

Change and Evolution in the Plant Hardiness Zones of Canada

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We present 50-year updates for two plant hardiness models (maps), developed originally by Agriculture Canada and the US Department of Agriculture (USDA), that are widely used for plant selection decisions in Canada. The updated maps show clear northward shifts in hardiness zones across western Canada. Shifts are less dramatic in southeastern Canada, with modest increases in zone values associated with the Canadian map but modest declines associated with the USDA approach. Species-specific climate envelope models are an alternative to generalized hardiness zones. We generated climate envelopes for 62 northern tree species over the same 50-year interval and found an average northward shift of 57 kilometers. These changes signal an increase in the productivity and diversity of plants that can be grown in Canada. However, late spring frosts and other factors discussed herein may limit the extent to which this potential is realized.

Keywords: plant hardiness zones, climate change, climate envelopes, spring frost damage

Plant hardiness zone maps are iconic tools that make very practical connections among plants, climate, and people. Most gardeners know the hardiness zone in which they live and use this information to select climatically appropriate species for their location. In Canada, there are two zonation systems, a Canadian multivariate approach and the US Department of Agriculture (USDA) extreme-minimum-temperature model. Comparable products, many of which are based on the USDA system, have been developed for other parts of the world (see Widrlechner et al. 2012). Here, we examine changes in Canada's plant hardiness zones from several perspectives and some of the complexities arising from simple interpretations of these changes.

The Canadian plant hardiness system was developed by Agriculture Canada in the early 1960s and involved field-based assessments of plant responses to Canadian climate (Ouellet and Sherk 1967a, 1967b, 1967c). 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 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 (table 1), thus allowing plant hardiness estimates to be generated at any location for which the requisite climate data were available. The original plant hardiness zone map was produced by calculating the hardiness index at 640 climate stations. These values were then hand-interpolated onto separate maps of eastern and western Canada (Ouellet and Sherk 1967c). For presentation, the hardiness values

(which ranged from 0 to 92) were classified into 10 zones of 10 units each (labeled 0–9), and each zone was further divided into 2 subzones of 5 units each (indicated by the letters a and b).

A version of the hardiness zone map for the 1961–1990 normal period was created using thin-plate smoothing splines (McKenney et al. 2001). This map had several advantages over the original, including the incorporation of more and higher-quality climate station data, complete spatial coverage across the country, and a much higher spatial resolution. Importantly, the thin-plate smoothing spline approach was also applied to climate data for the original 1931–1960 climate period, and the patterns of the original map were accurately reproduced (McKenney et al. 2001); therefore, changes over time are probably related to changes in climate rather than to changes in the methods used to generate the updated map.

The USDA hardiness zone map, which is based solely on the annual extreme minimum temperature, is also used to guide planting decisions in Canada. An early version of this map was produced in the 1960s (USDA 1960, Skinner 1962) using annual extreme-minimum-temperature values, which, depending on regional data availability, were averaged over various intervals within the 1899–1952 time period. Ten zones were defined (1–10) on the basis of 5.6-degree-Celsius (°C) temperature intervals. This model was recently updated (Daly et al. 2012) and is available at an 800-meter resolution for the United States (including Alaska and Hawaii) and Puerto Rico for the 1976–2005 period (Daly et al. 2012). The most recent USDA map has 11 zones of 5.6°C intervals

Table 1. Climate variables and regression coefficients used in the original derivation of the Canadian plant hardiness zones.

Variable abbreviation	Variable description	Regression coefficient
Int	Model intercept	-67.62
MINTCM	Monthly mean of the daily minimum temperatures (in degrees Celsius [°C]) of the coldest month	1.734
FFP	Mean frost free period above 0°C in days	0.1868
RAIN1	Amount of rainfall (<i>R</i>) from June to November, inclusive, in terms of $R/(R + a)$, where $a = 25.4$ if <i>R</i> is in millimeters and $a = 1$ if <i>R</i> is in inches	69.77
MAXTHM	Monthly mean of the daily maximum temperatures (°C) of the warmest month	1.256
RAIN2	Winter factor expressed in terms of $(0^\circ\text{C} - \text{MINTCM}) R_{\text{Jan}}$, where R_{Jan} represents the rainfall in January expressed in millimeters	0.006119
SNOW	Mean maximum snow depth (<i>S</i>) in terms of $S/(S + a)$, where $a = 25.4$ if <i>S</i> is in millimeters and $a = 1$ if <i>S</i> is in inches	22.37
WIND_MAX	Maximum wind gust (kilometers per hour) in 30 years	0.01832

Note: The information in this table is from Ouellet and Sherk 1967a, 1967b, 1967c. Abbreviation: °C, degrees Celsius.

(1–11) within the continental United States, which are further subdivided into 2.8°C half zones (also indicated by letters).

The Canadian and USDA hardiness zone maps summarize gradients in climate variables that, in a general way, influence the survival and growth of perennial plants. Climate envelope models offer an alternative and customized approach for mapping the range limits (or hardiness zone) of a particular species. In support of this approach, plant distribution data from across North America have been gathered through a combination of citizen science and data-sharing agreements (McKenney et al. 2007a). These data have been used to examine potential shifts in tree species in relation to climate change (McKenney et al. 2007b, 2011a) and to generate climate profiles for almost 3000 North American plant species (<http://planthardiness.gc.ca>).

Selecting appropriate species and varieties in the face of rapid climate change can be extremely challenging—both for small-scale horticultural and for large-scale agricultural and forestry operations (Pedlar et al. 2012). One phenomenon that contributes to this situation is the increasing variability that may accompany warming temperatures (Seneviratne et al. 2012), such that certain aspects of climate (e.g., average temperatures) may be changing in ways that encourage the introduction of less-hardy varieties, whereas other aspects (e.g., temperature extremes) may hinder such efforts. For example, an extreme cold event was implicated in the widespread mortality of pine plantations in France that were established using less-hardy stock from Portugal (Benito-Garzon et al. 2013). Similarly, unusually late spring frosts have caused extensive damage to North American fruit crops and forest plants in recent years (Gu et al. 2008, Ault et al. 2013).

Here, we update the Canadian and USDA plant hardiness zone maps (for Canada) using climate data from the most recent normal period (1981–2010) and compare them with maps generated using data from around the time

the products were originally developed (1931–1960)—an interval of approximately 50 years. We also report on geographical shifts in the climate envelopes of 62 northern tree species over this same time period. Finally, we illustrate the challenges involved in plant species selection by presenting trends in the date of sugar maple (*Acer saccharum*) budburst and the risk of late spring frost. By summarizing changes in well-known plant hardiness systems in this context, we hope to communicate climate change impacts and complexity in a way that resonates with the general public, the science community, and policymakers.

Plant hardiness map updates

The development of the Canadian plant hardiness zone map for the 1931–1960 period has been described in detail elsewhere (see Ouellet and Sherk 1967a, 1967b, 1967c, McKenney et al. 2001). For the 1981–2010 normal period, climate data (monthly and daily minimum and maximum temperatures, monthly precipitation, maximum monthly wind speed, and maximum monthly snow depth) were obtained from Environment Canada, and spatial models were developed using trivariate (latitude, longitude, elevation) thin-plate smoothing splines in ANUSPLIN (version 4.37; Australian National University, Canberra). A particular strength of this method of climate mapping is its incorporation of stable dependencies on elevation. When applied to monthly mean climate data, it has been found to perform well in comparison with other interpolation approaches, particularly in mountainous regions with limited climate station data (Haylock et al. 2008). Monthly mean errors associated with the smoothing spline approach (McKenney et al. 2011b) are comparable to those of PRISM (Daly et al. 2008)—a local regression-based approach that incorporates elevation effects (as well as other physiographic influences) that was used in a recent update of the USDA plant hardiness zone map for the United States (Daly et al. 2012).

The number of Canadian climate stations varied, ranging from 242 for wind speed to more than 3400 for temperature-related variables. Model errors, as measured by the square root of the generalized cross-validation (GCV) statistic (akin to a spatially averaged standard error estimate), were 0.8°C–1.2°C for monthly temperature variables, 8.5–11.1 millimeters (mm) for monthly rainfall variables (approximately 12%–23% of the surface means, depending on the month), 14 days for frost free period, 17 centimeters for maximum snow depth, and 25 kilometers (km) per hour for maximum wind speed (see supplemental table S1 for model diagnostics). The models were resolved on a 0.01667–arc second (approximately 2-km) geographic grid and combined (using the table 1 regression coefficients) to generate the hardiness index value for each grid cell.

The updated hardiness zones were compared with the 1931–1960 zones in two ways: first, by overlaying the two maps in a geographic information system to generate a difference map and, second, by converting both grids to an Albers equal-area projection and calculating the areal coverage of each zone in each time period. Note that the Canadian hardiness formula was originally developed for the southern part of the country and, in fact, generates negative values for the far north. For display purposes, these values have been combined with the 0 hardiness class; further effort is required to properly calibrate the index for far northern regions.

The USDA extreme-minimum-temperature hardiness zone map has also been described in detail elsewhere (Daly et al. 2012). For the 1981–2010 normal period, daily minimum temperature data were processed from 2307 Canadian climate stations and 6545 American climate stations. Trivariate spline models were also developed from this station data and resolved at the same grid resolution. The root GCV error associated with this surface was 1.79°C (see table S1). A similar procedure was followed for the 1931–1960 period, using 873 and 5208 climate stations in Canada and the United States, respectively; the root GCV error was 1.88°C. Although we report findings only for Canada, climate stations from the United States were included in the models to ensure high-quality estimates in the vicinity of the Canada–United States border, where much of Canada's population resides and the interest in hardiness zones is highest. Areas in the far north had extreme-minimum-temperature values that were lower than the range defined for the lowest USDA hardiness zone (–51.1°C to –48.3°C). Therefore, we delineated a zone 0 to track shifts in cells with temperatures below –51°C. The maps were compared across time periods in the manner described above.

Generating tree climate envelopes

Occurrence locations from across North America for 62 northern tree species were obtained from a variety of sources, including government resource management agencies, nongovernmental environmental organizations, and research data sets (see McKenney et al. 2007a). To ensure that

the occurrence data had a reasonable likelihood of reflecting the species' distributions from earlier in the century, only those data points that fell within the historical range limits of each species (as defined by Little 1971) were included in the analysis. Each tree species selected for the analysis had occurrence data that were well distributed across its historical range limits and had a northern distribution (i.e., more than half of its range lying north of 40° north [N]). Using North American climate models (McKenney et al. 2011b), the values for the 1931–1960 normal period were estimated at each tree occurrence location for six climate variables: the annual mean temperature, the minimum temperature of the coldest month, the maximum temperature of the hottest month, annual precipitation, precipitation of the warmest quarter, and precipitation of the coldest quarter. For each tree species, the minimum and maximum values of each climate variable across that species' occurrence locations were determined for the 1931–1960 time period using the ANUCLIM software package (Xu and Hutchinson 2013). Cells with climate conditions that fell within this six-variable climate envelope were then located on climate grids of the 1981–2010 time period (as was described in McKenney et al. 2007a). Shifts were quantified by subtracting the latitude of the climate envelope centroid for the 1931–1960 period from that of the 1981–2010 period. In recent years, there has been rapid expansion in the methods used to generate climate envelope models (Elith et al. 2006); however, we present our results using an early generation approach (i.e., ANUCLIM), which is simple, transparent, and well suited to horticultural applications (McKenney et al. 2007a).

Calculating budburst and a false spring index

Daily minimum and maximum temperature data for the 1950–2010 period were obtained at 190 high-quality climate stations located within the Canadian portion of the sugar maple's range. For each year, the date of sugar maple leaf emergence was estimated using a published phenology model (Raulier and Bernier 2000), which calculates the number of warming degree days (base 10°C) in the spring required to induce budburst as a function of the number of chilling days (base 10°C) accumulated over the course of the winter. On average, this model predicted budburst within 1.5 days of the measured budburst date at sites across the sugar maple range (Raulier and Bernier 2000). A false spring index (*sensu* Marino et al. 2011) was calculated as the Julian date of the last hard frost (i.e., a minimum daily temperature lower than –2.2°C) minus the Julian date of leaf emergence. Large positive numbers indicate a hard freeze that happened well after budburst, which would have put fragile spring foliage at risk. Trends in the mean annual leaf emergence date and the false spring index were calculated using an autoregressive model to correct for serial correlation in the error term. The order of the autoregressive model used for each climate variable was determined using backward elimination starting with a 10th order autoregressive model.

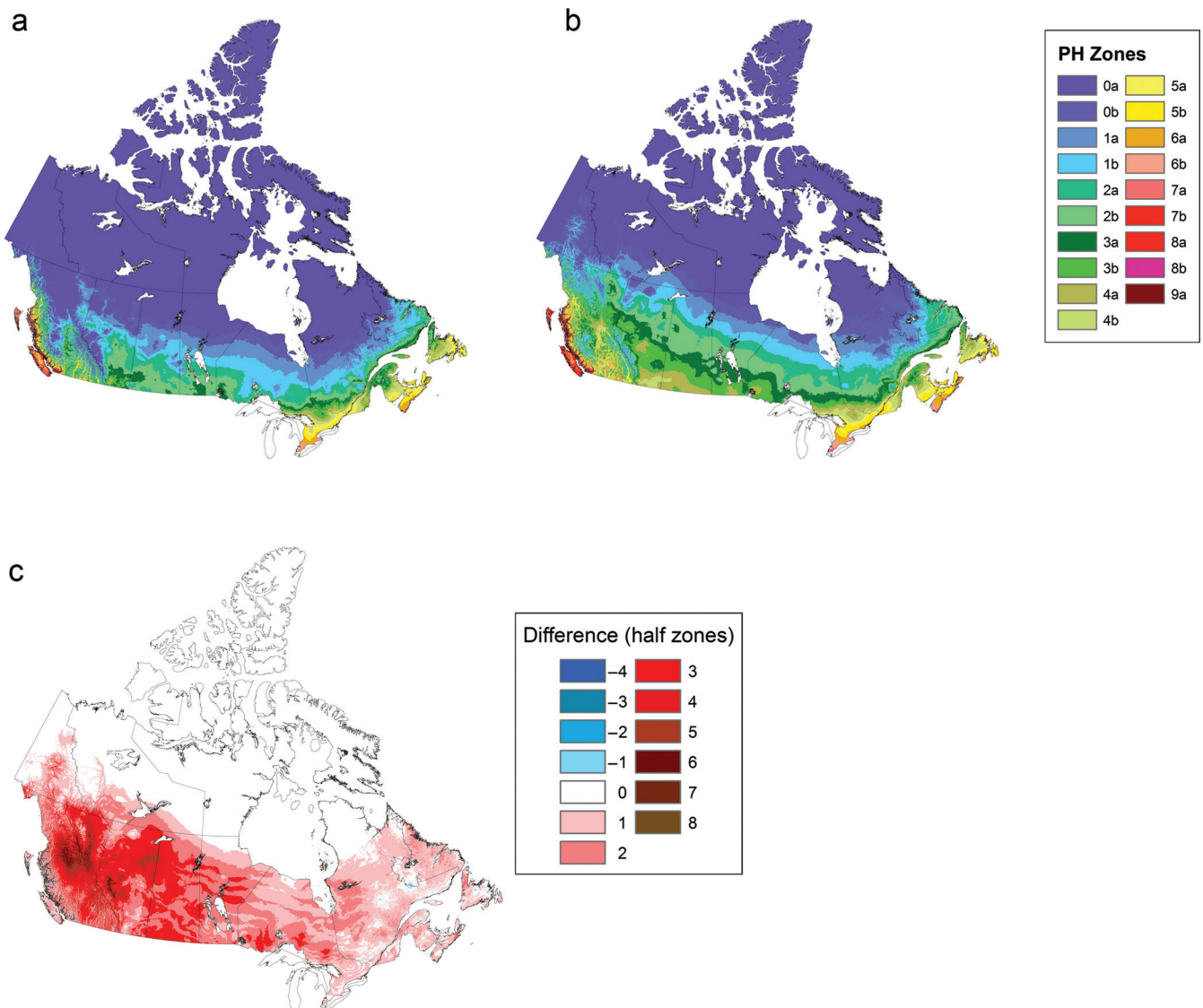


Figure 1. Canadian plant hardiness (PH) zone maps for (a) 1931–1960, (b) 1981–2010, and (c) the difference between those (1981–2010 minus 1931–1960). The difference map shows the number of half-zone differences between the two maps.

Changes in hardiness zones

The Canadian hardiness zones for the 1981–2010 period were substantially different from those of the 1931–1960 period (figure 1). The northward shift in zone limits was particularly obvious in western Canada, with changes of up to three zones (0a to 3a) apparent in northern British Columbia (figure 1c). The climate has changed less rapidly in eastern Canada (Zhang et al. 2000), but increases of a half to a full hardiness zone were common across this region. These regional patterns were apparent in the hardiness zone shifts associated with selected major cities across the country (moving from west to east): Vancouver (7a to 8b), Calgary (2b to 4a), Winnipeg (3a to 3b), Toronto (6a to 7a), Montreal (5a to 5b), and Halifax (6a, no change). Furthermore, shifts of a half to a full hardiness zone were common along the Canada–United States border, where much of Canada’s

population resides. The apparent lack of change in hardiness values for much of the far north (i.e., north of 60°N) was, as was noted above, due to the Canadian plant hardiness system’s not having been calibrated for this region.

Table 2 provides areal coverage estimates for each hardiness subzone for the two time periods. Noteworthy changes include a 31% reduction in the areal coverage of subzone 0a in the northern regions, the expansion of zones 2b–4b by 70%–240%, and the sharp increase in areal coverage of zones 7b and higher—two of which (8b and 9a) did not exist on the original map. Overall, these shifts point to a coherent climate change signal across the seven climate variables that are integrated into the hardiness zone index values. Previous efforts (Ouellet and Sherk 1967a, McKenney et al. 2001) have demonstrated that, the temperature-related variables (i.e., MINTCM, FFP, and MAXTHM; see table 1 for their

Table 2. Areal coverage of Canadian plant hardiness subzones for the 1931–1960 and the 1981–2010 normal periods.

Hardiness subzone	Area covered (km ² × 10 ³)		Change in coverage	
	1931–1960	1981–2010	Area (km ² × 10 ³)	Percentage
0a	5600.9	3862.8	-1738.1	-31.0
0b	655.2	827.0	171.8	26.2
1a	785.0	773.2	-11.8	-1.5
1b	784.5	665.3	-119.1	-15.2
2a	601.2	718.8	117.6	19.6
2b	494.3	831.3	337.0	68.2
3a	284.5	651.1	366.5	128.8
3b	169.6	575.7	406.2	239.5
4a	132.9	394.0	261.0	196.4
4b	124.4	217.9	93.5	75.1
5a	140.9	134.7	-6.1	-4.4
5b	97.3	139.3	42.0	43.2
6a	61.3	92.3	31.0	50.6
6b	37.2	59.1	22.0	59.1
7a	39.9	35.7	-4.2	-10.4
7b	28.8	42.3	13.5	46.9
8a	4.2	27.5	23.3	549.6
8b	0.0	8.4	8.4	-
9a	0.0	0.8	0.8	-

Abbreviation: km², square kilometers.

full names) have the greatest impact on the calculated index value. At the 476 climate stations that were common to the two time periods (see supplemental table S2), MINTCM, FFP, and MAXTHM increased by 1.5°C, 11 days, and 0.3°C, respectively, on average. Of secondary importance are the precipitation-related variables (i.e., RAIN1, RAIN2, and SNOW), which increased by 43, 2, and 0.02 mm, respectively, on average across the two time periods. Finally, WIND decreased in the later time period by 12 km per hour; because of the negative regression coefficient associated with this variable (table 1), this change also contributed to the widespread increase in hardiness index values. Although each climate variable contributes uniquely to the final hardiness index values, on average, all the climate variables changed in the direction of increasing the plant hardiness zone designation.

The USDA zones also showed significant northward shifts over time (figure 2). Again, change was most apparent in the west, where increases of a full zone were common (figure 2c). Shifts were less drastic in southeastern Canada, and significant portions of this region actually exhibited declines of about half a hardiness zone (figure 2). These findings are consistent with those of Daly and colleagues (2012), who reported little change or even declines in the USDA plant hardiness index from several northeastern states that border Canada. Specifically, the area covered by the three coldest zones (0, 1a, and 1b) decreased by 75%–95%, whereas the area of zones 2–5 increased by 11%–96% (table 3). Zones 8b

and 9a increased in area by 61% and 148%, respectively, and zone 9b did not exist in Canada during the 1931–1960 period.

There were considerably more climate stations available in the later time period for generating both the Canadian and the USDA plant hardiness maps. To examine whether these changes in station availability affected the shifts in hardiness zones described above, we generated regional summaries of the plant hardiness index values using climate stations that were available for both time periods—a total of 476 and 348 stations for the Canadian and USDA systems, respectively (table S2). At these stations, raw values of the Canadian plant hardiness index increased on average by eight units (or nearly one full zone) in the west, two units (less than half a zone) in the east, and five units (half a zone) for all of Canada. Similarly, extreme minimum temperatures increased on average by 2°C in the west, 0.5°C in the east, and 1°C overall. Although the limited number of stations prevents a detailed spatial comparison, these results support the general patterns observed in the plant hardiness maps (figures 1 and 2), which were generated using all available stations in each time period.

Our findings, based on two widely used plant hardiness systems, suggest that the Canadian land base has generally become hospitable to a wider range of perennial plant species over the past 50 years. This has implications for horticulture: Growers may be able to cultivate new

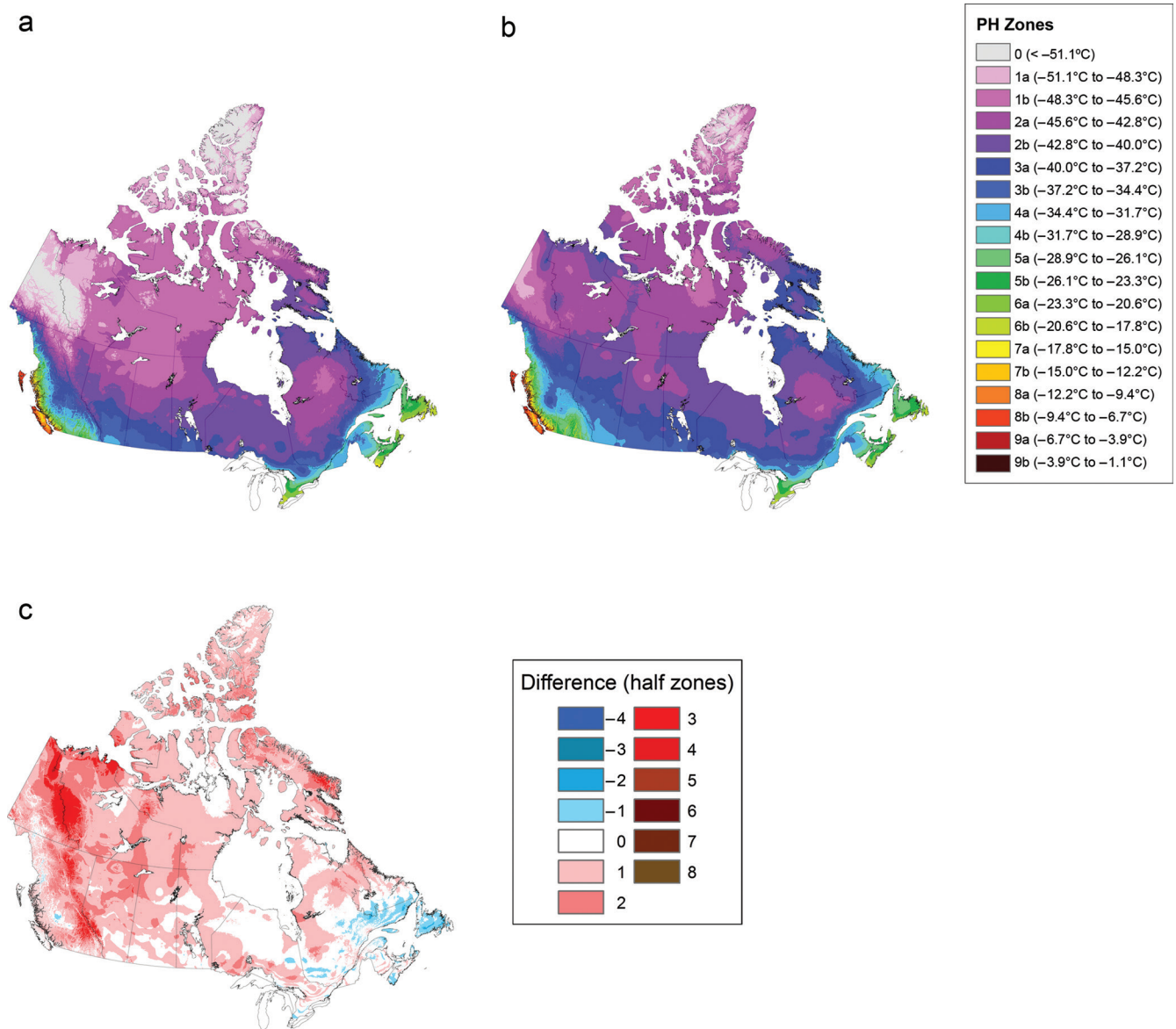


Figure 2. US Department of Agriculture plant hardiness (PH) zone maps for (a) 1931–1960, (b) 1981–2010, and (c) the difference between those (1981–2010 minus 1931–1960). The difference map shows the number of half-zone differences between the two maps.

plants in a given location. For instance, on the basis of the updated USDA plant hardiness map, there are sites in southern British Columbia where pindo palms (*Butia capitata*) and orchid trees (*Bauhinia variegata*)—plants indicative of USDA zones 8 and 9—could now be grown. Furthermore, the appearance of zone 9b on Vancouver Island suggests the potential to grow hardy citrus crops at select locations—a phenomenon that is, in fact, already occurring in a limited way (Cole 2013). At the opposite extreme, the climate around Yellowknife (located on Great Slave Lake, in the Northwest Territories) now appears suitable for hardy varieties of apple, pear, and plum where soil conditions allow.

The Canadian prairies, situated at the northern edge of the Great Plains of North America, produce globally significant quantities of cereal grains (wheat, barley, and rye) and oil seeds (canola, mustard, and flax). These annual crops are not directly affected by extreme winter temperatures as quantified in the USDA hardiness system. However, recent increases in soybean, pulse, and corn production in this region are likely related, at least in part, to changes in the frost-free period and summer heat accumulation (Nadler and Bullock 2011), both of which are incorporated into the Canadian hardiness index. Southeastern Canada (southern Ontario, Quebec, and the Atlantic provinces) is an important region for a variety of grain and fruit crops. The expanding

Table 3. Areal coverage of US Department of Agriculture plant hardiness subzones for the 1931–1960 and the 1981–2010 normal periods.

Hardiness subzone	Temperature range (°C)		Area covered (km ² × 10 ³)		Change in coverage	
	Low	High	1931–1960	1981–2010	Area (km ² × 10 ³)	Percentage
0	-51.1	–	476.0	25.9	-450.1	-94.6
1a	-51.1	-48.3	656.3	158.1	-498.1	-75.9
1b	-48.3	-45.5	2604.6	545.1	-2059.5	-79.1
2a	-45.5	-42.8	1768.0	2662.9	895.0	50.6
2b	-42.8	-40.0	2054.7	2836.7	782.0	38.1
3a	-40.0	-37.2	804.0	1576.9	772.9	96.1
3b	-37.2	-34.4	555.7	854.8	299.1	53.8
4a	-34.4	-31.7	363.8	507.1	143.3	39.4
4b	-31.7	-28.9	227.5	253.0	25.4	11.2
5a	-28.9	-26.1	136.7	197.2	60.6	44.3
5b	-26.1	-23.3	120.8	160.6	39.8	33.0
6a	-23.3	-20.6	107.9	110.6	2.7	2.5
6b	-20.6	-17.8	81.1	58.3	-22.8	-28.1
7a	-17.8	-15.0	22.3	19.2	-3.1	-13.9
7b	-15.0	-12.2	21.1	17.6	-3.5	-16.4
8a	-12.2	-9.4	30.5	26.0	-4.5	-14.8
8b	-9.4	-6.7	21.1	34.0	12.9	61.3
9a	-6.7	-3.9	5.3	13.1	7.8	148.3
9b	-3.9	-1.1	0.0	0.1	0.1	–

Abbreviations: km², square kilometers; °C, degrees Celsius.

wine industry in this area has been attributed, in part, to the milder winter temperatures and longer growing seasons associated with climate change (Jones 2012). However, the decline in USDA hardiness index values in this region indicates that the introduction of less-hardy grape varieties still involves considerable risk. Widrlechner and colleagues (2012) provided a detailed example of using the USDA plant hardiness zone map to identify potential vineyard sites in the US Pacific Northwest region.

Changes in tree climate envelopes

Tree climate envelopes shifted northward by 57 km on average (with a standard deviation of 42.5 km) and 58 of the 62 tree species under study exhibited northward shifts (see supplemental table S3 for the full list of tree species and results). The largest northward shift (183.3 km) was associated with the climate envelope of the grand fir (*Abies grandis*), whereas the climate envelope of the red spruce (*Picea rubens*) exhibited the largest southward shift (25.6 km). In general, the climate envelopes of western tree species (i.e., centroid of geographic range lying west of 100° west [W]) shifted further north (74.7 km on average) than those of eastern (centroid lying east of 100°W) tree species (38.1 km on average), which is further evidence of the hardiness zone shifts and climate trends noted above. Climate envelopes for a wide variety of plant species

and time periods can be viewed at <http://planthardiness.gc.ca>. We focus here on shifts in latitude, but results for longitude and climate envelope size are also provided in table S3.

Shifts in tree climate envelopes may have little impact on planting decisions in the context of ornamental horticulture, in which intense management can modify the range of suitable planting locations. However, such shifts are important in the field of silviculture, in which there is a long tradition of regenerating forests by using local seed sources. In many regions, management agencies have delineated seed zones, which limits the geographical distance that seeds can be moved and thus ensures that forest plantations are regenerated using genetic material that is well adapted to the climate at the planting site. However, under rapid climate change, the use of local seed sources may no longer be the best approach for generating productive, healthy, and resilient forest plantations (O'Neill and Nigh 2011). In recognition of both recent changes in climate (as was demonstrated here) and those expected to occur in the coming decades, forest managers in some regions of Canada have started to employ a form of assisted migration wherein seed zone limits are modified to allow seeds to be moved farther northward and upslope (Pedlar et al. 2012).

Although we focus here on horticultural or silvicultural systems, shifts in tree climate envelopes, plant hardiness

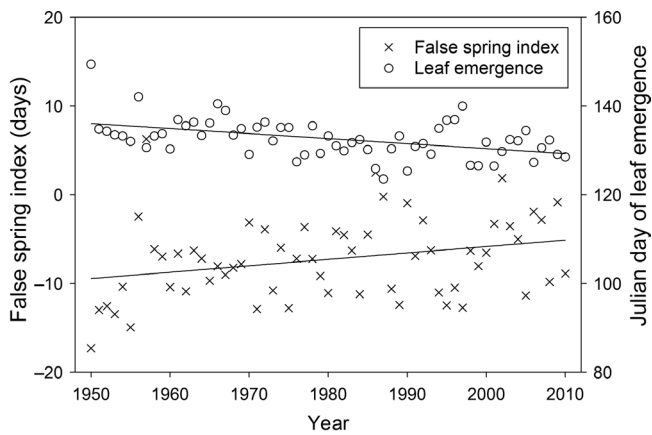


Figure 3. Trends in the date of sugar maple leaf emergence and in the false spring index over the 1950–2010 period. The leaf emergence dates were generated using an established sugar maple phenology model, and each data point is the average value across 190 climate stations that cover the range of sugar maple in Canada. The declining trend in the leaf emergence date indicates an earlier leaf emergence over time; the increasing trend in the false spring index indicates an increasing risk of late spring frost over time.

zones, and related climate variables clearly have implications for natural systems, as well. The expansion of the mountain pine beetle in western Canada—and the resulting devastation of lodgepole pine forests—is a high-profile example of how changes in extreme minimum temperature can affect natural ecosystems (Cudmore et al. 2010). In contrast, because of low migration rates, plants are not expected to shift in concert with climate; in fact, there was little evidence of northward migration in a study in which the latitudinal distribution of seedlings and adults were examined for 92 tree species in the eastern United States (Zhu et al. 2012). Therefore, for natural plant populations, persistence under rapid climate change may depend more on those species' ability to acclimate or adapt in place than on their ability to migrate to climatically suitable locations. This is a particular concern for rare and endangered species, which often require highly specialized—and often fragmented—habitats and which may lack adequate genetic diversity to allow rapid microevolutionary changes.

Plant selection challenges under climate change

Consistent with expectations under climate change, the date of sugar maple budburst (calculated using an established phenology model, as was described above) is occurring earlier (slope = -0.113 days per year, $p = .0002$; figure 3). Comparable trends were reported for the recorded budburst dates of three woody perennial species in the northeastern United States over the 1961–2005 period (Wolfe et al. 2005). However, the false spring index shows an opposing trend: Damaging frosts are occurring with higher frequency and severity over time (slope = 0.072 days per year, $p = .02$;

figure 3). This somewhat counterintuitive finding is due to the fact that budburst dates are advancing more rapidly than the date of the last frost, which is also happening earlier (slope = -0.074 days per year, $p = .02$; not shown in figure 3). Therefore, although some climate variables may be changing in a way that is amenable to planting less-hardy species and varieties, the timing of late spring frosts may limit the success of such plantings, at least in the short term. In support of this finding, an increased risk of frost damage over the past century has been reported in several recent studies (Marino et al. 2011, Augspurger 2013). Furthermore, extensive damage to forest plants and fruit crops has been reported in connection with false spring events across eastern and central North America in recent years (Gu et al. 2008, Ault et al. 2013).

The heightened risk of spring frost damage is one example of the increased weather variability that may accompany a change in average climate conditions (Seneviratne et al. 2012). Another example of this phenomenon is seen in the divergent patterns of change associated with the Canadian (figure 1c) and USDA (figure 2c) hardiness maps for southeastern Canada. This is an important region for grain and fruit crop production, which could benefit from the introduction of less-hardy crop varieties. The widespread zone declines seen on the USDA map imply that the extreme minimum temperature (which is the sole variable in the USDA system) is not increasing as consistently as are average monthly temperatures (which strongly influence the Canadian hardiness metric). This has important implications for plant selection in this region because ongoing extreme cold events present considerable risk to the introduction of less-hardy fruit varieties. For example, Cline and Norton (2012) tested 17 peach and nectarine cultivars in southern Ontario and reported winter freeze damage in 2 of 7 years. This issue is further complicated by the timing of extreme cold events; late fall or early winter events are more damaging to grape, apple, and cherry crops, whereas late winter events strongly influence pear, peach, and apricot yields (Quamme et al. 2010).

There are numerous other factors that may limit the extent to which the hardiness zone shifts presented here translate into expanded horticultural and agricultural opportunities. Increased moisture stress and drought have been identified as major concerns for both forest (Choat et al. 2012) and agricultural (Motha and Baier 2005) species under an evolving climate. Warmer winters may also facilitate the expansion of pest populations that are naturally controlled by extreme winter cold; this phenomenon is well documented in the recent mountain pine beetle outbreak (Cudmore et al. 2010). For temperate plant species, winter warming may mean that chilling requirements are not met, which can result in reduced crop yields (Atkinson et al. 2013). Furthermore, despite warming temperatures, winter damage to perennial crops could actually increase in parts of Canada because of reduced cold hardening during the fall, an increase in the frequency of winter thaw events, and

a decrease in protective snow cover (Bélanger et al. 2002). Finally, a critical limitation in Canada is the availability of arable land. Much of the northern part of the country is covered in thin soils, bare rock, or muskeg, none of which is likely to be suitable for crops in the near future, regardless of climate conditions.

Conclusions

Our findings present a complex picture of plant hardiness changes in Canada over the 50-year interval examined here. Shifts in both Canadian and USDA hardiness zones indicate that the Canadian land base—particularly in the west—has become suitable to a wider range of perennial species. Similarly, the climate envelopes of 62 tree species shifted northward by nearly 60 km on average, with western species again exhibiting larger shifts (75 km) than did eastern species (38 km). This finding also has implications for the field of silviculture, in which practitioners have traditionally limited seed movements to ensure that regenerative materials are well adapted to the climate at the planting site.

Extreme events, such as the increased incidence and severity of late spring frosts and the ongoing risk of extreme cold events in southeastern Canada, may limit the extent to which these shifts translate into planting success. In the gardening context, extreme events may be tempered by cultural practices (e.g., covering plants during frost, watering during drought), but, in larger agricultural and forestry operations, the selection of less-hardy species and varieties at a given location still involves considerable risk. The spatial products described here can be further explored at <http://planthardiness.gc.ca>.

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Supplemental material

The supplemental material is available online at <http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu016/-/DC1>.

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