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Author: Kilkenny, Francis F.

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Genecological Approaches to Predicting the Effects of Climate Change on Plant Populations

Francis F. Kilkenny[1,2]

[1]USDA Forest Service
Rocky Mountain Research Station
Boise, ID 83702

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ABSTRACT: Climate change threatens native plant populations and plant communities globally. It is critical that land managers have a clear understanding of climate change impacts on plant species and populations so that restoration efforts can be adjusted accordingly. This paper reviews the development and use of seed transfer guidelines for restoration in the face of global climate change, with an emphasis on the role of common garden studies in predicting climate change impacts. A method is presented for using genecological common garden data to assess population vulnerability to changing environmental conditions that includes delineation of geographical regions where habitats are likely to become marginal, assessment of shifting climatic selection pressures on plant traits, and identification of source material that is likely to be adapted to changing conditions. This method is illustrated using a genecological dataset for bluebunch wheatgrass (*Pseudoroegneria spicata*). The demonstration indicates that bluebunch populations will be vulnerable to extirpation in areas of their current range, that selection pressures will increase on a trait important to climatic adaptation, and that promising seed sources exist that may be able to persist under novel conditions. Additional avenues for expansion of the presented methods are discussed, and the use of common garden data for management in the context of evolution and changing climates is considered.

Index terms: assisted migration, common garden studies, natural selection, restoration, seed transfer guidelines

INTRODUCTION

Climate change threatens the continued persistence of many native plant populations (Thuiller et al. 2005), and may be detrimental to wildland restoration efforts if its effects are not taken into account (Harris et al. 2006). It is critical that land managers have a clear understanding of the probable effects of climate change on target species and populations so that restoration efforts can be adjusted accordingly. The global climate has warmed by an average of 0.6 °C over the last 30 years (IPCC 2007), and additional warming of 2-7 °C is expected by the end of the century (Stott and Kettleborough 2002), depending on the rate of anthropogenic carbon inputs and carbon-cycle feedbacks (Cox et al. 2000). While climates will warm generally, this process will not occur at the same rate everywhere, and change in other climatic variables, particularly precipitation, may be even more geographically and seasonally uneven (Rummukainen 2012). In addition, the likelihood of extreme weather events, such as drought frequency and severity, may surpass historical levels (Cook et al. 2004; Meehl and Tebaldi 2004).

As temperature and precipitation change from current norms, species that are locally adapted to current environments will have to adapt to novel conditions, or shift ranges to match the changing climate, in order to escape population extirpation and even species extinction (Aitken et al. 2008; Visser 2008). Already, human-caused climate change over the last century has triggered shifts in ranges and the phenology of growth and reproduction of a number of species (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan 2006). The rate of global warming is expected to increase (Cox et al. 2000), and some climate change models predict that plants will need to migrate as much as 3–5 km per year to match shifting climates (Davis and Shaw 2001; Aitken et al. 2008). This means that over time fewer species will be able to migrate or adapt rapidly enough to escape extinction. Climate change may result in a global loss of 9–13% of all species even with a minimal temperature rise and no limits to natural dispersal, but extinctions could rise to 38–52% of all species in worst-case climate scenarios with limited dispersal (Thomas et al. 2004).

A primary need in developing climate change management strategies is the assessment of ecosystem vulnerability to climate change (IPCC 2007). Because members of plant communities can have different climatic responses, it is necessary to identify the species and populations most under threat from climate change so that ecosystem conservation efforts can be targeted appropriately (Dawson et al. 2011). It has long been understood that plant species have climatic tolerances that limit the range of environments in which they can survive (Hutchinson 1957). Techniques that evaluate this environmental niche space can be

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[2] Corresponding author:
ffkilkenny@fs.fed.us; (208) 373-4376

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effective in assessing species extinction and population extirpation risks by identifying geographical regions where climates will shift beyond identified tolerance limits. Bioclimatic species distribution models derived from species presence/absence data have been used effectively for this purpose (Guisan and Thuiller 2005). However, each plant population has its own ecological and evolutionary history that drives genetic differences in climatic adaptation (Linhart and Grant 1996). This intraspecific adaptive variation may lead to both over- and underestimates of climate change vulnerability in species distribution models that are derived only from presence/absence data. Therefore, whenever relevant data is available, species distribution models should take the ecological genetics of target conservation and restoration species into account.

Plant community restoration success can often hinge on selecting the right plant material for the site being restored. In addition to selecting species that are important components of the degraded ecosystem, selecting specific source populations for introduction is expected to be essential for effective results (Lesica and Allendorf 1999). Native plant populations can be adapted to environmental conditions over a variety of spatial scales, from local to regional (Linhart and Grant 1996). Also, there is considerable evidence of population maladaptation where source phenotypes do not match local optimums (Crespi 2000). Therefore, the use of source populations that are adapted to the local environmental conditions at a restoration site is widely recommended (McKay et al. 2005). In many restoration efforts this is accomplished by reintroducing local source material, defined by close geographic proximity. However, introduction of local types may not be feasible in cases where restoration efforts are constrained by logistical, ecological, or economic factors that affect the availability of nearby sources (McKay et al. 2005), and may not be possible at all in changing climates (Peters and Darling 1985). Therefore, it is often necessary to consider plant materials sourced from populations at greater distances from a restoration site. To predict the fitness, or the adaptive match, of nonlocal sources at a restoration site, it is important to understand the strength of local adaptation and the geographic extent over which it occurs (McKay et al. 2005). Seed transfer guidelines, a management tool developed in forestry (Ying and Yanchuk 2006) and now being extended for use in other systems (Johnson et al. 2004), are a practical way to delineate the seed transfer distances that are expected to be adaptive for a given species. These guidelines take into account both genetic information from common garden studies and practical logistical considerations (Hamann et al. 2011).

In this paper I review the use of seed transfer guidelines in restoration, how these guidelines are developed, and the usefulness of seed transfer guidelines in coping with the effects of global climate change. I focus specifically on the role of common garden studies in seed transfer guideline development and use, with a particular emphasis on approaches to evaluating plant–climate associations. I also present a method for evaluating plant population vulnerability to climate change and how selection pressures on plant traits might shift due to climate change using genecological common garden data, where adaptive variation across a range of source environments is assessed using one or a few common gardens. Finally, I discuss additional avenues for expansion of these methods, and the use of common garden data for management in an evolutionary context under changing climates.

Seed Transfer Guidelines, Restoration, and Climate Change

Seed transfer guidelines are essential tools for identifying seed sources that are likely to be adapted to the environmental conditions at target restoration sites (Campbell 1991; Ying and Yanchuk 2006). The use of seed transfer guidelines to identify adapted seed sources has a long history in North American forestry dating back to the 1920s, when foresters recognized large differences in hardiness and growth of trees from different geographic origins (Thrupp 1927; Bates 1928). Recently, a number of studies have developed seed transfer guidelines for nontree species, including grasses (Erickson et al. 2004; R.C. Johnson et al. 2010; St. Clair et al. 2013), forbs (Johnson et al. 2013), and shrubs (Horning et al. 2010). Transfer guidelines often rely on contiguous fixed-boundary zones to regulate seed movement (Morgenstern 1996). Such zones were determined primarily through descriptive and qualitative means prior to 1974 (Ying and Yanchuk 2006). Campbell (1974) shifted the delineation of seed zones to a quantitative and predictive approach by employing regression analyses to describe adaptive clines that could be used in scaling zone sizes. In addition to fixed-boundary zones, "floating point" transfer guidelines can be developed using similar analytical techniques, where transfer distance limits are allowed to vary depending on the specific adaptive characteristics of the seed source (Rehfeldt 1983). These two delineation approaches roughly correspond with two different, but not mutually exclusive, conceptual approaches, where fixed-boundary delineations tend to aim at *minimizing risk* in seed transfers, while floating point delineations tend to aim at *maximizing fitness* in seed transfers (Hamann et al. 2011).

In practice, the delineation and conceptual approaches used in a given set of guidelines largely depend on the types of data available. Fixed-boundary and risk minimizing approaches are based on the assumption that source populations are locally adapted to the environments where they originate (Heslop-Harrison 1964; Endler 1986), and the primary goal is to match seed sources to climates where the risk of maladaptation is low (Hamann et al. 2011). This can be accomplished through several techniques that use a range of data types, from models that use only climate data, and are usually generalized rather than species-specific, to species-specific models that incorporate information on adaptive genetic variation.

A number of attempts have been made to create ecologically meaningful bioclimatic models that can be used as generalized transfer guidelines. For example, the ecoregion classification system used by the US Environmental Protection Agency (Omernik 1987) has been suggested as a potential basis for seed transfer zones (Jones 2005; Withrow-Robinson and Johnson

2006). Recently, the ecoregion approach has been extended globally (Potter and Hargrove 2012). Another example is the generalized provisional seed zone approach (Bower et al. 2014), which was developed using climatic variables that have been empirically associated with adaptive variation in plants (e.g., Chimura et al. 2011). Interestingly, when provisional seed zones were nested within level III ecoregion classifications, the combined model explained more variation in a set of species-specific seed zones than either system alone (Bower et al. 2014). Generalized guidelines can be especially useful in cases where genetic data are lacking, which include the vast majority of important nontree species (Bower et al. 2014), and have proven to be effective predictors of adaptive variation in at least some plant species (Horning et al. 2010; Miller et al. 2011).

Ideally, species-specific seed transfer guidelines should be used whenever possible (G.R. Johnson et al. 2010), because patterns of adaptive genetic variation can vary substantially among species, and species can be adapted to environmental conditions across small and large spatial scales (e.g., Sork et al. 1993; Fenster and Galloway 2000). Species-specific fixed-boundary and risk minimizing seed transfer guidelines are generally developed from genecological common garden studies. The term genecology was first used by Turesson (1923) to describe the study of intraspecific phenotypic variation in relation to source environments. In practice, genecological studies evaluate a large number of populations sourced from a range of geographic locations and environments in one, or a few, common gardens (St. Clair et al. 2013). Strong correlations between measured traits in the common gardens and conditions in the source environments indicate intraspecific variation in climatic adaptation. Adaptive variation is assumed to have a genetic basis due to past natural selection in local environments (Heslop-Harrison 1964; Endler 1986), but this assumption is not tested directly and may not always be valid (Mangold and Libby 1978; Mátyás 1990). This means that it is not possible to predict the distribution of fitness values across a range of environments for specific sources, but it is possible to determine associations between variation in phenotypic traits and environmental conditions across multiple sources. This then allows for the delineation of zones with similar adaptive associations in order to minimize the risk of maladaptation in within-zone transfer. The primary benefit of genecological studies is that a large number of populations can be sampled and tested cost effectively, such that adaptive differences can be determined across large areas of a species' range even when research budgets are limited.

Floating point and fitness maximizing approaches are generally pursued by developing source-specific response functions, which define the fitness distribution of each source population over a range of environments (Lindgren and Ying 2000; Wang, Hamann, Yanchuk, et al. 2006). Development of response functions requires data from reciprocal transplant studies, where sources are planted in a set of sites that are representative of the range of environmental conditions experienced by the target species. Reciprocal transplant studies are effective at testing whether specific source populations are adapted to their local environments or have nonlocal fitness optimums (Kawecki and Ebert 2004). However, testing multiple sources across multiple sites can be expensive and logistically challenging (O'Neill et al. 2007; Hamann et al. 2011), therefore many reciprocal transplant studies are spatially constrained and often represent only small portions of a species range (but see Wang et al. 2010; Kapeller et al. 2012).

A variety of approaches have been used in the development of seed transfer guidelines that account for the adaptive consequences of climate change. These approaches include the development of response functions from reciprocal transplants over a range of altitudes (e.g., Sáenz-Romero et al. 2006), combining information from multiple common garden studies into a single analysis in order to increase the range of population and climate values represented (Joyce and Rehfeldt 2013), and the use of large reciprocal transplant studies to develop a series of response functions to explore regional variation in climate impacts (Kapeller et al. 2012). Another promising approach is the development of universal response functions (Wang et al. 2010). Universal response functions combine both response functions, derived from trait × environment associations of specific source populations across multiple sites, and transfer functions, derived from trait × environment associations between multiple source populations and their source environments. Wang et al. (2010) developed a universal response function from a study on lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) in British Columbia initiated in 1974, which tested 140 sources at 60 sites. This study found that growth rates of lodgepole pine were likely to increase in much of the northern range, primarily because marginal habitats in that region would become more hospitable due to warming.

When large reciprocal transplant studies are not feasible, data from genecological studies with fewer common garden sites can be used to estimate the impact of future climate change on seed transfer guidelines. One approach is to re-project seed zones using geographically explicit future climate scenarios in place of current climate normals. For example, a study on white spruce (*Picea glauca* (Moench) Voss) in Ontario determined future seed zones under three different climate change scenarios (Thomson et al. 2010). Two out of the three of the scenarios predicted little change from current seed zones, but a third scenario predicted substantial shifts from current seed zones. This is illustrative of the inherent uncertainty in using future climate prediction models. Another approach is to use the underlying trait × environment regression models that are derived in the process of seed zone construction to assess population vulnerability and changing selection pressures. That technique is illustrated here.

METHODS

Here I describe a method for using genecological data to investigate vulnerability to climate change in plant populations, and give an example of its use. To perform the climate change vulnerability assessment, trait × environment regression equations, commonly generated in genecological studies (e.g., St. Clair et al. 2013), are mapped onto current and expected future climate surfaces for a region of interest, and used to generate geographically explicit trait surfaces. These surfaces describe values for expected population trait means for current climates, and predicted optimal values for future climates, under the assumption that measured trait × environment associations represent past natural selection for locally adapted traits. The current and future trait surfaces are then compared using map algebra in a GIS system; in this example I use ArcGIS 10 (ESRI 2011). Differences between current and future trait surfaces can be used to predict several aspects of climate change vulnerability. First, when current and future surfaces are compared for traits that are closely related to fitness, such as biomass or reproduction, geographic regions with a high vulnerability to population extirpation can be identified. Specifically, areas where a fitness trait is predicted to approach zero may indicate locations where climate will shift beyond the tolerance limits of the species in question. Second, the direction, and magnitude, of the changes in a trait surface under future climate conditions can been viewed as analogous to the expected direction, and strength, of natural selection on that trait, and under those conditions, for the time period in question. While the ability of particular plant populations to respond to identified selection pressures will need to be assessed by other means (Nyquist 1991), populations that face stronger directional selection pressures are likely to be at greater risk of running up against adaptive constraints, and are therefore more likely to be vulnerable to future maladaptation. Third, populations from tested sources can be compared to these models to identify sources that are more likely to be adapted to conditions in vulnerable habitats.

Data from a large common garden experiment on bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve (Poaceae); St. Clair et al. 2013, hereafter St. Clair et al.) are used to illustrate this technique (Appendices 1 and 2). The St. Clair et al. study was performed to determine seed transfer guidelines for bluebunch wheatgrass throughout the Intermountain West. Populations from 114 locations spanning a wide range of environments were planted in three common gardens (Central Ferry Research Farm, 46°40’9”N, 117°45’21”W; Pullman Plant Materials Center 46°43’9”N, 117°8’29”W; Lucky Peak Nursery, 43°34’57”N, 115°29’36”W), and morphological and phenological traits were measured in the summers of 2007 and 2008. Data from the common gardens were used to develop regression equations that describe trait × environment associations that were mapped using geographically explicit climate models obtained from Climate Western North America (Wang, Hamann, Spittlehouse, and Aitken 2006; Wang et al. 2012). Each trait of interest was modeled using a suite of climatic variables, and a single model was selected through a model selection procedure to find the model with the best goodness of fit and parameter complexity trade-off (Akaike Information Criterion, Akaike 1974). In this paper, I use the trait × environment regression equations developed for two traits (above-ground dry weight, hereafter referred to as biomass, and leaf length/width ratio) to demonstrate the climate vulnerability assessment procedure (Appendices 1 and 2).

To identify areas where there is a high probability of bluebunch extirpation, I projected the trait × environment regression model identified for biomass onto the current climate (1961–1990 norms) and two future climate models. Each future climate model represents a different carbon emission scenario, one high (A1B) and one low (B1), and derived from a consensus of available general circulation models (GCMs; Wang et al. 2012). I treat biomass as a fitness trait, similar to the treatment of plant height in seed transfer guideline studies on trees (Ying and Yanchuk 2006), and justified in the bluebunch system where size is strongly related to survival (Dalgleish et al. 2011). I identify habitats where projected biomass approaches or reaches zero, defined as projected biomass for each model that is below 20% of maximum projected biomass for the current climate. I then mapped these onto an area that represents the core of the bluebunch range tested in St. Clair et al., which is encompassed by the four following class III ecoregions (Omernik 1987): Blue Mountains, Columbia Plateau, Northern Great Basin, and Snake River Plain.

To assess how changing climate will affect selection pressure on a morphological trait in future climates, I projected the trait × environment regression model identified for leaf length/width ratio onto the current and future climate models described above. Leaf length/width ratio measures relative leaf narrowness, with greater values indicating greater narrowness. Leaf length/width ratio had the strongest trait × environment associations of all traits measured in St. Clair et al., which makes sense given that it is likely an adaptation to reduce water loss in arid environments (Westoby et al. 2002). The differences between current expected values of leaf length/width ratio and future predicted values were determined using map algebra in ArcGIS 10, and describe the predicted shift in optimal trait values over the time interval between the common garden measurements and 2050. The change in optimal values were then converted into selection differentials (*S*), which are used to indicate the overall directional change in phenotype over time (Lande and Arnold 1983). *S* values were constructed by standardizing trait values across all three projection models to a mean of 0 and a standard deviation of 1, and then subtracting the mean values of the current climate projection from the mean values of both future climate projections. To allow for comparisons between different environments within the study area, *S* values were derived for each seed zone delineated in St. Clair et al., nested in all four ecoregions. The advantage of this technique is that the relative strength of selection can be compared between regions with different initial phenotypic starting points. Also, when scaled by generation time, derived selection differentials can be compared with those found in other phenotypic selection studies. In this paper, I do not scale the *S* values because generation times of wild bluebunch populations are currently unknown, but see Dalgleish et al. (2011) for a dataset where these values could be derived.

To illustrate how these techniques can inform future seed movement decisions, I plotted projected optimal values of leaf length/width ratio against the projected values of two climate variables, mean annual temperature (MAT) and annual heat moisture index (AHM), for the high emissions scenario (A1B) across the entire study area. These two climate variables represent the two component parameters in the St. Clair et al. trait × association regression for leaf length/width ratio. Points are derived from gridded sampling locations at 20 arc minute intervals and are coded to show whether they were sampled from marginal or non-marginal habitats, derived from the A1B biomass analysis. In addition, the percentage of projected points from marginal habitats is shown at one degree intervals for MAT and every 10 index points for AHM. As a comparison, I plotted the measured leaf length/width ratio relationship of tested bluebunch seed sources (test sources) against values of MAT and AHM for the current climate onto the same graphs as the future projection data. The correlation between leaf length/width ratio of tested seed sources and each climate variable is also plotted ($r = 0.53$ for MAT, $r = 0.63$ for AHM; St. Clair et al. 2013). These plots allow for a number of visual comparisons, including the relationship between optimal leaf length/width ratios and marginal habitat and the relationship between the climatic associations of tested seed and projected associations for future climates.

RESULTS

The extent of marginal bluebunch habitats is likely to spread under changing climates in both low and high emissions scenarios (Figure 1). Marginal habitat area doubled in the B1 emissions scenario, and increased by six-fold in the A1B scenario, indicating that bluebunch extirpation vulnerability will increase even under optimistic emissions scenarios. Nearly the entire area of the Snake River Plain is predicted to become marginal habitat in the A1B scenario, as are significant portions of the Columbia Plateau. The extent of marginal habitat is likely to spread in the Northern Great Basin between the Owyhee Mountains and Steens Mountain. In the Blue Mountains, current bluebunch habitat will be maintained and remain marginal only at high elevations.

Selection differentials for leaf length/width ratio varied by emission scenario, ecoregion, and seed zone (Table 1). *S* values were higher for the A1B emissions scenario than the B1 emissions scenario by an average of 0.19, which makes sense given that climate change is expected to be more rapid with higher carbon emissions. For both emissions scenarios, *S* values were higher and more variable for the Northern Great Basin and the Snake River Plain ecoregions than for the Blue Mountain and Columbia Plateau ecoregions. Seed zones 6b and 7b had the lowest projected *S* values in both emissions scenarios, and seed zone 2a had the highest *S* values in both emissions scenarios.

In the plotted comparisons, the density of projected sample points for the A1B emissions scenario is shifted towards drier and hotter values in comparison to the values for tested source locations for the current climate, indicating climate shifts, and to higher projected leaf length/width ratios, indicating a shift towards narrower optimum leaf length/width ratios (Figure 2). The percentage of projected points from expected marginal habitats is greatest at the lowest and highest values for both MAT and AHM. In general, tested sources do not persist in climate conditions that are equivalent to the projected points with the highest values of MAT and AHM, and high percentages of marginal habitat. This indicates that many sites will shift outside of the range of climates that bluebunch populations currently experience. Interestingly, a number of tested sources have leaf length/width ratios that are similar to those projected for most of the extreme projected climate values.

DISCUSSION

In this paper I reviewed the role of seed transfer guidelines in restoration and climate change assessments, with a particular emphasis on the types of studies and datasets that underlie the development of seed transfer guidelines. I also presented an approach for using genecological common garden data to predict the impact of climate change on plant species by defining geographical regions where populations are at risk of local extirpation, evaluating the predicted strength of selection on key adaptive traits, and identifying test sources that are likely to harbor traits that are adapted to changing conditions. The presented approach is meant to demonstrate how genecological data can be leveraged, rather than be an exhaustive survey of possible techniques or a complete assessment of bluebunch wheatgrass. Here, I discuss the results in a restoration and methodological context and suggest ways to further extend the usefulness of these techniques. I will end with a discussion on two developing conservation paradigms, *evolutionarily enlightened management* and *assisted migration*, where data on adaptive genetic variation from common garden studies will prove particularly useful.

Climate Change Vulnerability, Natural Selection, and Seed Source Identification

Bluebunch wheatgrass habitats will become increasingly marginal as climates continue to shift away from current norms. Bluebunch populations in the Snake River Plain and the Columbia Plateau will be particularly vulnerable to extirpation risk. Much of the area of these two level III ecoregions is covered in basin topography, which already experiences greater temperature and aridity relative to the mountainous regions surrounding them, and will likely reach bluebunch climate tolerance thresholds earlier. As expected, the geographic extent of extirpation risk will depend on the amount of anthropogenic carbon emissions, with the high emission A1B scenario exhibiting three times the extent of marginal habitats in comparison to the low emission B1 scenario. This demonstrates the importance of emission model choice in climate change vulnerability assessments. In the vulnerability assessment I treated biomass as a fitness proxy. This is justified in bluebunch because above ground size is highly correlated with survival (Dalgleish et al. 2011), but may not be justified in other systems. The use of above-ground biomass as a fitness proxy could be particularly problematic for species where fitness is more correlated to biomass allocation to roots than allocation to shoots (e.g., Rowe and Leger 2011). The maps produced by projecting fitness

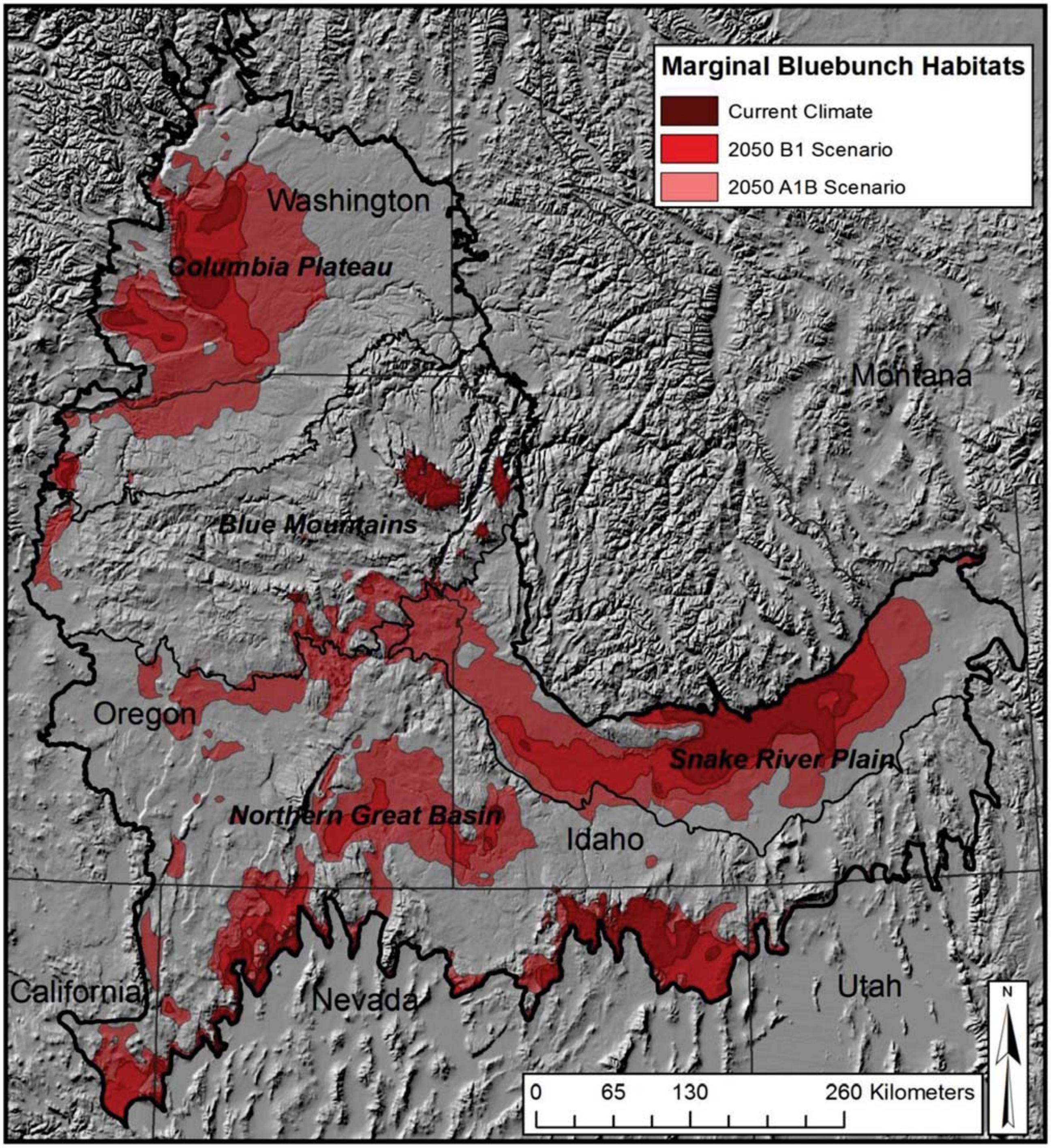

Figure 1. Map of predicted marginal habitats of bluebunch wheatgrass (*Pseudoroegneria spicata*) for the current climate (1961–1990 norms, shown in dark red) and two predicted climate models for 2050 (B1 emissions scenario with consensus circulation model, shown in medium red; A1B emissions scenario with consensus circulation model, shown in light red) within the four following level III ecoregions: Blue Mountains, Columbia Plateau, Northern Great Basin, and Snake River Plain. Marginal habitats are defined as areas where predicted biomass is below 20% of the maximum in current conditions. Predicted biomass values were modeled using regression equations developed in St. Clair et al. (2013).

× environment associations onto spatially explicit climate surfaces are very similar to the maps produced in species distribution modeling from presence/absence data, and can be compared when calibrated properly (Joyce and Rehfeldt 2013).

Predicted selection differentials on leaf length/width ratios exhibited considerable differences between emission scenarios, ecoregions, and seed zones. In general, zones that were lower in elevation had higher *S* values than zones at higher elevations. Selective differences between emission scenarios can help managers to identify a range of expectations for future climatic selection on plant traits, and differences between ecoregions and seed zones can help managers target conservation and restoration areas. Ideally, prediction of selection differentials should allow for cross-comparisons with other species subject to changing conditions. To evaluate the effective strength of climatic selection on plant populations, calculated *S* values should be scaled by generation time (Lande and Arnold 1983). This is because the rate of evolutionary response to selection is expected to be strongly related to generation times (Rosenheim and Tabashnik 1991). While generation times are not known for bluebunch, it is a long-lived clonal bunch-forming grass with high survival rates for large individuals (Dalgleish et al. 2011), meaning that generational turnover in wild populations may take considerable time. On the other hand, when grown in agricultural settings, significant seed production in bluebunch starts at 2–3 years and remains highly productive for only 4–5 years (Tilley and St. John 2013), suggesting that a large amount of reproduction occurs at early life-history stages and that effective generation times could be short.

Temperature and aridity in some areas of the bluebunch wheatgrass range will likely shift toward extremes that are not currently experienced by any of the tested bluebunch sources. The shift into extreme values coincides with a high percentage of marginal habitats predicted for the A1B scenario. The shift of climates toward values that are outside known climatic tolerances could pose challenges to land managers seeking to conserve species and ecosystems as these

Table 1. Estimated selection differentials (*S*) for bluebunch wheatgrass (*Pseudoroegneria spicata*) leaf length/width ratio in a changing climate under two emissions scenarios (B1 and A1B). *S* values represent the strength of selection for the interval between the common garden plantings (2006–2008) and 2050, and are not scaled by generation time. *S* values are estimated for each bluebunch seed zone nested within level III ecoregion: Blue Mountains (BLU), Columbia Plateau (COL), Northern Great Basin (NGB), and the Snake River Plain (SRP).

	Emissions scenario B1					Emissions scenario A1B				
	Level III ecoregion					Level III ecoregion				
Seed zone	BLU	COL	NGB	SRP	Zone mean	BLU	COL	NGB	SRP	Zone mean
1	n.a.	0.47	0.54	0.56	0.52	n.a.	0.72	0.81	0.76	0.76
2a	0.49	n.a.	0.57	0.6	0.55	0.72	n.a.	0.82	0.81	0.78
2b	n.a.	0.41	0.53	0.52	0.49	n.a.	0.57	0.71	0.68	0.65
3a	0.46	0.45	0.54	0.55	0.5	0.67	0.65	0.81	0.77	0.73
3b	0.44	0.41	0.47	0.48	0.45	0.6	0.56	0.64	0.64	0.61
4	0.46	0.43	0.53	0.58	0.5	0.69	0.61	0.79	0.78	0.72
5	0.42	0.4	0.51	0.5	0.46	0.58	0.55	0.69	0.66	0.62
6a	0.45	0.43	0.5	0.44	0.45	0.67	0.62	0.72	0.59	0.65
6b	0.43	0.41	0.47	0.43	0.43	0.58	0.56	0.65	0.58	0.59
7a	0.44	0.43	0.49	n.a.	0.45	0.65	0.62	0.74	n.a.	0.67
7b	0.41	0.42	0.45	0.44	0.43	0.56	0.57	0.62	0.58	0.59
Ecoregion mean	0.44	0.43	0.51	0.51		0.64	0.6	0.73	0.69	

types of changes become more common. These shifts may also pose challenges in data-driven analyses, because the shape of trait × environment associations are likely to change across multiple environmental values, and modeled associations may not be predictive outside the range of the data. Nevertheless, using trait × environment associations to predict optimal trait values for novel climatic conditions makes it possible to identify source populations with matching trait values, even if those sources persist in nonmatching environments. In the case of bluebunch, several tested sources had leaf length/width ratios that matched optimal values predicted for hotter and more arid conditions.

An important extension of the analytical methods presented in this paper would be to incorporate variance in trait × environment associations and climate change predictions to evaluate the sensitivity of these analyses to initial assumptions. A number of methods exist to assess the variance distributions of trait × environment associations. In particular, posterior distributions of variance in trait × environment associations could be computed from data on, within, and between population variation using Bayesian multilevel models (Webb et al. 2010; Laughlin et al. 2012). This would allow for the generation of a set of trait × environment association models where the model parameters are probabilistically distributed and allowed to vary. The sensitivity of species vulnerability assessments to assumptions in climate models is usually assessed by comparing the outcomes of multiple models (e.g., Thomson et al. 2010). While this is informative, it does not allow for the probabilistic analysis of outcomes. In addition, the models used in multiple comparison risk-assessments are usually heavily averaged to begin with and may hide considerable variance (Knutti et al. 2010). A number of recent climate studies have developed downscaled probabilistic scenarios for specific regions by using multimodel ensembles (reviewed in Tebaldi and Knutti 2007). However, significant challenges remain, particularly the need to develop metrics that separate "good" and "bad" models, so that input datasets can be weighted with a high degree of confidence (Knutti et al. 2010).

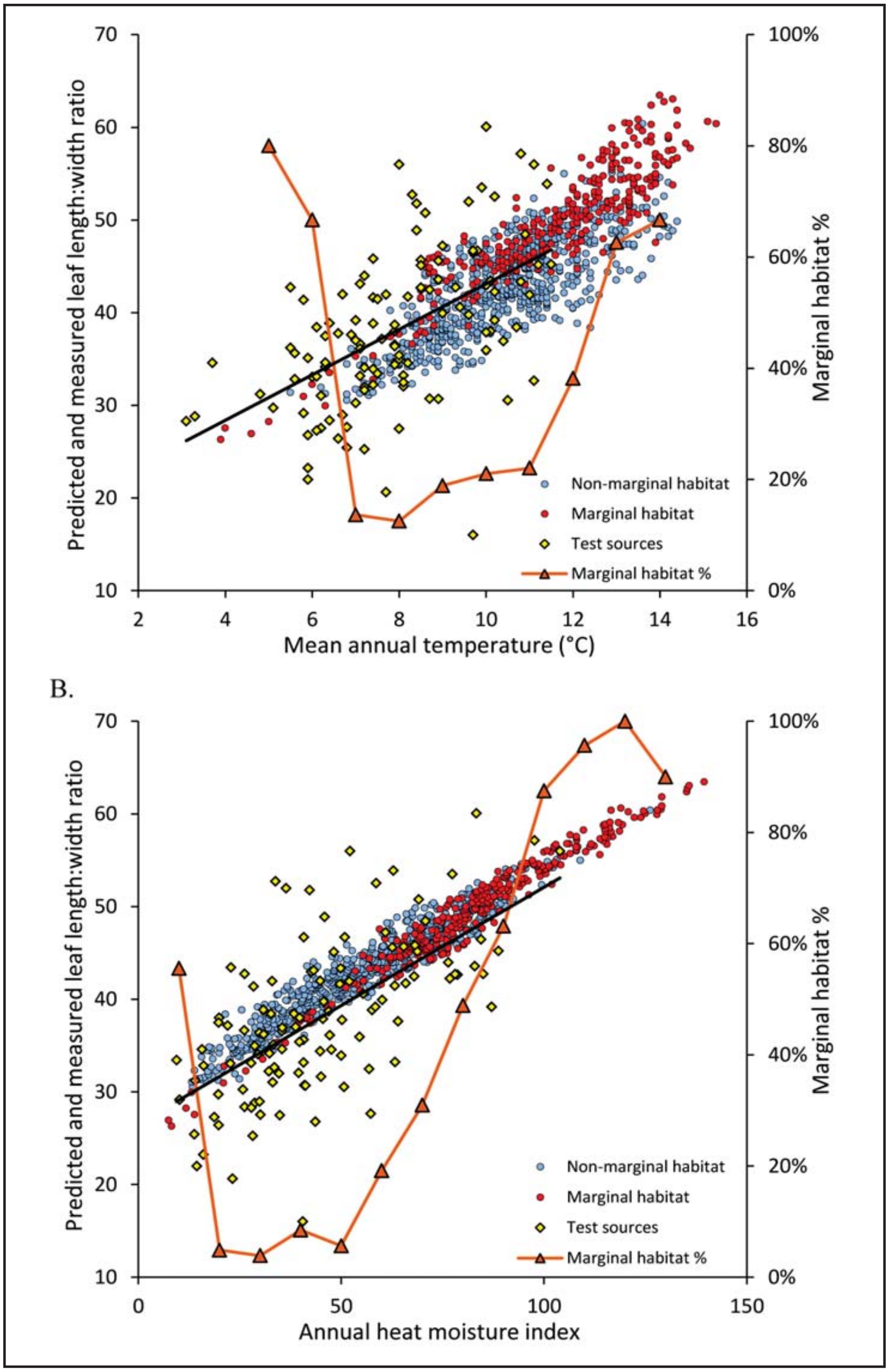

Figure 2. A comparison of mean annual temperature (MAT; A) and annual heat moisture index (AHM; B) with predicted optimal leaf length:width ratio for marginal and non-marginal habitats of bluebunch wheatgrass (*Pseudoroegneria spicata*) for a predicted climate model in 2050 (A1B emissions scenario with consensus circulation model, see text for details). Also shown is the climate × leaf length/width ratio relationship of tested bluebunch seed sources (test sources) for the current climate (1961–1990 norms). Points for the predicted climate were selected from a grid spaced at 20 arc minute intervals. Predicted leaf length/width ratio values were modeled using regression equations developed in St. Clair et al. (2013). Marginal and non-marginal habitats were determined through an analysis of predicted biomass, where points below 20% of maximum size in current conditions (see text for details) were considered marginal. A trend line (solid black line) is plotted for the tested seed sources trait × climate correlation (MAT *r* = 0.53, AHM *r* = 0.63; see St. Clair et al. 2013). The percentage of marginal habitats is pooled by degrees of MAT or AHM (orange triangles).

Evolutionarily Enlightened Management

Ensuring the resilience of native plant communities will require managers to consider the evolutionary consequences of changing climates on restoration practice (Ashley et al. 2003; Hufford and Mazer 2003; Rice and Emery 2003; Harris et al. 2006). This will include both the identification of plant material sources that are adapted to predicted conditions, and assessments of the selective pressures of a changing climate on native plant populations. The use of local or nearby seed sources is generally recommended because these sources are likely to be adapted to conditions in the habitats targeted for restoration (McKay et al. 2005). In addition, local seed sources are expected to be less likely to cause (1) genetic swamping, where genotypes of local remnants are replaced by introduced genotypes; (2) outbreeding depression, where hybridization with local remnants leads to a loss of fitness due to the dilution of adapted genes; or (3) epistatic complications, through the disruption of co-adapted gene complexes (Hufford and Mazer 2003). However, any number of logistical, ecological, and economic constraints can limit local seed supply (McKay et al. 2005). One suggested alternative is to plant high quality genetically variable material, even if it is nonlocal, under the assumption that it will allow for a favorable response to selection (Broadhurst et al. 2008). Although managing for genetic variation can increase evolutionary potential, it can also increase risks of extinction and extirpation due to "genetic load," where a large amount of the available genetic variation is maladaptive (Lande and Shannon 1996). Therefore, it will be important to find source material that is both genetically variable and adapted. Seed transfer guidelines help delineate which source populations are likely to be adapted to environmental conditions at a restoration site, as well as indicate a range of possible sources so that genetically variable sources can be selected from available populations or constructed through source pooling.

Restoration practice will also benefit from predicting shifts in the direction, and magnitude, of climate-based selection pressures on native plant traits and populations. This can lead to better targeting of conservation areas, through vulnerability assessments, and to better targeting of plant material use, by matching sources to changing climates in an evolutionarily relevant time frame. Indeed, even in current practice, a lack of consideration of natural selection at a restoration site can lead to failures or near-failures in population establishment, especially when site conditions select for trait values that are significantly different from the source material (Kulpa and Leger 2013). Prediction of changing selection pressures will be all the more important as the rate of climate change continues to increase.

Assisted Migration

Assisted migration, also known as assisted colonization, is a conservation strategy for managing the impacts of rapid climate change that seeks to deliberately translocate organisms from locations with deteriorating climate conditions to locations with better climate matches, in order to lower the risk of population maladaptation and loss (Peters and Darling 1985). Assisted migration strategies can encompass a broad range of goals, from minimizing loss of biodiversity to preventing species extinction (Williams and Dumroese 2013), and resides on a continuum of restoration practice that includes all deliberate translocations, though generally it refers to translocations outside a species historical range (Seddon 2010). While this strategy is controversial, due to invasion risks, impacts on host ecosystems, and other unintended consequences (Mueller and Hellmann 2008; Ricciardi and Simberloff 2009), it may become a necessary part of the conservation toolkit if climate change continues to accelerate (Vitt et al. 2010). Decision tree approaches have been recommended that take into account the species vulnerability, potential negative impacts, alternative management tools, and feasibility of assisted migration strategies (Hoegh-Guldberg et al. 2008). Data from common garden studies will be critical to informing decisions on the necessity and efficacy of assisted migration as climates continue to change.

Dr. Francis Kilkenny is a USFS Research Biologist and lead of the Great Basin Native Plant Project, an interagency project between the BLM Plant Conservation Program and the USFS Rocky Mountain Research Station. His research interests include the ecological and evolutionary impacts of climate change on native and invasive plant species; the evolution of local adaptation in native and invasive plant species; pollination biology of herbaceous and long-lived clonal plants; evolutionary consequences of density and intraspecific competition; and fundamental niche modeling and the projection of species range shifts due to climate change.

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Appendix 1. Model selection procedure for bluebunch wheatgrass dry weight. The top 20 models are shown. Data are from St. Clair et al. 2013.

Rank	Int	MAT	MWMT	MCMT	TD	MAP	MSP	AHM	SHM	bFFP	FFP	PAS	EMT	Eref	CMD	Adj R^2	AIC
1	1138.9		-13.51		7.24	0.05			-0.16	-3.22	-1.91	-0.20	7.90			0.51	751.5
2	1138.9		-6.27	-7.24		0.05			-0.16	-3.22	-1.91	-0.20	7.90			0.51	751.5
3	1138.9			-13.51	-6.27	0.05			-0.16	-3.22	-1.91	-0.20	7.90			0.51	751.5
4	1163.8					0.05				-3.70	-2.55	-0.21	4.98		-0.15	0.49	751.9
5	1124.9		-8.26			0.05			-0.15	-3.60	-1.85	-0.17	4.19			0.50	752.0
6	1201.0		-3.16			0.06			-0.14	-3.76	-2.29	-0.21	5.02	-0.08		0.51	752.2
7	1192.9					0.07		0.17	-0.17	-3.70	-2.45	-0.21	5.45	-0.12		0.50	752.4
8	1190.2			-3.06		0.06			-0.15	-3.53	-2.41	-0.22	6.92	-0.10		0.50	752.4
9	1173.5	4.45				0.06			-0.15	-3.60	-2.51	-0.21	4.91	-0.16		0.50	752.4
10	952.5	22.66	-11.44			0.05			-0.16	-2.99	-1.86	-0.18		-0.18		0.50	752.5
11	1213.2					0.07			-0.16	-3.75	-2.47	-0.21	5.54	-0.14	0.03	0.50	752.6
12	1211.0				-0.65	0.06			-0.14	-3.79	-2.46	-0.21	5.10	-0.12		0.50	752.6
13	1202.8					0.06	0.01		-0.14	-3.72	-2.47	-0.21	5.52	-0.12		0.50	752.6
14	1026.2	8.97	-20.84		9.95	0.04			-0.18	-2.72	-1.60	-0.18	7.27			0.51	752.7
15	1026.2	8.97	-10.89	-9.95		0.04			-0.18	-2.72	-1.60	-0.18	7.27			0.51	752.7
16	1026.2	8.97		-20.84	-10.89	0.04			-0.18	-2.72	-1.60	-0.18	7.27			0.51	752.7
17	1140.9					0.04			-0.07	-3.61	-2.44	-0.18	5.26		-0.12	0.49	752.8
18	1098.0	11.98	-6.69			0.05			-0.16	-3.39	-2.16	-0.18	2.91	-0.14		0.51	753.0
19	1153.7		-5.40			0.04			-0.10	-3.67	-2.11	-0.18	4.56		-0.05	0.50	753.3
20	1124.7		-13.44		6.82	0.06		0.16	-0.18	-3.21	-1.87	-0.20	7.61			0.51	753.3

Note: Tested climate variables include: mean annual temperature in °C (MAT), mean warmest month temperature in °C (MWMT), mean coldest month temperature in °C (MCMT), temperature difference between MWMT and MCMT in °C (TD), mean annual precipitation in mm (MAP), mean annual summer (May to September) precipitation in mm (MSP), annual heat:moisture index ((MAT+10)/(MAP/1000); AHM), summer heat:moisture index ((MWMT)/(MSP/1000); SHM), the Julian date on which FFP begins (bFFP), frost-free period (FFP), precipitation as snow in mm between August in previous year and July in current year (PAS), extreme minimum temperature over 30 years (EMT), Hargreaves reference evaporation (Eref), Hargreaves climatic moisture deficit (CMD).

Appendix 2. Model selection procedure for bluebunch wheatgrass leaf length/width ratio. The top 20 models are shown. Data are from St. Clair et al. 2013.

Rank	Int	MAT	MWMT	MCMT	TD	MAP	MSP	AHM	SHM	bFFP	FFP	PAS	EMT	Eref	CMD	Adj R^2	AIC
1	20.3	1.11						0.20								0.44	422.9
2	10.9		0.97					0.19								0.43	423.6
3	8.3		0.74					0.18						0.01		0.44	424.2
4	17.1	0.88						0.19						0.01		0.44	424.3
5	12	1.44						0.19		0.04						0.44	424.4
6	15.9	0.75	0.40					0.19								0.44	424.6
7	21.1	1.36						0.19			-0.02					0.44	424.6
8	16.8	1.12			0.18			0.19								0.44	424.6
9	11.2							0.19			0.04			0.02		0.44	424.6
10	14.2	1.41						0.19					-0.14			0.44	424.6
11	19.6	1.03						0.18							0.00	0.44	424.7
12	18.1	1.37		-0.27				0.19								0.44	424.7
13	18.8	1.21						0.21				0.00				0.44	424.8
14	20.1	1.17						0.22	-0.01							0.44	424.8
15	14.2			1.16	0.83			0.19								0.44	424.8
16	14.2		0.83	0.33				0.19								0.44	424.8
17	-3.4		1.44					0.17		0.11			0.32			0.45	424.8
18	1.7				1.71			0.18		0.21			1.25			0.45	425.0
19	30.9			-1.50				0.18					0.82	0.02		0.45	425.0
20	22.2		1.35					0.17			-0.06		0.34			0.45	425.1

Note: Tested climate variables include: mean annual temperature in °C (MAT), mean warmest month temperature in °C (MWMT), mean coldest month temperature in °C (MCMT), temperature difference between MWMT and MCMT in °C (TD), mean annual precipitation in mm (MAP), mean annual summer (May to September) precipitation in mm (MSP), annual heat:moisture index ((MAT+10)/(MAP/1000); AHM), summer heat:moisture index ((MWMT)/(MSP/1000); SHM), the Julian date on which FFP begins (bFFP), frost-free period (FFP), precipitation as snow in mm between August in previous year and July in current year (PAS), extreme minimum temperature over 30 years (EMT), Hargreaves referen
evaporation (Eref), Hargreaves climatic moisture deficit (CMD).