate climate profiles for nearly 3000 North American plant species that can be downloaded at Canada's Plant Hardiness Website <http://planthardiness.gc.ca/>. These climate profiles, generated using the software ANUCLIM (Xu and Hutchinson, 2013), provide simple statistics (min, max, mean, and various percentiles) that summarize a wide range of climate variables at the occurrence locations of each species. When mapped, a "full" climate range identifies all pixels with climatic conditions that fall between the minimum and maximum values occupied by the species for one or more climate variables of interest (Figs. 3 and 4). These full climate ranges invariably extend outside the typical range limits of the species and are probably best interpreted as an approximation of the fundamental climate niche — the potential environmental space occupied by a species in the absence of biotic constraints such as predation and competition (Hutchinson, 1957). Alternatively, users can select percentile cut-offs to eliminate outlying data points and identify a core range that more closely resembles the species' realized niche (Figs. 3 and 4).

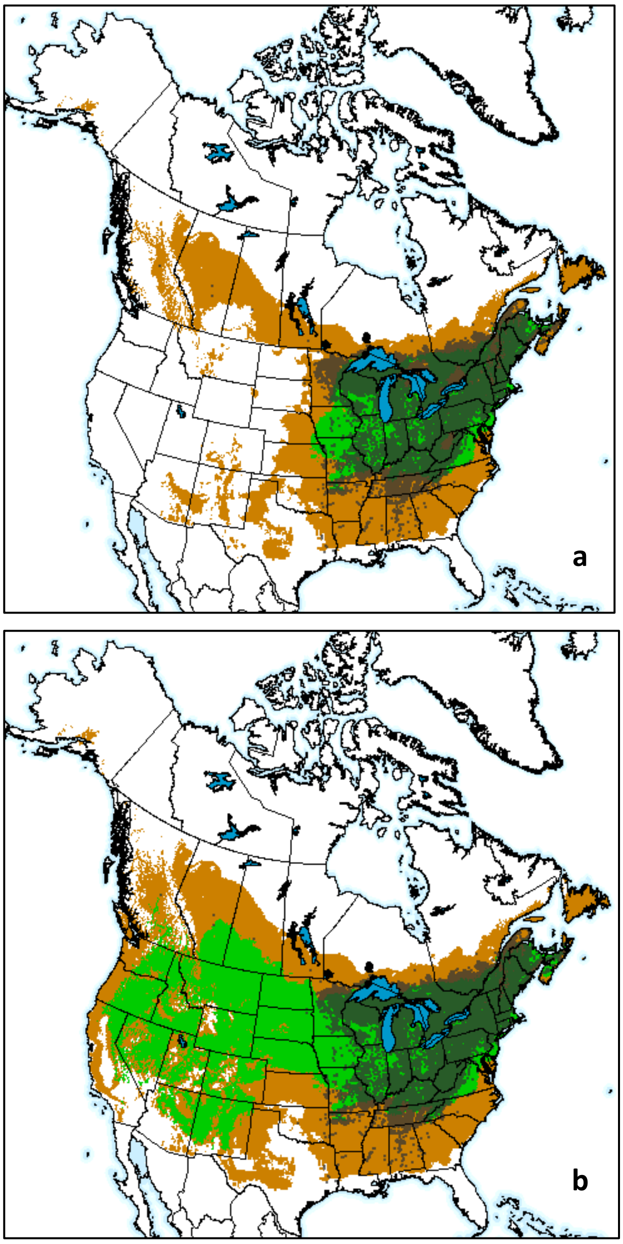

Fig. 3. Sugar maple climate envelope maps showing 41,764 occurrence observations (gray dots), full climatic range (orange), and core climatic range (green) for models based on (a) precipitation and temperature, and (b) temperature only.

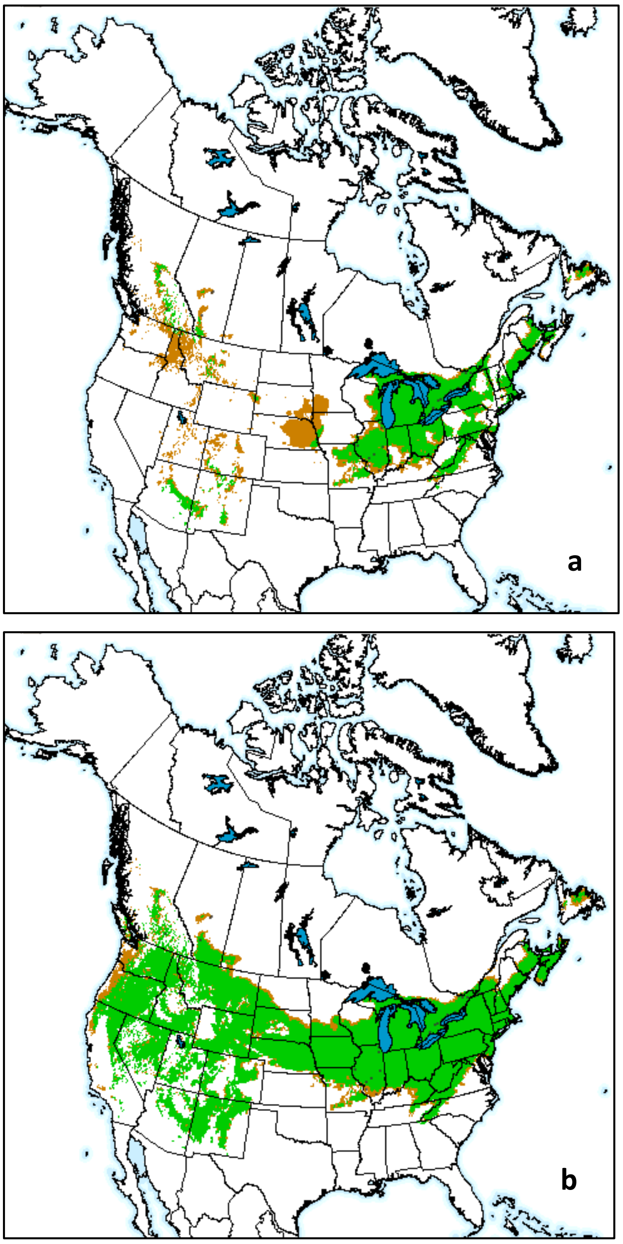

Fig. 4. Horse chestnut climate envelope maps showing 39 occurrence observations (gray dots), full climatic range (orange), and core climatic range (green) for models based on (a) precipitation and temperature, and (b) temperature only.

Several types of climate envelope models have been produced and are available for viewing at the plant hardiness web site. These include models that are based on both temperature and precipitation variables as would be experienced in natural settings (Figs. 3a and 4a), as well as temperature-only models which are aimed at horticultural situations where water can be added by the grower/gardener (Figs. 3b and 4b). A recent addition to the website is a set of distribution models generated using a machine learning method called Maxent (Phillips et al., 2006). This approach, which provides a sophisticated estimate of site suitability by comparing occurrence locations against a random selection of background points, has performed well in comparison to other distribution modelling techniques (Elith et al., 2006).

COMPARING CLIMATE ENVELOPES AND HARDINESS ZONES

Figures 5a and b show climate envelope models for two tree species (sugar maple — *Acer saccharum* and horse chestnut — *Aesculus hippocastanum*) overlaid on the Canadian plant hardiness map. These species were selected because they were part of the original indicator species used by Ouellet and Sherk (1967a) and they illustrate other attributes associated with the species modelling approach. The sugar maple model has over 40,000 georeferenced locations in our plant hardiness database, including places well outside its known natural range (Little, 1971). In contrast, the horse chestnut model is based on only 39 observations. Sugar maple is an indicator species for Canadian plant hardiness Zone 4a, while horse chestnut is an indicator species for Zone 5a. The climate envelope models (and actual observations used in the models) suggest that the species are in fact hardy to areas outside these zone designations in certain regions. The horse chestnut model is clearly a work in progress — as new observation data are obtained the models are updated. The preliminary nature of models with very few observations is intended to help spur contributions.

PLANT HARDINESS ZONES UNDER A CHANGING CLIMATE

McKenney et al. (2014) demonstrated that climate changes over the past century have resulted in significant changes in plant hardiness zones. Specifically, both systems exhibited: increases of 1 to 3 hardiness zone designations across western Canada; relatively small increases of up to 1 zone across eastern Canada (with some areas even showing slight declines); and the appearance of new zones (8b and 9a) on Vancouver Island that had not previously been found in Canada. The prospects for climate change in the coming century (IPCC, 2013) suggest ongoing changes to plant hardiness zones, however, future plant hardiness zone maps have not been generated due to difficulties in obtaining reliable future estimates of certain climate variables required to calculate the plant hardiness indices (e.g., maximum snow depth, maximum wind gust, and extreme minimum temperature).

Climate envelope models are well suited to climate change analysis; models based on current climate can be projected onto grids of future climate to visualize where suitable climate is expected to migrate during the course of this century. Numerous studies have applied this approach to examine changes in potential distributions of plant species. For example, McKenney et al. (2007b) undertook an analysis of 130 North American tree species; based on climate projections that assume continued high levels of greenhouse gas emissions, the average northerly shift in the climate habitat for all species by the latter part of the current century was approximately 700 km. This is not to say the species will migrate these distances, but it does suggest that a remarkable degree of migration pressure will be placed on species over the coming century. Projecting how species will actually shift in response to climate change is incredibly challenging, and involves considerations such as species' migration rates, biotic interactions, disturbance regimes, and human interventions.

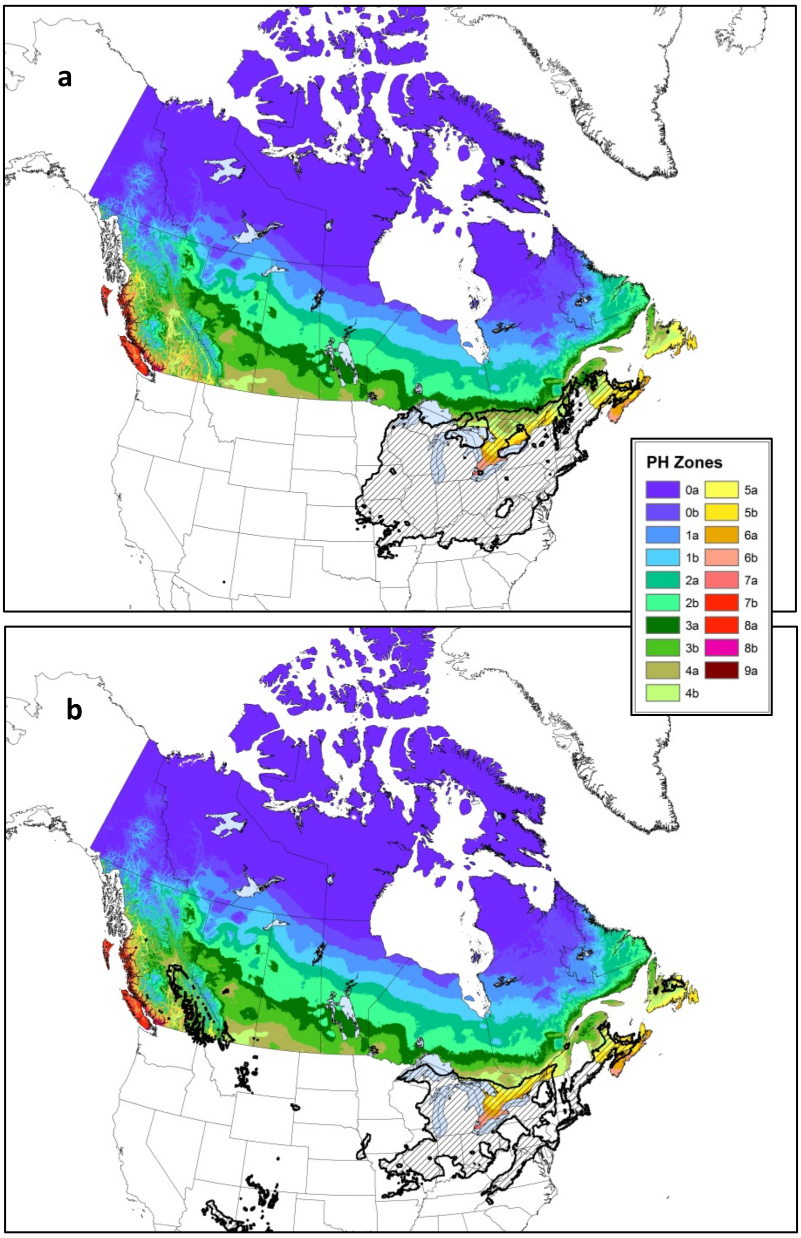

Fig. 5. Current climate envelope of (a) sugar maple, and (b) horse chestnut overlaid on the 1981-2010 Canadian plant hardiness zone map.

Figures 6a and b show the projected climate envelopes for sugar maple and horse chestnut by mid-century, overlaid on the current hardiness zones. Both species show significant northward shifts, such that locations currently designated as Zone 1 may become suitable for sugar maple, while locations currently designated as Zone 2 appear to become suitable for horse chestnut. If climate change progresses as projected, there will clearly be significant changes in planting opportunities throughout Canada. These planting opportunities may already be occurring but trends in factors such as late spring frosts may also limit success (McKenney et al., 2014). The spatial complexity of the future climate envelopes, as shown in the example here for sugar maple, indicates that temperature and precipitation are not simply projected to shift northward in synchrony under climate change; rather, certain climate combinations are expected to be lost, while novel climate combinations may also be formed (Williams and Jackson, 2007).

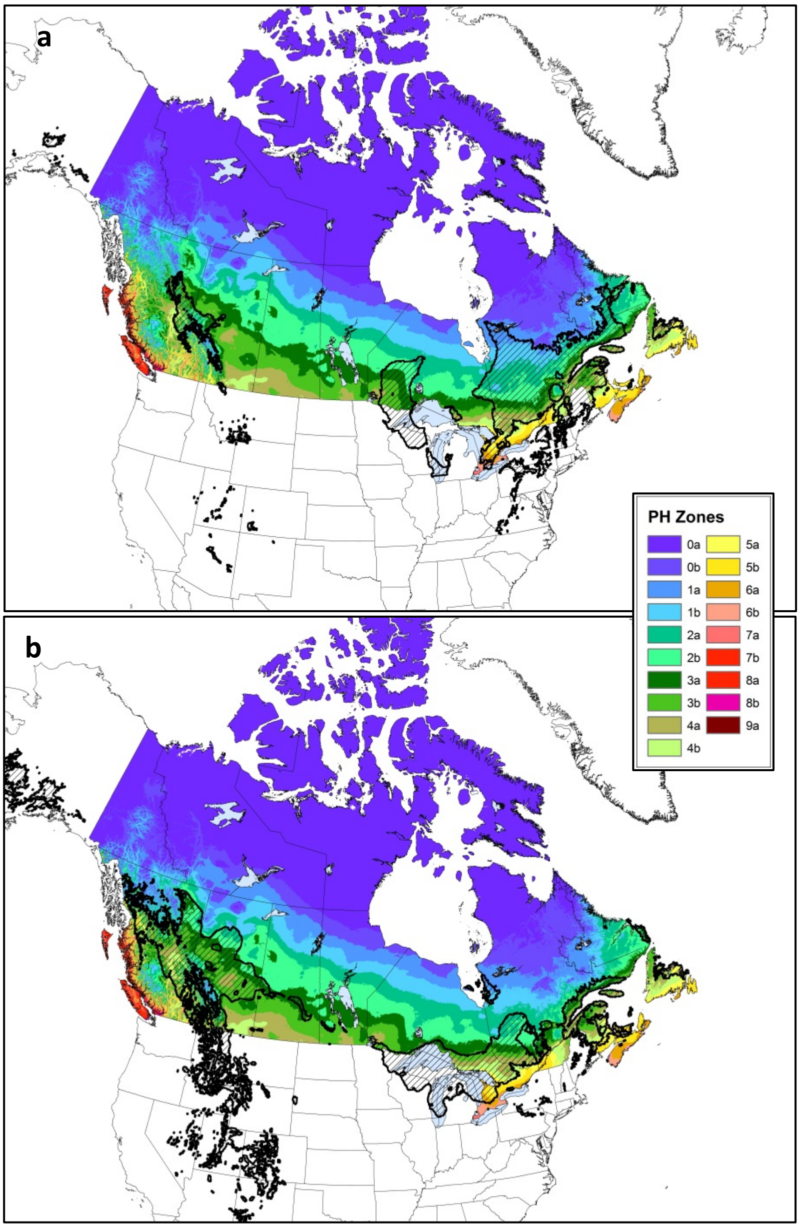

Fig. 6. Future (2041-2070) climate envelope of (a) sugar maple, and (b) horse chestnut overlaid on the 1981-2010 Canadian plant hardiness zone map.

CONCLUSIONS

Although the hardiness map of Oulette and Sherk (1967c) was seminal for its time and represented a robust approach to hardiness modelling and mapping for Canada, there are important limitations to general hardiness zones. First, the map applied a single formula for the entire country, ignoring possible interactions in bioclimatic variables that may vary spatially, temporally, and by individual plant species. For example, as the climate evolves, warmer temperatures may be useful for plant survival in western coastal areas but could decrease snow cover in other parts of the country exposing plants to lethal minimum temperatures and damaging winter rains. Furthermore, the hardiness zone designation for a particular plant is often not based on extensive testing in the field, which limits the overall effectiveness of the system.

Given that plant species respond to climate in individualistic ways, species-specific distribution models are increasingly practical and offer a flexible and rapid approach to mapping potential distributions. Through data gathered as part of our plant hardiness project <http://planthardiness.gc.ca>, we have developed climate envelope models for nearly 3000 species to date that cover both the USA and Canada. This work is ongoing as time and resources allow. A much larger set of plant species models could be developed with fairly minimal coordination between nursery growers and citizens and models such as those described here. Indeed it would appear that some form of citizen science would be the most effective way to build, maintain and modify plant hardiness zones in the future. Collaborations are invited.

Literature Cited

Booth, T.H., Nix, H.A., Busby, J. and Hutchinson, M.F. 2014. BIOCLIM: the first species distribution modelling (SDM) package, its early applications and relevance to most current MaxEnt studies. Diversity and Distributions 20:1-9. <http://onlinelibrary.wiley.com/doi/10.1111/ddi.12144/pdf>.

Daly, C., Widrlechner, M.P., Halbleib, M.D., Smith, J.I. and Gibson, W.P. 2012. Development of a new USDA plant hardiness zone map for the United States. J. Appl. Meteor. Climatol. 51:242-264.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S. and Zimmermann, N.E. 2006: Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Elton, C.S. 1927. Animal Ecology. University of Chicago Press.

Hutchinson, G.E. 1957. Cold Spring Harbor Symposium on quantitative biology. Concluding Remarks 22:415-427.

IPCC. 2013. Summary for policymakers. In: T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA.

Little, E. 1971. Atlas of United States Trees, Vol. 1: Conifers and Important Hardwoods. Washington (DC): US Department of Agriculture. Miscellaneous publication no. 1146.

McKenney, D.W., Hutchinson, M., Kesteven, J.L. and Venier, L.A. 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Can. J. Plant Sci. 81:129-143.

McKenney, D.W., Hutchinson, M., Papadopol, P., Campbell, K. and Lawrence, K. 2006. The generation of USDA-equivalent extreme minimum temperature models and a comparison with Canada's plant hardiness zones. Can. J. Plant Sci. 86:511-523.

McKenney, D.W., Pedlar, J.H., Lawrence, K.L., Campbell, K. and Hutchinson, M.F. 2007a. Beyond traditional hardiness zones: using climate envelopes to map plant range limits. Biosci. 57(11):929-937.

McKenney, D.W., Pedlar, J., Lawrence, K., Campbell, K. and Hutchinson, M.F. 2007b. Potential impacts of climate change on the distribution of North American Trees. BioSci. 57(11):939-948.

McKenney, D.W., Hutchinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J.H., Campbell, K. and Owen, T. 2011. Customized spatial climate models for North America. Bull. Amer. Meteorol. Soc. 92(12):1611-1622.

McKenney, P., Lawrence, K., Papadopol, P., Campbell, K.L., Hutchinson, M.F. 2014. Change and evolution in the plant hardiness zones of Canada. BioSci. 64(4):341-350.

Ouellet, C.E. and Sherk L.C. 1967a. Woody ornamental plant zonation I. Indices of winter hardiness. Can. J. Plant Sci. 47:231-238.

Ouellet, C.E. and Sherk L.C. 1967b. Woody ornamental plant zonation. II. Suitability indices of localities. Can. J. Plant Sci. 47:339-349.
Ouellet, C.E. and Sherk, L.C. 1967c. Woody ornamental plant zonation III. Suitability map for the probable winter survival of ornamental trees and shrubs. Can J. Plant Sci. 47:351-358.
Phillips, S.J., Anderson, R.P. and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190(3):231-259.
Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. and Samson, F.B. 2002. Predicting species occurrences: issues of scale and accuracy. Island Press, Washington, DC, USA
Skinner, H.T. 1962. The geographic charting of plant climatic adaptability. p.485-491. In: J.-C. Garnaud (ed.), Advances in Horticultural Science and Their Applications, Vol. 3. Proc. 15th Intl. Hort. Congr., Nice, France, 1958. Macmillan.
Widrlechner, M.P., Daly, C., Keller, M. and Kaplan, K. 2012. Horticultural applications of a newly revised USDA Plant Hardiness Zone Map. HortTechnol. 22(1):6-19.
Williams, J.W. and Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers Ecol. Environ. 5(9):475-482.
Xu, T. and Hutchinson, M.F. 2013. New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. Environ. Model. Software 40:267-279.