

Assisted migration to address climate change: recommendations for aspen reforestation in western Canada

LAURA K. GRAY, TIM GYLANDER, MICHAEL S. MBOGGA, PEI-YU CHEN, AND ANDREAS HAMANN¹

University of Alberta, Department of Renewable Resources, 751 General Services Building, Edmonton, Alberta T6G 2H1 Canada

Abstract. Human-aided movement of species populations in large-scale reforestation programs could be a potent and cost-effective climate change adaptation strategy. Such large-scale management interventions, however, tend to entail the risks of unintended consequences, and we propose that three conditions should be met before implementing assisted migration in reforestation programs: (1) evidence of a climate-related adaptational lag, (2) observed biological impacts, and (3) robust model projections to target assisted migration efforts. In a case study of aspen (*Populus tremuloides* Michaux.) we use reciprocal transplant experiments to study adaptation of tree populations to local environments. Second, we monitor natural aspen populations using the MODIS enhanced vegetation index as a proxy for forest health and productivity. Last, we report results from bioclimate envelope models that predict suitable habitat for locally adapted genotypes under observed and predicted climate change. The combined results support assisted migration prescriptions and indicate that the risk of inaction likely exceeds the risk associated with changing established management practices. However, uncertainty in model projections also implies that we are restricted to a relatively short 20-year planning horizon for prescribing seed movement in reforestation programs. We believe that this study exemplifies a safe and realistic climate change adaptation strategy based on multiple sources of information and some understanding of the uncertainty associated with recommendations for assisted migration. Ad hoc migration prescriptions without a similar level of supporting information should be avoided in reforestation programs.

Key words: bioclimate envelope modeling; climate change; ecological genetics; reforestation; remote sensing; seed transfer guidelines; seed zones.

INTRODUCTION

Climate change is projected to eliminate suitable habitat of many endemic or range-restricted species (e.g., Hannah et al. 2005, Parmesan 2006), which suggests that assisted movement of endangered species outside their historic range may be necessary for conservation purposes (e.g., Millar 2004, McLachlan et al. 2007). However, proactive mass translocation of a wide variety of species to mitigate loss of biodiversity under changing climate is a contentious issue and conflicts with well-established conservation principles (Hunter 2007, Ricciardi and Simberloff 2009). The concept of assisted migration may also be applied to translocation of populations within a species range. Populations within wide-ranging species are usually adapted to local environmental conditions (e.g., Kawecki and Ebert 2004, Savolainen et al. 2007) and maladaptation due to climate change may require population movement to matching habitat in new locations to maintain ecosystem health and productivity. This version of assisted migration, too, has been subject

to debate (Marris 2009), and it also conflicts with well-established forest resource management principles and legislation that restrict the movement of seed sources in reforestation programs (e.g., Morgenstern 1996, Ying and Yanchuk 2006, McKenney et al. 2009).

We find it useful to differentiate the movement of species far outside their range for conservation purposes (*assisted colonization*), and population movement within a species range or somewhat beyond the leading edge (*assisted migration*). Under this definition, assisted migration would usually apply to common and widespread species for the purpose of maintaining ecosystem health and productivity, whereas assisted colonization aims at conserving endemic or range-restricted species. Although there are exceptions, this definition largely reflects previous usage of terminology in conservation biology (e.g., Hunter 2007, Hoegh-Guldberg et al. 2008, Ricciardi and Simberloff 2009) and forest resource management (e.g., Millar et al. 2007, O'Neill et al. 2008b, McKenney et al. 2009). For both assisted migration and assisted colonization, the contentious issue is the risk of unintended consequences associated with large-scale management interventions as well as a lack of rigorous scientific knowledge to guide the movement of species or genotypes. While predictive habitat modeling and observed biological impacts suggest an obvious general need for assisted migration

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¹ Corresponding author. E-mail: andreas.hamann@ualberta.ca

(e.g., Parks and Bernier 2010 and associated conference papers), we usually do not know if this need applies to a particular population of a species, and where exactly appropriate target habitat would be under uncertain future climates.

Our view is that assisted migration of common species is a promising and effective climate change adaptation strategy with good chances of successful implementation. First, movement of planting stock is already a well-established management practice in reforestation programs, although the current principle of seed transfer is to limit the distance of seed movement to ensure that reforestation stock is well adapted to planting environments (Ying and Yanchuk 2006). Second, there is a substantial body of research on how populations of commercially important tree species are adapted to local environments (Morgenstern 1996), and we can further draw on existing programs for commercial forestry species that monitor forest growth and health to determine the need for assisted migration (Parks and Bernier 2010). Third, robust predictive habitat models to reliably guide assisted migration are far easier to develop for common species than for rare endemics that lack census data for model parameterization (Kadmon et al. 2003). Fourth, most common tree species have a high degree of within-population genetic variation in addition to substantial environmental plasticity (Hamrick 2004). Slightly missing the optimal habitat of a planting stock in an assisted migration program is therefore unlikely to have serious consequences. Lastly, implementing assisted migration at a large scale requires little or no additional financial resources when put into operation through existing reforestation programs.

Nevertheless, patterns of adaptive genetic variation and response to environmental change can be quite species specific in trees, and we think that generic and ad hoc assisted migration efforts should be avoided. A moderate research effort is required to determine whether assisted migration is necessary and how it should be implemented. Ideally, we should rely on a population-specific case-by-case evaluation if the benefits associated with a management intervention outweigh the potential risks. In a case study for aspen in western Canada, we develop a framework to guide assisted migration that draws on reciprocal transplant experiments to detect adaptational lag of populations, remote sensing to identify populations that are potentially vulnerable to climate change, and predictive habitat modeling to target assisted migration efforts both in terms of species choice and at the level of locally adapted populations within a species. Our intention is to develop more dependable guidelines for assisted migration by synthesizing information from a variety of data sources and by drawing on independent modeling, experimental, and empirical research approaches.

METHODS

Reciprocal transplant experiments

Regional genetic differences and adaptational lag of aspen populations were examined with a provenance trial series established by a forest industry cooperative at five locations in western Canada. The planting locations were chosen to represent major ecosystem classes including the eastern Rocky Mountain foothills (test site coordinates, 52°50' N, 114°53' W), the southern boreal plains of Alberta (54°45' N, 113°10' W) and of Saskatchewan (53°26' N, 105°35' W), and the northern boreal plains of Alberta (56°46' N, 117°38' W) and of British Columbia (58°34' N, 122°22' W). Three to 11 bulked commercial seed lots from collection locations in the broad vicinity of each test site were grown in a forest nursery in 1997, and seedlings representing a total of 38 provenances (seed lots) were planted at all five test locations in the spring of 1998. At each test site, provenances were planted in a randomized complete block design with six replications in five-tree row plots. Tree height at age 9 was recorded in 2006. Means of five-tree row plots were used as experimental units for analysis of variance implemented with PROC GLM of the SAS statistical software package (SAS Institute 2008). Averages and standard errors of provenances by source location were calculated with the least squares means method, taking advantage of the nested sampling and blocked experimental designs. Subsequently, we calculated a matrix of probabilities that provenances transferred from different ecoregions (representing assisted migration) matched or exceeded the growth of provenances collected near the test site (representing local genotypes).

Remote sensing

To infer forest productivity through remote sensing we use the Enhanced Vegetation Index (EVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) of NASA's Terra satellite. We obtained the 16-day interval 500-m grid resolution EVI product (Huete et al. 2002, Gao et al. 2008) from the MODIS-for-NACP data products web site (NASA 2008). Original MODIS/EVI data were cropped to western Canada and filtered for grid cells that primarily contained aspen stands. For the filtering we explored the use of Alberta Vegetation Inventory database (ASRD 2005), and 25-m grid resolution land cover data for western Canada (Wulder et al. 2008). Summarized at 500-m grid resolution corresponding to MODIS/EVI data, the deciduous class of 25-m land cover data could closely reproduce aspen frequency data from Alberta's forest inventory database. This is plausible because aspen is the predominant deciduous forest species throughout the study area (representing 75–95% of deciduous trees for boreal ecosystems). We therefore use deciduous forest cover as a proxy for aspen frequency over the entire study area, since forest inventory data for

the study area were regionally incomplete and not available for most parts of Saskatchewan.

To infer potential vulnerability of aspen populations to climate change, we took advantage of a major regional drought that led to dieback of aspen stands in western Canada in 2002 (Bonsal and Wheaton 2005, Hogg and Bernier 2005, Hogg et al. 2008). First, 16-day interval MODIS/EVI data that were available from 2001 to 2006 was processed with the TIMESAT software package, using an adaptive Savitzky–Golay function to fit EVI values as a function of Julian date over the course of each year (Jonsson and Eklundh 2004). We use the large integral under the Savitzky–Golay function to generate remotely sensed proxies of forest productivity. The large integral represents the cumulative amount of green vegetation, measured as EVI, over the course of the growing season. This measure can be used to estimate net primary productivity with additional predictor variables (Huete et al. 2002), but we analyze raw integral data in this study. Integral values were generated for 700 000 aspen grid cells for six years, and subsequently converted to annual anomalies from the six-year average. The anomaly values were mapped to evaluate geographic variation of EVI values integrated over the course of the growing season in response to the 2002 regional drought.

Climate trends and projections

Our baseline climate data were derived from monthly precipitation and temperature grids that were generated by Daly et al. (2008) using the Parameter-elevation Regression of Independent Slopes Model (PRISM) to interpolate climate normal data observed at weather stations for the period 1961–1990 for the United States and Canada. We enhance this database with lapse-rate-based down-sampling to 1-km resolution and estimation of biologically relevant climate variables (Hamann and Wang 2005, Wang et al. 2006a, Mbogga et al. 2009). Climate variables were selected to avoid pairs of highly correlated variables as much as possible. We included mean annual temperature, mean warmest month temperature, mean coldest month temperature, continentality (difference between mean January and mean July temperature), mean annual precipitation, mean growing season precipitation (May–September), the number of frost-free days, growing degree days above 5°C, and annual and summer dryness indices according to Hogg (1997). The climate variables are described in more detail by Wang et al. (2006a).

A measure of observed climate change was calculated as the difference between the 1961–1990 climate normal and the 1997–2006 decadal average, which corresponds to the period when trees were grown in the reciprocal transplant experiment (described in *Reciprocal transplant experiments*). Climate projections for the sample sites for the 2020s, 2050s, and 2080s were generated by overlaying projections from general circulation models expressed as difference from the 1961–1990 normal

period. We used 18 future projections based on four major SRES emission and population growth scenario families (A1FI, A2, B1, B2) (IPCC 2000) and implementations of these scenarios by five modeling groups (CGCM2, Canada; HADCM3, UK; ECHAM4, Europe; CSIRO2, Australia; and PCM, United States). Two model–scenario combinations were not available (ECHAM4-A1FI and ECHAM4-B1). The difference between the 1961–1990 climate normal and the 1997–2006 average can further be interpreted as observed climate change over a 25-year period (ca. 1975–2000) and was used for predictive habitat modeling in the same way as projections from general circulation models (Mbogga et al. 2009).

All grid manipulations of climate data, lapse rate elevation adjustments, data extraction from grids for sample locations, overlays of historical anomalies and climate projections just described were carried out with a custom software application that we make freely available. The database and software for western Canada has been released (Mbogga et al. 2009), while an extension of this database to western North America is available online as a beta version (T. Wang, A. Hamann, D. L. Spittlehouse, and T. Murdock, *unpublished manuscript; available online*).²

Predictive habitat modeling

For projections of aspen habitat and aspen seed zones that represent locally adapted aspen populations, we use an ecosystem-based bioclimate envelope modeling technique developed by Hamann and Wang (2006) and Mbogga et al. (2010). Predictions were carried out with classification trees implemented by the RandomForest software package (Breiman 2001, Cutler et al. 2007) for the R programming environment (R Development Core Team 2008). RandomForest grows multiple classification trees from bootstrap samples of the training data and determines the predicted class by majority vote over all classification trees. As the dependent ecosystem class variable we used the finest available ecosystem delineations for western Canada and the United States. For British Columbia we use the Biogeoclimatic Ecological Classification system version 4 (Meidinger and Pojar 1991); for Alberta, we use the Natural Regions and Subregions System, 2005 release (NRC 2006); the National Ecological Framework for Canada was used for Saskatchewan and Manitoba (Selby and Santry 1996); and the United States Ecoregion System was used for the area west of 100° longitude and north of 42° latitude (EPA 2007). In total, 771 mapped ecosystems were rasterized at 1-km resolution, and 100 of the resulting grid cells were randomly sampled from each ecosystem to characterize its climatic envelope for subsequent modeling.

² (<http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html>)

TABLE 1. Regional climatology of five ecological regions based on 1961–1990 normal data, with observed climate change over the last 25 years in parentheses.

Climate variable	Acronym	Aspen Parkland	Foothills	Boreal Plains	Northern Boreal	Taiga Plains
Mean annual temperature (°C)	MAT	1.9 (+0.8)	1.9 (+0.8)	0.5 (+1.1)	−0.6 (+1.1)	−2.5 (+1.4)
Mean July temperature (°C)	MWMT	17.5 (+0.3)	13.9 (+0.4)	16.5 (+0.6)	15.4 (+0.6)	15.6 (+0.8)
Mean January temperature (°C)	MCMT	−16.7 (+1.9)	−11.5 (+1.8)	−18.7 (+2.0)	−20.2 (+1.9)	−23.9 (+2.4)
Temperature difference (°C)	TD	34.2 (−1.6)	25.4 (−1.4)	35.2 (−1.4)	35.6 (−1.3)	39.5 (−1.6)
Mean annual precipitation (mm)	MAP	437 (−3%)	620 (−5%)	472 (−6%)	454 (−9%)	392 (−7%)
Mean summer precipitation (mm)	MSP	294 (−1.6%)	395 (−4%)	316 (−4%)	284 (−5%)	238 (+0.2%)
Precipitation as snow (mm)	PAS	106 (−12%)	183 (−13%)	127 (−13%)	145 (−17%)	144 (−16%)
Annual heat–moisture index	AHM	27.4 (+2.9)	19.5 (+2.5)	22.3 (+3.9)	20.8 (+4.9)	19.3 (+5.5)
Summer heat–moisture index	SHM	60.1 (+1.9)	35.7 (+2.6)	52.8 (+3.8)	55.9 (+4.9)	67.8 (+3.0)
Chilling degree-days below 0°C	DD0	1776 (−290)	1289 (−252)	2049 (−346)	2233 (−375)	2778 (−466)
Growing degree-days above 5°C	DD5	1519 (+12)	1028 (+26)	1333 (+479)	1177 (+30)	1129 (+41)
Number of frost-free days	NFFD	164 (−1.0)	144 (+0.4)	156 (+0.1)	148 (+0.1)	142 (+1.5)
Frost-free period (days)	FFP	107 (−0.4)	79 (+1.5)	97 (+2.8)	87 (+2.6)	83 (+4.3)
Extreme minimum temperature	EMT (°C)	−47.4 (+1.2)	−44.2 (+1.9)	−48.4 (+1.0)	−48.6 (+0.8)	−49.6 (+0.6)

Notes: Observed change is calculated as the difference between the 1961–1990 reference period and the 1997–2006 decadal average. Ecological regions are shown as maps in Fig. 1, except the Aspen Parkland which is located south of the Boreal Plains.

An ecosystem-based climate envelope modeling approach has some disadvantages. For example, spatial autocorrelations in the ecosystem response variables require a different approach to model validation (Hamann and Wang 2006), and community-based modeling methods may restrict individualistic species response to climate change (Baselga and Araujo 2009). However, there are also important advantages to the approach: species frequencies (in addition to probability of presence) can be inferred by replacing the ecosystems modeling units with known species frequencies (Hamann and Wang 2006), and crucially, we can aggregate modeling units into higher hierarchical groups that represent similarly adapted genotypes. Although accounting for within-species genetic structure in bioclimate envelope modeling has previously been proposed (e.g., Botkin et al. 2007), to our knowledge this is the first study that implements this idea. A final practical advantage is that the ecosystem modeling units are also the framework for current natural resource management prescriptions, and model projections can therefore be directly linked to a set of applicable management practices under anticipated future climates.

RESULTS

Regional climatology and climate change

For subsequent interpretation of experimental, empirical, and modeling results, it is instructive to examine the climatology of western Canada. The foothills ecosystem (Table 1, Fig. 1) stands out, with higher precipitation and a more maritime climate (cooler summers and warmer winters) than all other zones. For the rest of the study area we find a latitudinal temperature gradient and a unimodal precipitation gradient that has a maximum at ~56°N latitude, corresponding to the summer position of the polar jet stream storm track that defines the climatology of the Boreal Plains region (Alberta Environment 2005).

Precipitation declines both toward the northern boreal ecosystems and the aspen parklands in the south.

The average climate during the decade 1997–2006 when trees of the reciprocal transplant experiment were grown in the field is substantially warmer and drier than the 1961–1990 reference period (Table 1). Temperature increases were more pronounced in the north (+1.4°C) than in the south (+0.8°C), with more warming in winter than in summer temperatures. Observed temperature trends approximately correspond to patterns described in the IPCC fourth assessment report (IPCC 2007) and also match regional climate change projections by general circulation models for the 2020s in direction and magnitude (Table 2). In contrast, observed precipitation trends are opposite in direction to projections by most general circulation models. The trend toward drier climate conditions was more pronounced in winter, and together with warmer winter temperatures have resulted in major reductions in precipitation as snow (Table 1).

Taking climate trends observed over the last 25 years into account, the Boreal Plains for the 1997–2006 period (MAT = 1.6, MAP = 444) starts to resemble the 1961–1990 climatology of the Aspen Parkland. The Northern Boreal zone under the 1997–2006 period is very dry, but does not reach the 1961–1990 temperature values of the Aspen Parkland. Similarly, the Taiga Plains under the 1997–2006 period, does not reach the temperature values of the current Northern Boreal zone, but exceeds it in dryness. This implies a general north shift of climatically defined habitat conditions for a recent 10-year period, which is driven by reduced precipitation and increased temperatures.

Genetic differentiation and adaptational lag

Growth of aspen provenances that have been subjected to assisted migration in a reciprocal transplant experiment indicate an apparent adaptational lag (Fig. 1). Provenances from the Taiga region in northeast British Columbia (color code: olive) perform poorly

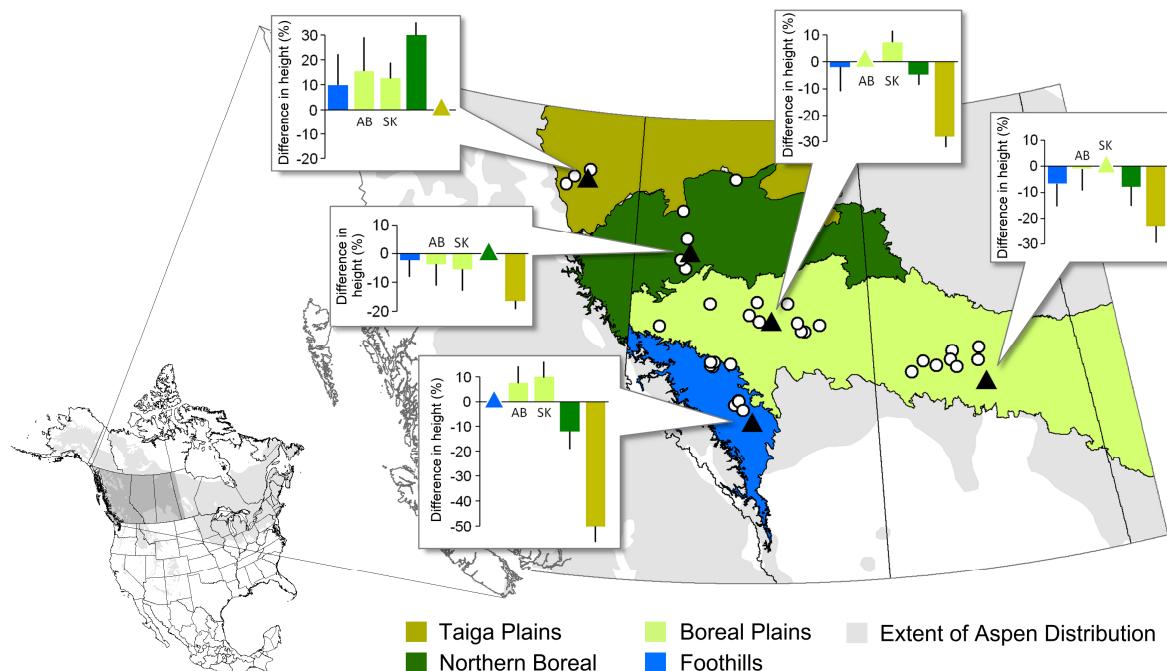


FIG. 1. Bar charts show height of transferred provenances expressed as percentages relative to the local sources from the vicinity of five test sites (solid triangles). Seeds from locations throughout the study area (open circles) were grown in a common garden environment to reveal genetic differences. Within-region variation among provenances is indicated by error bars showing +SD. AB represents seed sources in Alberta; SK represents Saskatchewan.

when transferred south, with the relatively lowest height growth at the most southern test site (33). The group of five provenances from northern Alberta (dark green) performs somewhat more poorly than local sources at the southern test sites (33, 60, 90), but is the relatively best performer when transferred to the most northern test site (70). The remaining provenances from the Boreal Plains region of central Alberta and Saskatchewan (light green) and the Foothills (blue) show similar growth across all test sites. They outperform the local sources when transferred to the most

northern test site (70), but they are slightly inferior to the local sources when transferred to the Northern Boreal test site (10). The Rocky Mountain Foothills provenances are weakly distinguished from Boreal Plains provenances by lower performance at several test locations, including their local test site (33).

The probabilities of provenance groups matching or exceeding the local sources following an assisted migration treatment are listed in Table 3. The probability values reflect both the magnitude of the provenance transfer effect and the sample size for each region (i.e., it

TABLE 2. Range of 18 regional climate change projections from five general circulation models (CGCM2, HADCM3, ECAHM4, CSIRO2, and PCM) implementing four SRES emission scenarios (A1FI, A2, B1, and B2) (IPCC 2000).

Period and climate variable	Foothills	Boreal Plains	Northern Boreal	Taiga Plains
2020s				
Mean annual temperature (°C)	+0.5 to +1.9	+0.6 to +2.0	+0.5 to +2.1	+0.6 to +2.1
Mean annual precipitation (%)	+0.3 to +3.2	-0.2 to +3.1	-0.4 to +3.9	-0.1 to +4.2
Summer heat-moisture index	+1.6 to +5.6	+1.0 to +6.0	-0.9 to +5.5	-2.2 to +5.8
2050s				
Mean annual temperature (°C)	+1.0 to +3.1	+1.2 to +3.8	+1.1 to +3.4	+1.3 to +3.6
Mean annual precipitation (%)	+0.5 to +5.8	-0.4 to +5.1	-0.7 to +6.4	-0.3 to +6.9
Summer heat-moisture index	+2.7 to +13.7	+1.9 to +14.5	-0.6 to +13.2	-3.2 to +13.7
2080s				
Mean annual temperature (°C)	+1.5 to +5.3	+1.8 to +6.4	+1.9 to +5.6	+1.4 to +5.9
Mean annual precipitation (%)	+0.8 to +9.6	-0.8 to +7.5	-1.4 to +11	-13 to +11.6
Summer heat-moisture index	+3.5 to +24	+2.0 to +25	+0.7 to +22	-2.6 to +22.4

Notes: Projected changes are expressed relative to the 1961–1990 reference period. Ecological regions are shown as maps in Fig. 1.

TABLE 3. Probability of matching or exceeding the performance of local provenances.

Transferred to:	Taiga Plains	Northern Boreal	Boreal Plains (AB)	Boreal Plains (SK)	Foothills
Site 70, Taiga Plains	...	>0.99	0.91	0.96	0.71
Site 10, Northern Boreal	<0.01	...	0.29	0.26	0.41
Site 60, Boreal Plains (AB)	<0.01	0.13	...	0.95	0.52
Site 90, Boreal Plains (SK)	<0.01	0.21	0.54	...	0.29
Site 33, Foothills	<0.01	0.26	0.74	0.91	...

Notes: The lower left section of the table represents a southward transfer, and the upper right section a northward transfer.

is essentially a confidence interval calculation). The probabilities of matching or increasing productivity relative to local sources are very pronounced for movement to and from the most northern region (Taiga, Site 70), with northward transfer very likely to be beneficial and southward movements certain to be disadvantageous. However, the results are less clear-cut for the Northern Boreal test location (Site 10). Here, a southward transfer from the region is clearly disadvantageous, but a northward transfer to the region is unlikely to have a benefit. Smaller positive effects associated with a high probability include transfers from the Boreal Plains to the Foothills and transfers from Saskatchewan to Alberta. All other probability values are intermediate, indicating either a minor transfer effect size or uncertainty due to low sample sizes.

Drought impacts on aspen populations

Remotely sensed EVI values integrated over the course of the growing season show two main areas of negative anomalies during the 2002 regional drought (Fig. 2). Within the Northern Boreal zone we find an area of reduced productivity in western Alberta that approximately corresponds to the Dry Mixedwood and Peace River Parkland ecological subregions (Fig. 2, DM indicated by dotted lines). Within the Boreal Plains of Saskatchewan and Alberta the southern fringe has negative integral and peak value anomalies (Fig. 2, DM). The negative anomalies extend further south into the Aspen Parkland ecoregion (not delineated in Fig. 2) toward the southern range limit of aspen. Another region that showed substantial negative anomalies is the eastern part of the Boreal Plains in Saskatchewan.

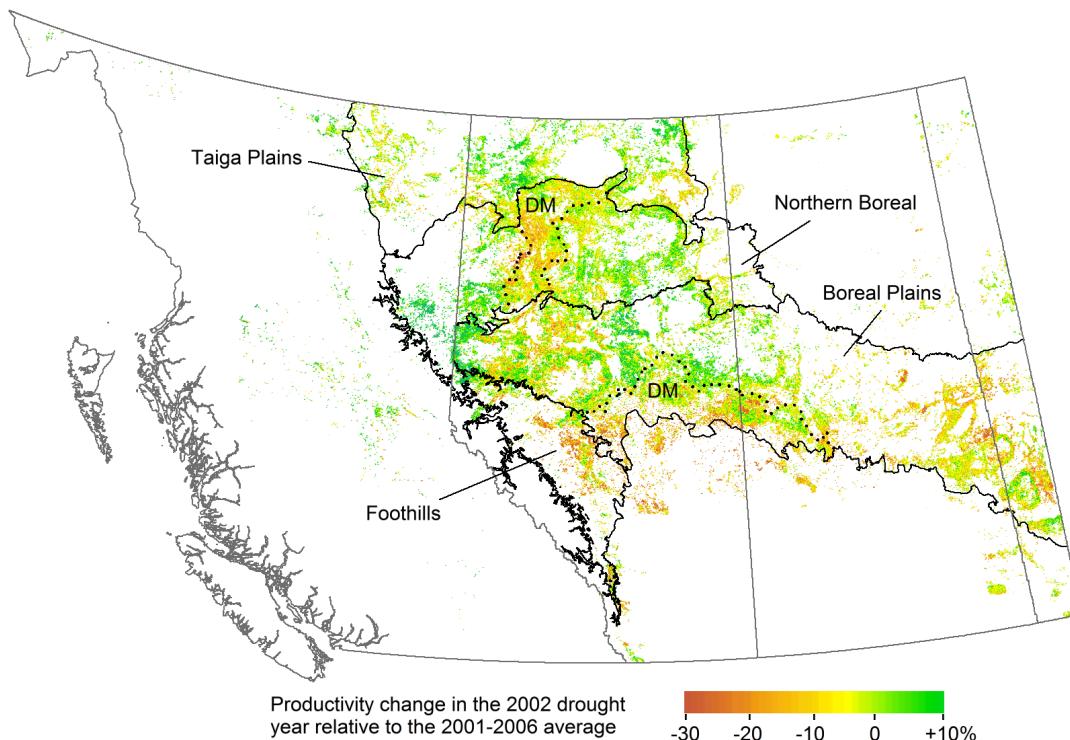


FIG. 2. Inferred productivity loss of aspen stands during a regional drought event in 2002 relative to the 2001–2006 average. The map displays the 2002 anomaly from the large integral parameter of the adaptive Savitzky–Golay function of TimeSat, fitted to 16-day interval 500-m resolution MODIS/EVI data and filtered for deciduous (aspen-dominated) grid cells. Productivity loss is pronounced in the Dry Mixedwood subregions (DM) of the Boreal Plains and Northern Boreal regions.

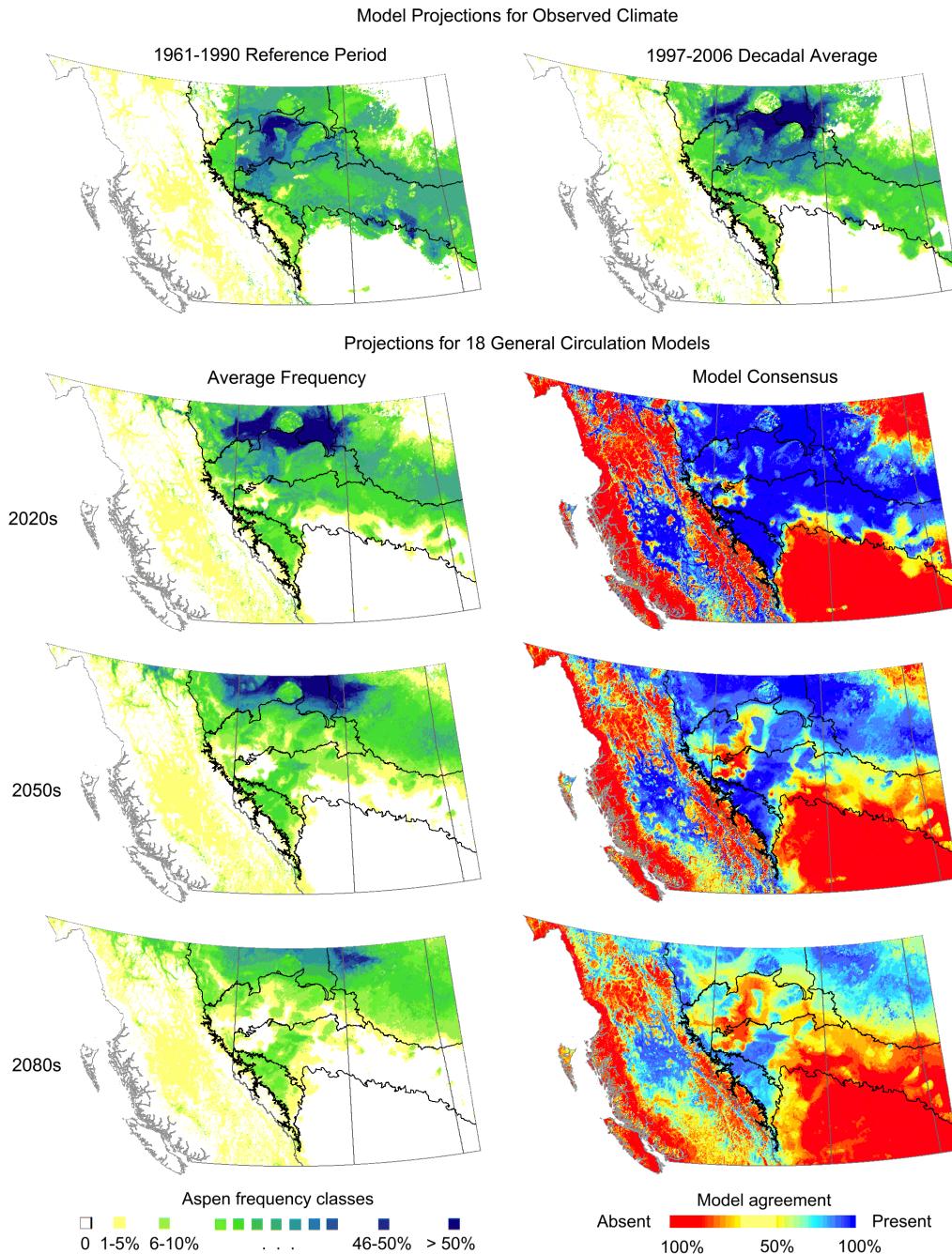


FIG. 3. Aspen frequency under baseline (1961–1990), recent decade (1997–2006), and projected future climate scenarios for the 2020s, 2050s, and 2080s time slices. General circulation model (GCM) agreement for modeled aspen frequency under future climate is also provided. Current aspen seed zones (as in Fig. 1) are included as black outlines for orientation.

Bioclimate envelope shifts

Composite results of predictive habitat models are shown in Fig. 3. Predicted species frequencies indicate where aspen is expected to be a major forest component. Counts of predicted presence or absence from multiple bioclimate envelope model projections indicate the risk (or uncertainty) of future habitat loss. Aspen is currently

most frequent in the Northern Boreal zone and the western portion of the Boreal Plains of Alberta (Fig. 3, 1961–1990). The majority of model runs, however, project a complete loss of habitat for aspen over much of this area (Fig. 3, the 2080s). In contrast, the Foothills and the Taiga Plains are projected to maintain aspen habitat. Also, moderately high aspen frequencies and

low probability of habitat loss are expected along a band across the Boreal Plains that originates in the Rocky Mountain Foothills and crosses Alberta in a northeast direction. Interestingly, projected habitat shifts for the 1997–2006 decadal average approach model projections for the 2020s quite closely. Notably, aspen appears to have already lost climatically suitable habitat along the southern fringe of its distribution (Fig. 3, 1961–1990).

In Fig. 4 we break the same projections down into climate envelopes of seed zones represented by major ecological regions (rather than into aspen frequency classes as in Fig. 3). In this case, the model consensus maps for future projections reflect confidence in seed zone recommendations. High confidence (towards 100%), means that all model runs result in the same seed zone recommendation. At the low end of confidence, 6 out of 18 model runs (~30%) project the same seed zone for a grid cell, with the remaining 12 model runs composed of various other seed zone projections. For the 2020s and the 1997–2006 average, we observed a general north shift of seed zone bioclimate envelopes by 1°–2° latitude, and for the 2020s, there is generally high confidence in seed zone projections, with areas of uncertainty restricted to boundaries between projected seed zone envelopes. For the 2050s and 2080s, we find that the Northern Boreal and Boreal Plains climate envelopes are primarily replaced by Aspen Parkland climates. However, there is a very high degree of uncertainty associated with these predictions.

DISCUSSION

Adaptational lag causes suboptimal growth

Adaptational lag refers to a mismatch of genotypes and environments, caused by a relatively fast environmental change and a comparably slow evolutionary response (Matyas 1990). Adaptational lag is not uncommon, and is in fact part of any evolutionary change through directional natural selection. Even if adaptational lag does not pose a threat to a species' overall survival, it is a concern for forest management because it can result in suboptimal growth, poor forest health, and high rates of tree mortality. Even though these impacts could be viewed as a natural part of evolutionary change, proactive climate change adaptation strategies should aim at maximizing forest health and productivity through intervention.

Adaptational lag can be detected with reciprocal transplant experiments if transferred seed sources outperform local seed sources. Given the regional climatology and observed climate trends described in Table 1, we would expect nonoptimality due to temperature changes to be most pronounced in the Taiga plains, where the warming signal was strongest (+1.4°C mean annual temperature). The expectation is that southern sources, adapted to warmer environments, outperform local provenances when transferred north. With respect to precipitation we have generally seen a trend towards drier conditions, which was most

pronounced in the Northern Boreal Plains (–9% mean annual precipitation). This means that provenance adapted to drier environments may outperform local sources when transferred to originally wetter sites that now match their conditions of origin.

Results from the reciprocal transplant experiment generally conform to these expectations. For example, local sources at the northern Taiga Plains test site were outperformed by all other provenances that were transferred north to this site (Fig. 1). The Northern Boreal provenances, which are a very good match in both temperature and precipitation for the new Taiga plains environment, outperform the local sources by a large margin (30% increase in height relative to the local Taiga Plains provenances). Conversely, a transfer of provenances southward generally leads to poor performance, e.g., Northern Boreal and Taiga provenances to any southern test site.

Transfer results with respect to changes in precipitation partially conform to expectations. For example, local Foothills sources were outperformed by Boreal Plains sources, which are adapted to drier environments (Fig. 1). However, sources from the wet Foothills ecosystem outperform local sources when transferred to the dry Taiga Plains environment. A plausible explanation arises from the fact that evolutionary fitness is not necessarily reflected by growth measured in short-term common garden trials. Some environments require survival adaptations that result in a trade-off with adaptations that maximize growth (Mangold and Libby 1978). Taiga Plains provenances likely have conservative growth strategies that may include late bud break, early bud set, and wood properties to avoid frost damage in harsh northern environments. While such damage did not occur to Foothills provenances at the Taiga Plains site during the testing period, the local provenances may still have a long-term evolutionary advantage in surviving extreme climate events. It would therefore be instructive to evaluate adaptive traits in the common garden experiments before recommending such transfers to non-matching environments.

Another example that indicates more than one climatic factor drives local adaptation of genotypes is the Northern Boreal test site. Here, local sources outperformed all introduced provenances, even though the Boreal Plains provenances would be a good match after a temperature increase of 1.1°C (Table 1). However, these sources also came from wetter environments that did not match the test site conditions with respect to precipitation. The transplant experiment did not include provenances from the dry and warm Aspen Parkland region, but we can speculate these sources could outperform local sources because they climatically match the observed 1997–2006 climate of the Northern Boreal region. This points to the potential value of other approaches to complement limited information from sample-based reciprocal transplant experiments.

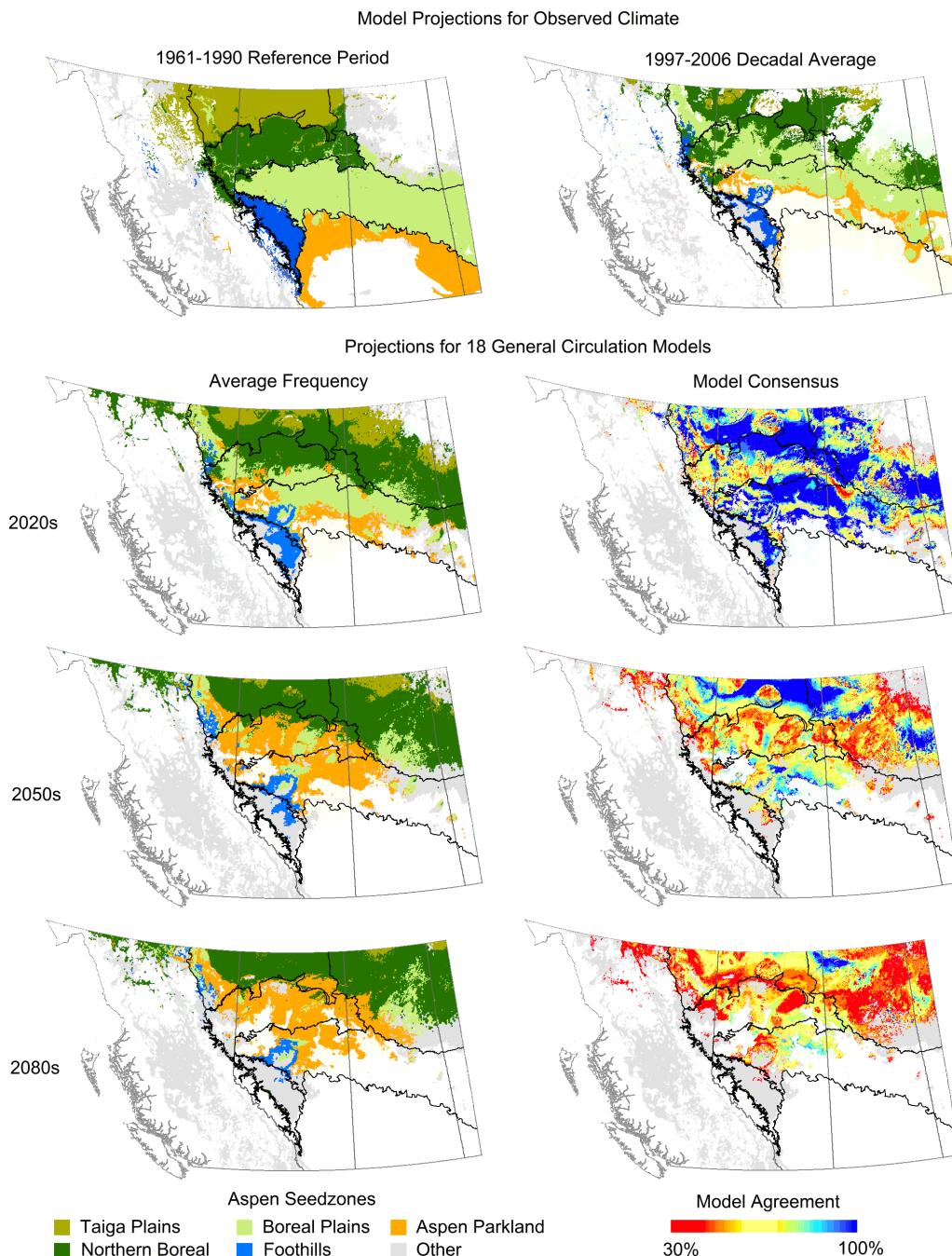


FIG. 4. Aspen seed zone climate envelope under baseline (1961–1990), recent decade (1997–2006), and future climate scenarios for the 2020s, 2050s, and 2080s, and general circulation model (GCM) consensus for predicted shifts under future climate. Current aspen seed zones (as in Fig. 1) are included as black outlines for orientation.

Indirect indicators of maladaptation

In addition to the reciprocal transplant experiment, bioclimate envelope modeling and remote sensing provide independent data that can guide assisted migration efforts. Negative anomalies in remotely sensed EVI values during a regional drought in 2002 identify two general areas where aspen populations are

vulnerable to climate change: the southern fringe of the Boreal Plains and Dry Mixedwood subregion of the Northern Boreal ecosystem (Fig. 2). Remarkably, the remotely sensed negative anomalies correspond to loss of habitat inferred from bioclimate envelope modeling (Fig. 3, 1997–2006). In addition, reduced productivity and dieback of aspen forests along the southern range

limit of aspen in Alberta and Saskatchewan has been found through field observations (Hogg et al. 2002, Hogg and Bernier 2005). For the southern fringe, the realized niche model corresponds to empirical data from fundamental niche observations (negative EVI anomalies), suggesting that the limits of the fundamental and realized niche are the same at the southern range limit of aspen.

Bioclimate envelope model projections for the 1997–2006 period did not show a loss of habitat for the Dry Mixedwood subregion of the Northern Boreal ecosystem, the second region where we observed remotely sensed negative anomalies (Fig. 2). However, substantial loss of aspen habitat is predicted in this area for the 2050s and 2080s (Fig. 3). The discrepancy among the realized niche projections for the 1997–2006 period and fundamental niche observations (reduced productivity in the northern Dry Mixedwood subregion) is not surprising. By treating species as homogenous units, bioclimate envelope models essentially allow translocation of climate envelopes within the species range from southern/low-elevation populations to northern/high-elevation locations. This is equivalent to assuming unlimited migration of genotypes within a species range, and thereby underestimating potential climate change impacts on northern and high-elevation populations (Chen et al. 2010). In Fig. 4 we visualize, for the first time, the translocation of populations by a bioclimate envelope model within a species range. The species-level model (Fig. 3) could correctly account for climate change impacts at the southern fringe, but failed to account for impacts in the dry mixedwood subregion, where habitat was maintained at the species level, but lost for the Northern Boreal genotype (Fig. 4).

Climate envelope models should guide seed transfer

Although reciprocal transplant experiments can theoretically be used to determine optimal transfer distances for seed sources (Wang et al. 2006b, O'Neill et al. 2008a), we propose that bioclimate model projections are a better and safer approach to make such inferences. Bioclimate envelope models have many limitations that have been thoroughly discussed (e.g., Hampe 2004, Araujo and Guisan 2006, Botkin et al. 2007). However, many of these limitations do not apply in a reforestation context. For example, management practices can “migrate” as rapidly as bioclimate envelope model results suggest. Also, competition and species interactions are usually controlled through spacing of plantations and choice of planting stock. Perhaps most importantly, the limitation that bioclimate envelope models project the realized niche and not the fundamental niche of tree species turns out to be an advantage in a reforestation context.

For example, consider the results of a reciprocal transplant experiment to determine growth across the fundamental niche of lodgepole pine, *Pinus contorta* (Wang et al. 2006b, O'Neill et al. 2008a). These studies

showed that the species may grow well under projected climate warming in many areas as long as there are no moisture limitations. However, warm and moist growing conditions can also lead to severe needle cast caused by the native fungus *Dothistroma pini* (Woods et al. 2005). This biotic interaction reduces the fundamental niche space of lodgepole pine to a more restricted realized niche. A judicious recommendation for reforestation under climate change should exclude warm and wet climate conditions, i.e., a conservative approach to species choice for reforestation should be guided by projections of the realized niche, not the fundamental niche. While this approach may possibly forgo some potential gains in tree growth due to climate change, it is less risky and corresponds to the widely adopted reforestation policy of not planting species outside their observed range.

Another disadvantage of using data describing the fundamental niche of tree populations from common garden trials has been mentioned before. Long-term evolutionary fitness is not necessarily reflected by growth measured in short-term common garden trials. In contrast, the realized niche inferred from distribution data should be a reasonable approximation of environmental conditions under which a species (or populations of a species) are competitive in the long term.

Recommendations for aspen

Bioclimate envelope projections at the seed zone level for the 2020s and 1997–2006 period suggest that aspen seed sources may be moved north by 1° to 2° latitude (Fig. 3). However, we do not need to change seed zone boundaries or other delineations that currently serve as framework for forest resource management. Instead we find it more useful to provide general seed source recommendations for established forest management areas or even individual planting sites. In Table 4 we list the most appropriate climatic regions where seed should be obtained for reforestation. For example, for the Alberta forest management unit NM 1.1 we can see that aspen habitat in this unit is fully maintained until the 2080s (100% of the management unit). The recommended seed source for the 1961–1990 normal period is the Taiga Plains (TP, 100% of the management unit). However, under currently observed climate and 2020s projections, 24% and 32% of this management unit is climatically best suited for seed sources from the Northern Boreal climate region.

In many instances, the recommendations for 2020 projections and the climate observed over the last decade are very similar (Table 4, Fig. 3). However it should be noted that this similarity is based on slightly different climatologies: for the recent decade, precipitation values are lower, but this is compensated by cooler temperatures compared to the 2020s projection. A relatively short-term 25-year trend in observed precipitation cannot be extrapolated into the future, and we should not make the assumption that the trend will continue.

TABLE 4. Seed transfer recommendations for Alberta's seed management units of the natural region and subregion system.

Management unit†		Aspen habitat (%)					Seed source recommendation‡		
Name	Size (km ²)	Normal	1997–2006	2020s	2050s	2080s	Normal	1997–2006	2020s
NM 1.1	23 803	100	100	100	100	100	TP(100)	TP(70), NB(24)	TP(67), NB(32)
CM 1.1	16 756	100	100	100	100	100	TP(99)	NB(98)	NB(98)
CM 1.2	12 098	100	100	100	100	100	TP(55), NB(45)	NB(94)	NB(100)
CM 2.1	12 436	100	100	100	99	74	NB(82), TP(17)	NB(70), BP(15)	NB(64), BP(35)
CM 2.2	13 849	100	100	100	98	85	NB(93)	NB(94)	BP(55), NB(42)
CM 2.3	11 036	100	100	100	100	76	NB(91)	NB(86), BP(14)	BP(53), NB(47)
CM 2.4	17 861	100	100	100	80	55	BP(53), NB(47)	BP(46), NB(41)	BP(76), AP(17)
CM 3.1	25 246	100	92	89	48	29	BP(94)	BP(70), AP(27)	BP(59), AP(41)
CM 3.2	13 015	100	74	89	90	94	BP(99)	BP(60), AP(36)	BP(60), AP(37)
CM 3.3	14 022	100	100	100	99	95	BP(96)	BP(63), AP(22)	BP(95)
CM 3.4	9928	100	100	98	94	91	BP(86)	BP(39), FH(32)	BP(47), AP(27)
DM 1.1	14 764	100	100	100	100	87	NB(78), TP(22)	NB(87), BP(13)	NB(100)
DM 1.2	17 361	99	94	79	45	17	NB(92)	NB(56), BP(31)	NB(41), AP(34)
DM 1.3	17 042	100	97	76	19	14	BP(67), NB(33)	BP(46), NB(29)	AP(84), BP(10)
DM 2.2	19 512	100	27	51	55	57	BP(96)	AP(75), BP(20)	AP(64), BP(32)
LF 1.4	7795	100	100	100	100	100	FH(88)	M(56), FH(43)	FH(83), M(14)
LF 1.5	9996	100	100	100	100	100	FH(99)	FH(85), M(15)	FH(99)
LF 2.1	6639	100	100	100	100	100	FH(98)	M(61), FH(37)	FH(87), M(13)
LF 2.2	3352	100	100	100	100	100	FH(100)	M(53), FH(46)	FH(99)
LF 2.3	2110	100	100	100	96	79	FH(100)	M(97)	FH(59), AP(35)

† Seed management units are based on the finest subdivisions of the Alberta Natural Subregion classification: NM, Northern Mixedwood; CM, Central Mixedwood; DM, Dry Mixedwood, LF, Lower Foothills.

‡ The values represent the percentage area of the management unit for which the seed source is predicted as optimal. In case of multiple recommendations, either seed source may be used. Recommended seed sources are based on major ecological regions also shown in Fig. 1, including: TP, Taiga Plains; NB, Northern Boreal; FH, Foothills; M, Montane; BP Boreal Plains; and AP, Aspen Parkland.

Nevertheless, from an applied perspective, the combined information from GCM projections, climate trends that have apparently materialized, and observed biological response make a strong case for implementing adaptation strategies in the southern fringe of the Boreal Plains, and the Dry Mixedwoods of the Northern Boreal region. Reforestation programs should rely on more drought-tolerant species or genotypes in the future, and aspen forestry should concentrate on the moister and more northern ecosystems.

Reforestation with aspen genotypes other than the local sources requires some confidence in the projections of which genotype should be used. Model consensus for seed zones is generally high for the 2020s, but shows dramatic reductions toward the 2050s and 2080s (Fig. 4). Does this suggest that we should develop relatively “short-sighted” adaptation strategies, i.e., focus on the 2020s projection and dismiss longer-term projections as too uncertain for practical resource management? We think the answer to this question is “Yes.” Despite consideration of their long lifetime, it is important to realize that the most vulnerable phase of trees remains their seedling and sapling stage. In a changing environment, we should not focus on optimizing planting stock for maximum growth during midrotation, when this means that seedlings planted today will not survive because climate conditions predicted for the 2050s have yet to materialize. The high degree of uncertainty in longer-term climate projections is an additional argument to develop adaptation strategies for the immediate future with a 10–20 year planning horizon.

While there is a high degree of uncertainty in determining optimal seed sources for deployment by the 2050s and 2080s, we recognize that applied tree improvement programs regularly have planning horizons of several decades or even a century. What can be recommended with respect to developing long-term breeding programs and establishment of seed- and cutting orchards for improved aspen planting stock? It certainly appears that there will be limited future demand for aspen planting stock that is adapted to moist environments of the Rocky Mountain Foothills ecosystems and the adjacent Boreal Plains zone (Fig. 4, blue and light green). These areas, which currently receive relatively high summer precipitation, are predicted to be more suitable for genotypes adapted to warmer and drier growing conditions by the 2050s and 2080s (Fig. 4, orange). At the same time the climate envelope of the current Foothills and Boreal Plains regions are predicted to largely disappear from the study area. A breeding program or seed zone corresponding to the parkland ecoregion (Fig. 4, orange) currently does not exist, and we think that the establishment of a tree improvement programs with genotypes from this region would be a worthwhile consideration.

CONCLUSIONS

In this paper we advocate assisted migration prescriptions for common tree species to address climate change within a framework of normal reforestation programs. However, patterns of adaptive genetic variation and response to environmental change can be quite species-

specific in trees, and we think that generic and ad hoc assisted migration efforts should be avoided. A moderate research effort is required to determine if assisted migration is necessary and how it should be implemented.

To develop dependable, species-specific guidelines for assisted migration we may draw on information from a variety of data sources and use independent modeling, experimental, and empirical research approaches. In a case study for aspen, we examined adaptational lag in a transplant experiment, in situ productivity anomalies through remote sensing, and population-specific habitat projections from bioclimate envelope models. Additional research approaches may be useful to develop population-specific prescriptions. For example, dendroclimatology approaches can be used to identify tree populations vulnerable to climate change. Monitoring problems such as failure of plantation establishment or pest and disease outbreaks can provide additional information where the risk of inaction likely exceeds the risk associated with changing established management practices.

To end on a positive note, we also would like to point out that for northern regions, climate change may be associated with opportunities as much as challenges to forest resource management. Results from the reciprocal transplant experiment suggest that major gains in productivity could be achieved by matching genotypes to new environmental conditions through assisted migration, arguably exceeding projected gains from current genetic tree improvement programs.

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