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*Traditional plant hardiness zone maps identify areas that are relatively homogeneous with respect to climatic conditions that affect plant survival. Plants are typically categorized according to the most northerly, and sometimes the most southerly, zone in which they can successfully grow. This approach suffers from a number of limitations, including the coarse spatial nature of the zones and the relatively unsystematic assignment of plants to zones. Here we propose using climate envelopes to map the potential ranges of plant species in North America in wild and cultivated settings. We have initiated a major data-gathering effort that currently includes over 1.8 million georeferenced observations for more than 4100 plant species. We demonstrate the approach using sugar maple (*Acer saccharum*) and show the ease with which predicted climate-change impacts can be incorporated into the models.*

Keywords: plant hardiness zones, climate envelopes, plant distribution, climate change, Acer saccharum

Plant hardiness zones identify the location of environmental conditions under which a species or variety of plant can successfully survive and grow. Knowledge of the hardiness characteristics of plants is useful for disciplines such as horticulture, agriculture, and silviculture, in which high levels of plant survival and growth are desirable. The seemingly simple question of where a plant can grow can have important implications, given the magnitude of the horticultural sector, the introduction of new species, the viability of native species outside their natural ranges, and the prospect of rapid climate change over the course of this century.

Several systems have been developed for mapping plant hardiness in North America. In the United States, plant hardiness zones have traditionally been defined using extreme minimum temperature (USDA 1965), that is, the average coldest winter day for any given location. These zones were updated in 1990 using averages of the lowest temperatures recorded for each of the years 1974–1986 in the United States and Canada and 1971–1984 in Mexico (Cathey 1990), and again in 2006 for the United States (National Arbor Day Foundation 2006; *www.freetrees.com/media/zones.cfm*). This system identifies 11 different zones, each of which represents a 10-degree-Fahrenheit (5.6-degree-Celsius [°C]) range in average annual minimum temperature. In Canada, Ouellet and Sherk (1967a) developed a map based on an index of winter hardiness using plant survival data on 174 woody plant species and cultivars at 108 stations across the country. Their model was generated using regression analysis that included seven climate variables: mean minimum temperature of the coldest month, frost-free period in days, rainfall from June through November, mean maximum temperature of the warmest month, rainfall in January, mean maximum snow depth, and maximum wind gust in 30 years (Ouellet and Sherk 1967b). The result was a map that defined 11 hardiness zones (0–10) across southern Canada (Ouellet and Sherk 1967c). Both of these approaches to mapping plant hardiness zones have also been updated using thin-plate smoothing spline interpolation techniques (McKenney et al. 2001, 2006). Finally, the Sunset climate zone system (Brenzel 2001) incorporates information on length of growing season, timing and amount of rainfall, extreme low and high temperatures, and humidity. Though this system provides a high degree of detail for some regions, here we focus on comparisons with the US Department of Agriculture (USDA) system because it is widely used and accepted throughout North America.

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Although plant hardiness systems are part of the lore of gardening in North America, there are a number of limitations to the systems employed in Canada and the United States. The USDA zones rely entirely on extreme minimum temperature, which, though important for plant survival, is not the only climatic factor that determines the suitability of a location. For example, snow cover can provide critical winter insulation in many regions. The Canadian system was in fact developed for trees and shrubs, but is used extensively for herbaceous perennials, which may not respond to the same climatic controls as woody plants. For instance, maximum wind gust is likely to be more important to a tree than to a low-growing, herbaceous plant. The categorical nature of both maps also introduces a degree of coarseness to the zone designations, particularly if the boundary of a plant's growing range falls in the middle of a hardiness zone. Finally, although both systems have been mapped to a high degree of detail and accuracy, the method used to designate plants into hardiness zones is not well defined. In some cases, hardiness ratings may be derived from trials at a few sites around the continent; in other cases, ratings may simply reflect the opinion of a select few horticulturalists. Often, in the rush to get new products to market, the gardens of the general public act as test plots for plants with poorly understood hardiness characteristics (John Valleau, Valleybrook Gardens/Heritage Perennials, Niagara-on-the-Lake, Ontario, Canada, personal communication, 14 November 2006).

In recognition of these limitations, it is our aim to go beyond the traditional plant hardiness zone approach and outline a generic, transparent, and repeatable process for delineating the potential distribution of large numbers of perennial species. Our approach involves developing climate envelopes (Nix 1986) for individual plant species using accurately georeferenced occurrence data and spatially continuous, continent-wide climate models. This method works by summarizing the climatic extents (defined as the ranges between the minimum and maximum values for different climatic variables) at locations where a species is known to survive and then mapping the potential range of the species by identifying all locations (i.e., grid cells on a map) with conditions that fall within those extents. Furthermore, the potential effects of climate change on a species' distribution can be explored by identifying where these climate conditions are located on maps of future climate as estimated by general circulation models (GCMs).

To place this work in an ecological context, we draw on the niche concept proposed by Hutchinson (1957). He defined the fundamental niche of a species as the potential space that it could occupy, based on the full set of environmental conditions (e.g., climate, soil) that it can tolerate. Conversely, the realized niche, which is a subset of the fundamental niche, is the actual space occupied by a species, given the further constraints of biotic factors such as competition and predation. The realized niche is typically represented in species' range maps. The approach used here defines the climatic niche (Pearson and Dawson 2003) of the species under study, which, in theory, should actually be larger than the fundamental niche, because it considers only climatic limitations to plant growth. In the horticultural context, the climatic niche should be a reasonable estimate of the full potential growing area of a plant, given that gardening activities often minimize both abiotic (e.g., fertilization to boost soil nutrients) and biotic (e.g., weeding to reduce competition) constraints on plant growth. Success in defining the potential growing area for any given species will depend on the extent to which the observed data encompass a plant's climatic tolerances and the chosen climate variables represent primary climatic controls on survival and growth.

An alternative approach to identifying a plant's fundamental niche is to employ physiologically based process models (Sykes et al. 1996, Chuine and Beaubien 2001, Porter et al. 2002, Walther et al. 2005). However, the physiological details required for such an approach are time-consuming and expensive to gather, and thus are not likely to be determined for very many species. The approach used here makes use of georeferenced distribution data, which are more readily accessible. We have therefore undertaken a major data-gathering effort that involves obtaining geographically referenced plant occurrence information from agencies, from botanically reputable experts, and from the enthusiastic gardening public across both Canada and the United States (McKenney 2006).

Here we advance the concept of using bioclimatic envelopes to define species-specific potential distributions as an alternative approach to defining hardiness zones for individual species across North America. Specifically, we have three objectives: (1) to summarize the current status of our data-gathering efforts, (2) to present results for a representative species and compare them to those using the standard hardiness zones, and (3) to demonstrate how predicted climate-change impacts can be incorporated into the climate-envelope approach. We demonstrate our approach using sugar maple (*Acer saccharum*)—a popular and economically important species, with well-established hardiness ratings in both Canada and the United States, and for which we have obtained extensive distribution data.

Climate envelopes: Concepts and considerations

Climate envelopes were generated using ANUCLIM computer software (Nix 1986, Houlder et al. 2000). This system works by first generating an estimate for all climate variables of interest at each location where the species was observed. The climatic extents of the species' range are then defined by obtaining the minimum and maximum value for each of the climate variables. ANUCLIM is an early-generation climate-envelope program that fits a simple rectilinear model—that is, it essentially fits a box around extreme values in multivariate ecological space. In recent years, ecologists have developed a variety of niche-modeling techniques (Segurado and Araújo 2004, Guisan and Thuiller 2005, Elith et al. 2006, Heikkinen et al. 2006, Pearson et al. 2006), many of which attempt to fit a more refined (i.e., nonrectilinear) envelope by incorporating patterns of covariance among the environmental variables. We note, however, that in a horticultural setting, typical climatic covariation (e.g., hot and dry conditions) may no longer hold because of human intervention (e.g., irrigation), and thus the simple, direct approach of ANUCLIM may be very suitable in this context. The transparency of the method also aids in generating interest and involvement from the general public.

It is common practice to delineate a "core range"—a subset of the full climatic range within which an organism is thought to maintain high rates of survival, growth, and reproductive success. Since climate values for a given species are summarized in the form of a cumulative frequency distribution, users can define upper and lower percentiles as limits for a reduced or core range. In this study, we defined the core range as the climatic space bounded by the 5th and 95th percentiles, thus encompassing 90% of the climate values for each species. Because the core range is quantified on the basis of the density of species observations in climate space, its shape and location can be sensitive to variations in observed spatial data density that may not reflect its possible distribution in climate space. For example, occurrence records for a tree species with a climatic niche centered in northern Canada may be biased toward the southern portion of the species' range because of a greater density of data collections in southern areas. To help reduce this geographic bias, we prefiltered the species occurrence data by overlaying them with a 300-arc-second (approximately 10-kilometer [km]) grid and randomly selecting a single observation from any grid cell that contained multiple data points. We explored several grid sizes for this operation and found that the 10-km grid represented a reasonable trade-off between the degree of coarseness required to filter out spurious data density effects and the degree of fineness needed to capture the range of climate variability contained in the species occurrence data.

Another important consideration for this approach is the set of climate variables used to define the envelope. ANUCLIM generates 19 climate variables by default when supplied with spatially continuous models of monthly mean daily maximum and minimum temperature and monthly mean precipitation. Differences in the size and shape of the predicted climatic niche can arise depending on the variables involved (Beaumont et al. 2005). Thus, the best choice of climate variables is a parsimonious set that defines important climatic constraints on plant survival and growth; larger sets can unnecessarily constrain potential plant ranges with climatic requirements that are superfluous to plant survival (Box 1981, Beaumont et al. 2005). On the basis of extensive testing, and of a literature survey on climate controls on plants (e.g., Woodward 1987, Shao and Halpin 1995, Stephenson 1998), we use six climate variables in the models presented here: annual mean temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, annual precipitation, precipitation in the warmest quarter, and precipitation in the coldest quarter. Irrigation is often provided in the horticultural setting, which removes water supply (i.e., precipitation) as a constraint. Therefore, we also generate potential distribution results using only the three temperature-related variables. The resultant pair of maps for each species can be interpreted as indicating potential distribution under irrigated (i.e., cultivated) and nonirrigated (i.e., wild) conditions.

The temperature variables listed above are highly correlated ($r > 0.90$) with other familiar climatic controls on plants, such as extreme minimum temperature, growing season length, and degree-days. Ideally, moisture constraints would be quantified with a water budget model rather than with precipitation variables. However, this would require high-resolution maps of soil water capacity, which are not available for much of Canada. Nevertheless, we have found high levels of correlation (i.e., r values of 0.7 to 0.8) between the precipitation variables outlined above and coarse-scale, global water budget variables (Willmott and Matsuura 2007).

Present and future climate

Climate data are provided in the form of spatially continuous models generated from 1971 to 2000 US and Canada-wide climate station data using the ANUSPLIN suite of programs (Hutchinson 2004). This approach employs thin-plate smoothing splines to model each climate variable as a function of latitude, longitude, and elevation; errors from withheld data tests for any given location are 10% to 20% for precipitation and less than 0.5°C for temperature (McKenney et al. 2006). Because the models are spatially continuous, climate estimates can easily be generated for any georeferenced entry in the plant database.

To map the climatic niche, we created regular grid estimates of the selected climate variables at a 300-arc-second (approximately 10-km) resolution. Although finer resolutions are possible—and arguably appropriate in regions with significant elevation gradients—we found this resolution to be a reasonable compromise between computational intensity, spatial relevance, and convenience for users. We note, however, that this resolution may not completely capture the abrupt climatic gradients that exist in the mountainous regions of the western United States and Canada. As our computing power increases, our map resolution will increase.

One advantage of the climate-envelope approach is that the effect of predicted changes in future climate can be easily explored. Here we compare the climate habitat for sugar maple in current climate conditions with the climate habitat predicted for the end of the century in the conditions projected by the Canadian Centre for Climate Modelling and Analysis's second-generation coupled global climate model (CGCM2; Boer et al. 2000) under the A2 emissions scenario outlined by the Intergovernmental Panel on Climate Change (IPCC; Nakicenovic and Swart 2000). This is considered by some to be a relatively extreme scenario that assumes, among other things, high human population, rapid rates of deforestation, and high levels of pollution and carbon dioxide emissions; however, recent evidence suggests that carbon dioxide levels have been increasing at rates higher than the most pessimistic

IPCC scenarios (Canadell et al. 2007). We have developed grids of future climate for several other GCMs, emissions scenarios, and time periods (see McKenney et al. 2006), but here we present only the findings for the CGCM2/A2 emissions scenario to demonstrate the approach.

The climate-envelope approach has been criticized as a method for studying the effect of climate change on species' distributions. The approach does not take into account nonclimatic factors that play an important role in determining species distributions, such as biotic interactions (Davis et al. 1998, Hampe 2004), dispersal limitations (Lawton 2000, Hampe 2004), and genetic adaptation in response to environmental change (Etterson and Shaw 2001, Hampe 2004). In response to these criticisms, Pearson and Dawson (2003, 2004) point out that most of these concerns are minimized when bioclimatic envelopes are employed at broad spatial scales, at which climate factors tend to be the primary controls on species distributions. Furthermore, as noted previously, issues such as dispersal and competition are often minimized in the horticultural setting.

Plant observations

We have adopted a two-part strategy to acquiring plant data for the project. First, we have approached various agencies that collect or store georeferenced plant observations. In Canada, these agencies are the Ministry of Natural Resources within each province; Conservation Data Centres; *ad hoc* vegetation surveys by experts; botanical gardens; herbaria; master gardeners; and other botanically reputable groups, such as community-based horticultural societies. In the United States, we have obtained information from similar sources and from the US Forest Service's Forest Inventory and Analysis program (Alerich et al. 2005). This data collection is ongoing.

Another source of plant occurrence data is submission from the general public, a form of citizen science. This approach has been facilitated by a Web application developed to accept the required information on plant distributions. Before submitting data, participants are asked to register and identify themselves as professional botanists/horticulturalists, master gardeners, or members of the general public. We recognize that there may be some concerns over the taxonomic skills of contributors; thus, this categorization will allow models to be generated using data with varying degrees of botanical certainty. The user interface then accepts information concerning the plant name and location of the sighting. Plants recorded in the database must have survived at a particular location for at least three years. All data submitted are confidential, in that the location coordinates are coarsened before being mapped for public viewing. This not only protects the location of sensitive plant species but ensures privacy for contributors.

To date, more than 1.8 million records for more than 4100 plant species have been gathered. A large majority of these records have come from data agreements with government agencies. Approximately 5000 records have been submitted online, and this number continues to grow as the project generates interest. At this point, 1499 species have more than 50 observations each (figure 1); previous work indicates that approximately that number of observations is required to produce reliable climate-envelope models, though this number varies depending on the dispersion of the data and the distributional qualities of the species under study (Kadmon et al. 2003). At *http://planthardiness.gc.ca,* users can view the occurrence data, potential range maps for both the "irrigated" and "nonirrigated" scenarios, and the projected future climate habitat for all species with at least 30 observations. We have chosen this number of observations (as opposed to 50) as a cutoff to provide preliminary models for a larger number of species and to encourage the submission of observations from data-sparse areas. Users are reminded that the models are preliminary and a work in progress.

An alternative approach to collecting occurrence records is to make use of published range maps (see Shafer et al. 2001). However, range maps do not exist for many plant groups and are usually relatively coarse representations of species' natural, not potential, range. As an example, figure 2 shows the natural range of sugar maple (digitized from Little 1971) overlaid with the data collected for this species. The data represent the natural range well, but they also include verified occurrences as far south as Texas (more than 1000 km south of its natural range; figure 2) and as far west as British Columbia (about 3000 km west of the published range limits; figure 2). Clearly, sugar maple, like most species, is

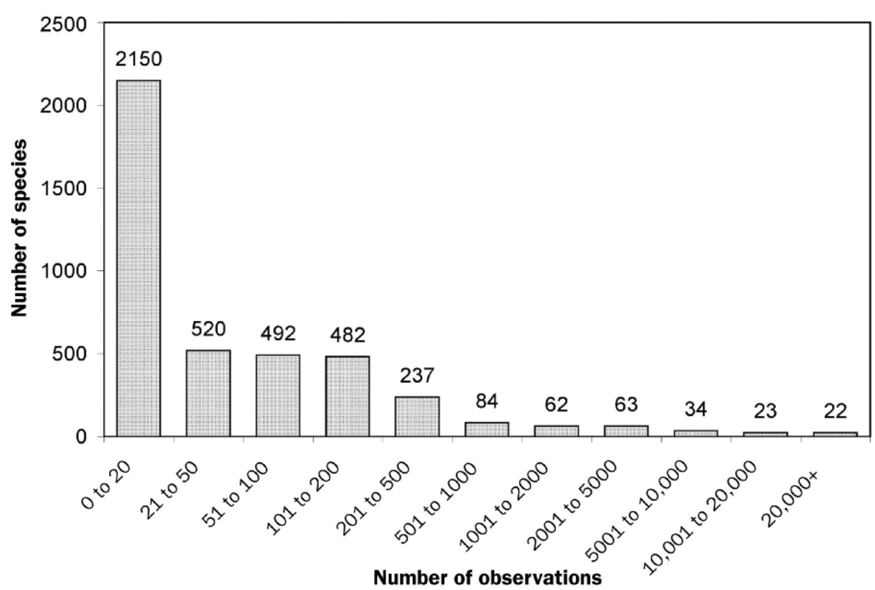

Figure 1. Number of species in each of 11 categories representing frequency of occurrence in the plant hardiness database.

capable of survival and growth far outside its accepted range limits, which underlines the importance of obtaining occurrence data from a wide range of locations when trying to map potential distributions.

The occurrence of sugar maple in novel locations raises a number of important general considerations. First, there is the issue of cultivars—that is, cultivated plant varieties that have been selected for a particular combination of desirable attributes. There are more than 10 sugar maple cultivars on the market, and some of these varieties have been selected specifically for heat tolerance (e.g., *A. saccharum* 'Astis') and cold tolerance (e.g., *A. saccharum* 'Unity'). This intervarietal variation with respect to climatic tolerances may explain some of the outlying data points in the current work. Ultimately, we would like to produce models for each cultivar, although considerably more data will need to be collected before maps can be produced at this level of taxonomic detail. Another consideration is that outlying data records, particularly in the north, may come from a location with a microclimate that is not representative of the surrounding area. For example, a planting site within an urban heat island or on the lee side of a building may experience temperatures that are several degrees warmer than the general surroundings. Although we do request information on proximity to buildings for the observations submitted through the Internet, there are currently too few observations to address this issue adequately for most species. Users may wish to exercise some caution when interpreting the models for planting outside the area defined by the core range, especially for species with very few observations. Finally, although contributions have been modest to date, the Internet mechanism allows for a more detailed quantification of climate tolerances than the typical approach of developing climate envelopes from digital range maps when such maps are available (e.g., Shafer et al. 2001). Information on successful growth from new locations will be valuable in a climatically changing world, providing both evidence of change and options for future planting efforts (McLachlan et al. 2007).

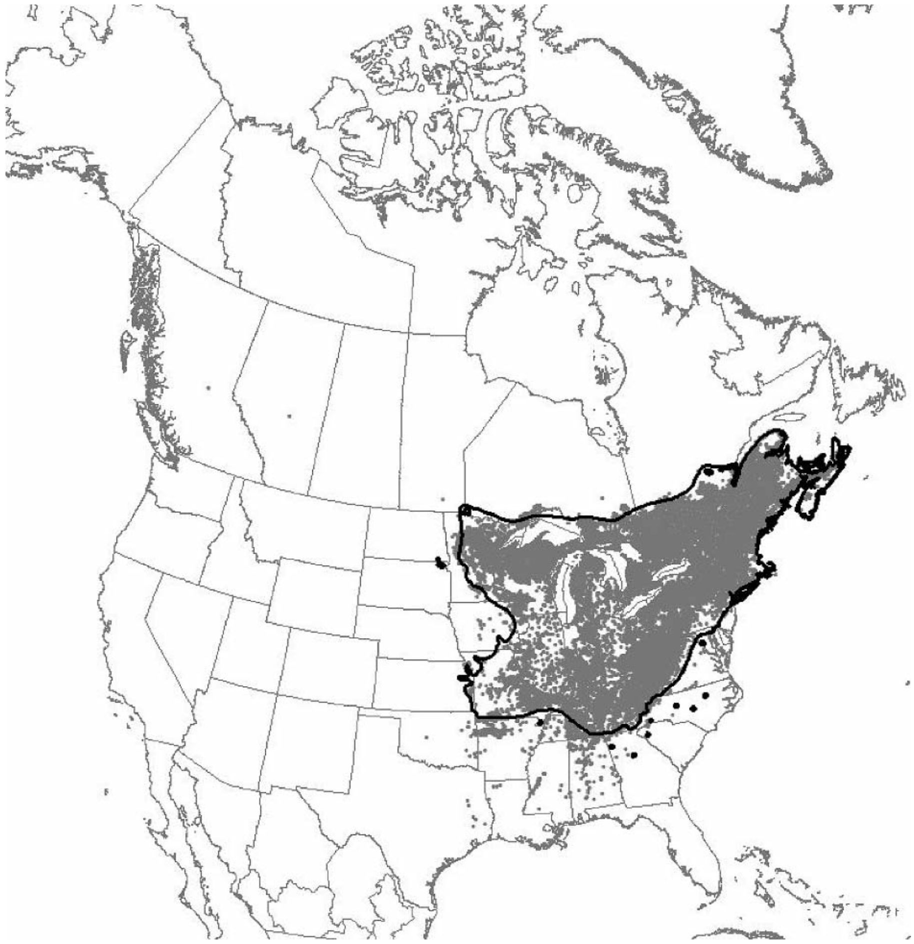

Figure 2. Occurrence records for sugar maple, overlaid by Little's (1971) range map.

Beyond traditional plant hardiness zones

The potential distribution model for sugar maple covers much of the eastern United States and southeastern Canada when both temperature and precipitation requirements are considered (figure 3a), and it covers nearly all of the United States and southern Canada when only temperature is taken into account (figure 3b). Both scenarios indicate a much broader potential range than sugar maple naturally occupies (cf. Little's [1971] range in figure 2). This is not surprising, given that climate envelopes identify all locations with suitable climatic conditions for growth, but do not take into account other factors, such as competition and historical dispersal limitations, that have restricted each species to only a subset of its distributional potential (Peterson 2003, Soberon and Peterson 2005). Incorporating available soil moisture variables into our models (as opposed to precipitation variables only) may also act to reduce the predicted potential ranges. In both scenarios, the core range follows the general pattern of the full climatic range but, of course, occupies only a subset of this geographic space. This subset may be considered a climatically safer planting area within which a species would be expected to exhibit higher rates of survival and growth.

On the basis of the traditional plant hardiness approach, sugar maple is designated to grow in USDA zones 4 through 8 (Mityga 2005). Figure 4 shows a comparison between this area and that defined by the climate envelopes for the irrigated and nonirrigated scenarios. The climate habitat identified

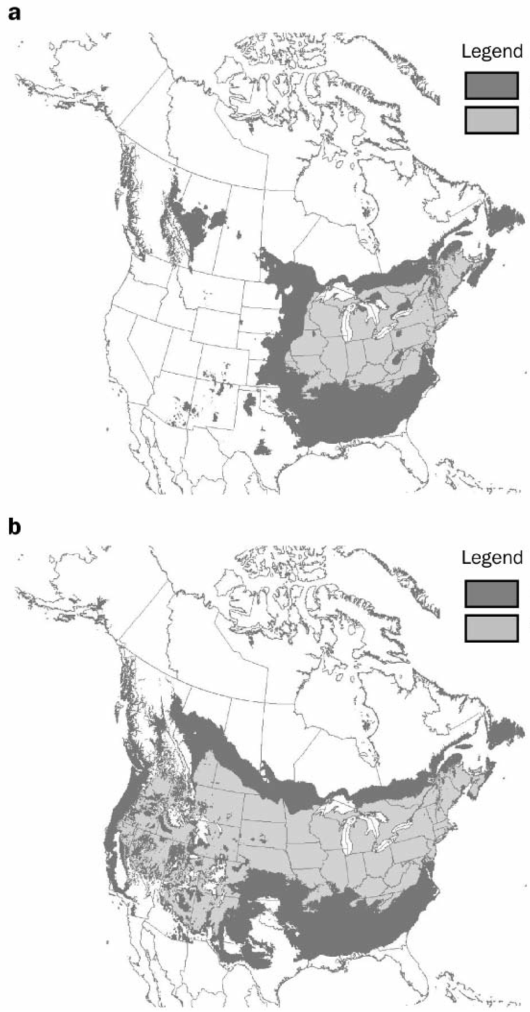

Figure 3. Climate envelopes (full and core range) for sugar maple, based on (a) temperature and precipitation variables (i.e., the nonirrigated scenario), and (b) temperature variables only (i.e., the irrigated scenario).

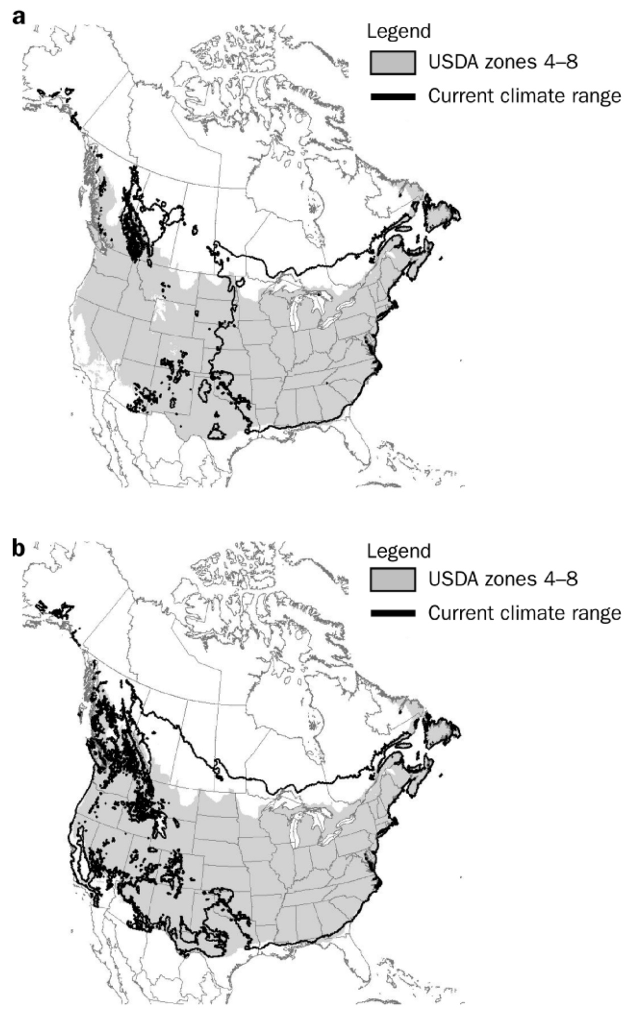

Figure 4. US Department of Agriculture plant hardiness zones 4–8 overlaid by the climate envelope for sugar maple, the latter based on (a) temperature and precipitation variables (i.e., the nonirrigated scenario), and (b) temperature variables only (i.e., the irrigated scenario).

by the nonirrigated scenario is considerably more restricted than that defined by the traditional approach (figure 4a), particularly in the western half of the continent. However, when precipitation is not a consideration (e.g., when irrigation is present), the climate envelope for sugar maple extends dramatically to the west, covering much of the area defined by zones 4 through 8 (figure 4b). The drastic difference between the irrigation scenarios suggests that much of the western half of the continent has favorable temperatures, but perhaps inadequate rainfall, to optimally support sugar maple. This distinction could be useful information for those interested in growing this species, but is not immediately apparent from the traditional plant hardiness zone approach.

Both irrigation scenarios identify extensive areas of potential habitat in Canada that lie well north of USDA zone 4 (figure 4). This pattern is driven by verified distribution records for sugar maple from locations in northern Ontario, southern Manitoba, and central British Columbia (figure 2). Generally, the northern range limits provided by the traditional zone approach tend to be conservative (i.e., err on the southern side). This is probably because most published references (e.g., books and magazines) are from southern locations with limited experience, and limited reader market, in truly cold winter regions (John Valleau, Valleybrook Gardens/Heritage Perennials, Niagara-on-the-Lake, Ontario, Canada, personal communication, 14 November 2006). That said, there are a number of ongoing hardiness trials that do gather useful data on plant survival at higher latitudes, such as the Regional Woody Plant Test Project in Alberta (Murray and Seymour 2005). We are endeavoring to make data agreements with any relevant and interested agencies to increase the number of observations and hence improve the veracity of models in all regions.

Incorporating climate change

With the climate-envelope approach, it is relatively straightforward to incorporate predicted impacts related to climate change. On the basis of projections from CGCM2, we mapped where the current climate envelope for sugar maple would be expected to occur by the end of this century (figure 5). The future climate habitat for sugar maple shows a significant northward shift of nearly 1000 km and overlaps the current habitat only in the northern portion of the current range (figure 5).

Clearly, this potential range is an unlikely outcome as a future natural distribution, given that suitable soil conditions are not likely to occur in much of this region by the end of this century. Furthermore, the magnitude of the predicted shift is well beyond generally accepted tree migration rates (Neilson et al. 2005). However, if climate warming progresses as projected, maps such as those shown in figure 5 may become increasingly important for identifying potential planting areas for negatively affected plant species.

A caveat is that, as atmospheric carbon levels increase, the water-use efficiency of plants may also increase (Wullschleger et al. 2002). This would mean that, in the future, plants may be able to persist in areas currently considered too dry. In this context, our models may be a conservative estimate of future range limits, particularly along southern and western edges that are strongly affected by precipitation.

Conclusions

Here we present the idea of using climate envelopes to map the potential range of North American plant species. This approach has several advantages over traditional plant hardiness zones, including (a) species-specific maps, (b) a more precise identification of potential growing space than that afforded by the traditional zone approach, (c) the ease of alternative interpretations (wild and cultivated), and (d) a transparent and repeatable method for defining and quickly updating the potential distribution of a species, requiring only georeferenced occurrence observations. The method also allows potential climate-change impacts to be incorporated in a relatively

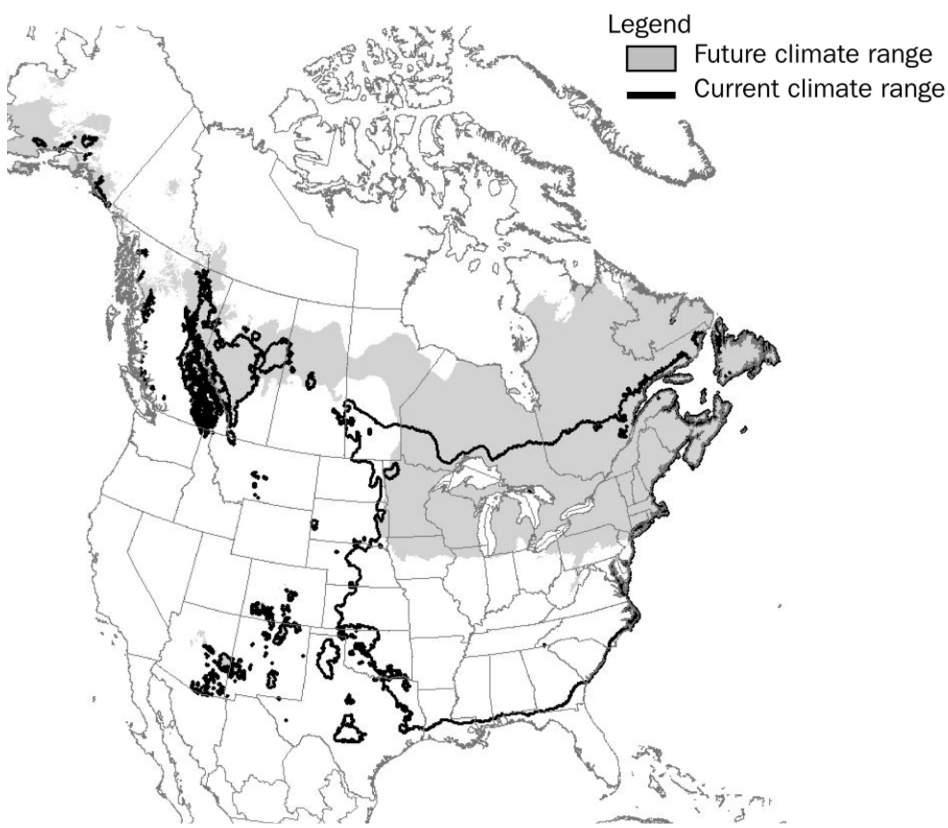

Figure 5. Current and future climate envelopes for sugar maple under the nonirrigated scenario. The future climate envelope is based on projected climate conditions for the period 2071–2100, using the Canadian Centre for Climate Modelling and Analysis's second-generation coupled global climate model and the A2 emissions scenario outlined by the Intergovernmental Panel on Climate Change.

simple way. In the long run, we hope the monitoring and data-acquisition aspects of this effort will provide insights into the impacts of climate change, migration rates, and intervention and adaptation strategies for native, nonnative, and invasive plant species.

The prospect of detailed laboratory studies to determine the climatic tolerances of large numbers of plant species seems unlikely. As an alternative, the approach presented here makes use of geographically widespread distribution data to map the climate habitat of plants. More than 1500 plant species have been modeled to date. This work in progress is intended to engage both experts and the general public on the topic of plant biogeography. The Internet provides a practical mechanism to enhance this participation. Those interested in supporting the project by submitting plant observations are encouraged to do so at the Web site *http://planthardiness.gc.ca/*.

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