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Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Reforestation

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ABSTRACT

Impacts of climate change on the climatic niche of the sub-specific varieties of *Pinus ponderosa* and *Pseudotsuga menziesii* and on the adaptedness of their populations are considered from the viewpoint of reforestation. In using climate projections from an ensemble of 17 general circulation models targeting the decade surrounding 2060, our analyses suggest that a portion of the lands occupied today primarily by coastal varieties of each species contain genotypes that should remain suitable for the future climate. A much larger portion, particularly for varieties occupying inland sites, should require either introduction of better suited species or conversion to better adapted genotypes. Regeneration strategies are considered with the goal of matching growth potential of contemporary populations to the future climate where that potential can be realized. For some lands, natural reproduction should be suitable, but most lands will require forest renewal to maintain forest health, growth, and productivity. Projected impacts also illustrate the urgent need for conservation programs for *P. menziesii* in Mexico.

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1. Introduction

Climate affects the distribution of species and molds adaptation of populations within species. Climate change, therefore, will impact land management objectives and procedures. Yet, targeting future climates currently moving along uncertain trajectories presents unprecedented challenges to managers, particularly when dealing with long-lived organisms. This paper is the third in a series dealing with plant-climate relationships for the sub-specific varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*. The first of the series, PART 1 (Comparative Genetic Responses to Climate for the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Realized Climate Niches, this issue), considered the realized climate niche, and the second, PART 2 (Comparative Genetic Responses to Climate in the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Clines in Growth Potential, this issue) addressed the clines in growth potential that occur within varieties. Both papers used future climate projections to assess potential impacts of climate change on these two widespread species. Herein we focus on impacts from the viewpoint of reforestation strategies and procedures.

Ample literature demonstrates that in time, directional shifts in climate will result in deterioration of growth, health and survival in forest ecosystems (e.g., Leites et al., 2012a,b). Climate-induced impacts are currently in evidence, and numerous analyses of potential impacts unanimously portend widespread disruption of forest ecosystems over the course of the current century. We state in PART 2: “Although little is known about the rates of demise as trees become maladapted, provenance testing has repeatedly demonstrated the process: loss of productivity, increased environmental stress, and mortality from numerous potential agents.” To managers, this may mean that operations such as salvage will rise toward the forefront, but our focus is on reforestation: the species,

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populations and genotypes to become established for the new generation.

In this paper, we synthesize the results of PART 1 and PART 2 to illustrate approaches for identifying contemporary sources of seeds having reasonable chances of being suited to forest landscapes of the future. While management strategies and options become more complex in a changing climate (see Millar et al., 2007), the underlying goal of reforestation should remain the same, that is, to optimize forest health, growth, and productivity by assuring that new generations are genetically suited to their environment. This goal is imbedded in the seed deployment strategies that are in use today.

For reference, the contemporary distribution of the varieties of these two species is illustrated in Fig. 1 where data points recording taxa occurrence (see PART 1) are mapped. Climatypes (PART 2) refer to climatic ecotypes of Turesson (1925) which, in our case, are delineated by classifying continuous genetic variation in growth potential within varieties. The classification considers the steepness of the cline and variation within populations such that individuals and populations within climatypes should be adaptively similar. Impacts from climate change are commonly viewed as occurring at the trailing edge where habitat is being lost and at the leading edge where new habitat is emerging. The area between the edges is commonly viewed as being stable with regard to the persistence of the contemporary inhabitants. In our work, projected impacts are based on output of an ensemble of 17 general circulation models (GCM) centering on the decade surrounding 2060 (see PART 1).

Central to our discussion of responses to the changing climate is the concept of *phenotypic plasticity*. We adopt the succinct presentation of Mátyás et al. (2010) who noted that the term originated with zoologists for describing an ability of individual genotypes to produce alternative phenotypes in disparate environments (see DeWitt and Scheiner, 2004). Bradshaw (1955), however, warned that in plants, plasticity should be interpreted in a broader context. The definition Mátyás employs was derived from the collective experience of plant breeders: phenotypic plasticity is the ability of the genotype or the population to maintain high fitness across a range of environments (also see Mátyás, 2007). The relative steepness of clines or the breadth of climatypes (PART 2) is indicative of the strength of local adaptation on the one hand and plasticity on the other as alternative mechanisms for accommodating environmental heterogeneity. If one views phenotypic plasticity as the ability of a genotype to express a different phenotype under different environmental conditions without considering fitness (e.g. Franks et al., 2013), then plastic and maladaptive responses are hopelessly confused.

2. Climate change impacts

2.1. Short- and long-term responses to climate change

Responses to a changing climate can be viewed as (a) short-term plastic responses that accrue in endemic populations as physiological systems adjust to change, and (b) as long-term evolutionary responses that realign genetic variation with environmental diversity (see Rehfeldt et al., 2004). Both responses are unquestionably occurring today (Franks et al., 2013). Immediate short-term responses draw on the innate plasticity that allows forest trees to endure temporal environmental variation during their long lives. Yet, as unequivocally demonstrated by provenance testing (see PART 2), plastic responses are limited to a finite range of environmental variability; exposure to climates beyond these limits will produce maladaptive effects, commonly involving dieback and mortality. Provenance tests also have demonstrated for

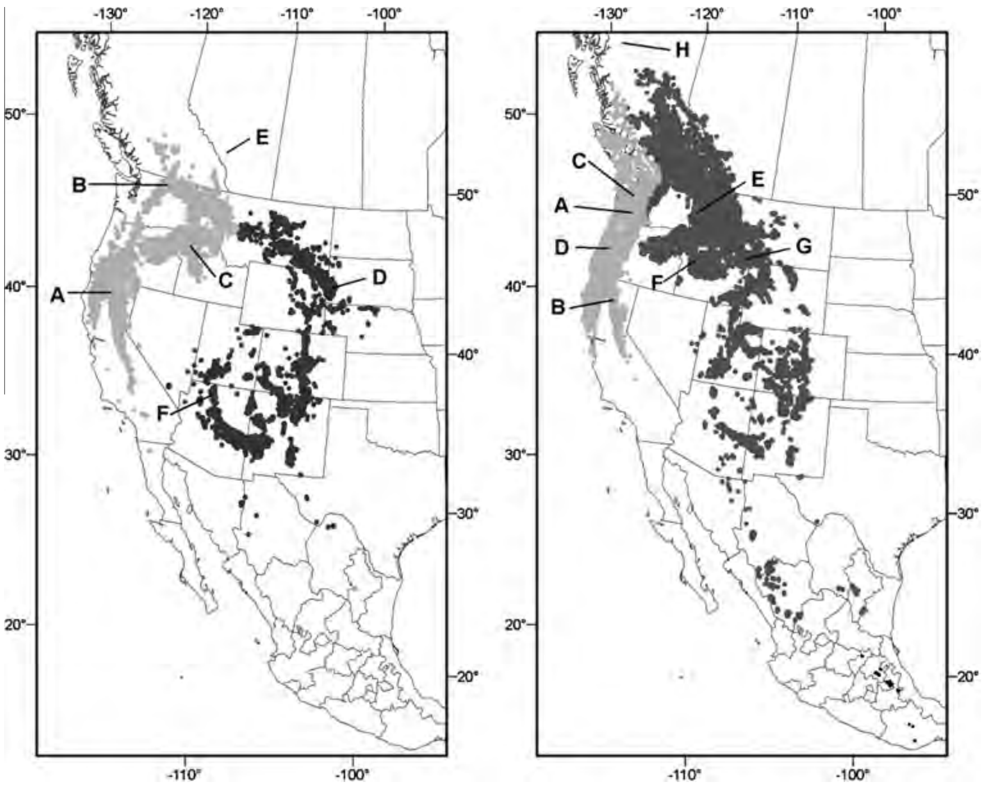

Fig. 1. Location of ground plots containing *Pinus ponderosa* (left) var. *ponderosa* (light gray) and var. *scopulorum* (dark gray) and *Pseudotsuga menziesii* (right) var. *menziesii* (light gray), var. *glauca* (dark gray), and the unnamed Mexican variety (black). Ground plots were used to construct the climate profile models (PART 1). Letters identify map locations enlarged in Figs. 5 and 6.

numerous species in North America (Mátýas and Yeatman, 1992; Rehfeldt et al., 1999, 2001; Leites et al., 2012a, b) and Eurasia (Rehfeldt et al., 2002, 2003) that populations tend to occur in climates that are cooler than where they exhibit optimal growth, but that the degree of suboptimality is greater toward the leading edge than at the trailing edge. Consequently, plasticity should be less capable of accommodating change on the trailing edge (Mátyás, 2007); impacts should occur first and be the strongest at the trailing edge (see Czúcz et al., 2011); and rates of forest demise should be greatest at the trailing edge (see Worrall et al., 2013). Nonetheless, continued directional changes eventually will result in maladaptation everywhere (see Leites et al., 2012a,b); phenotypic plasticity can only delay its expression.

When plastic responses are no longer able to buffer physiological processes against environmental variability, maladaption leads toward mortality. While rates of demise from maladaptation are problematic, responses to climate change eventually will invoke the evolutionary processes for redistributing genotypes across the new mosaic of heterogeneous environments (see Davis and Shaw, 2001; Davis et al., 2005; Jump and Peñuelas, 2005). Yet, because adaptedness of forest tree species is most commonly conveyed through the adaptation of populations along climatic gradients, the primary role of the evolutionary processes will be to re-establish a semblance of equilibrium between genetic variation and environmental heterogeneity, that is, maintenance of the clines.

2.2. Projected impacts to *P. ponderosa* and *P. menziesii*

Statistics summarizing projected impacts of climate change on the varieties of *P. ponderosa* and *P. menziesii* are compiled in Table 1 from the maps of Figs. 5–7 of PART 1 (Comparative Genetic Responses to Climate for the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Realized Climate Niches, this issue) and Figs. 3 and 4 of PART 2 (Comparative Genetic Responses to Climate in the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Clines in Growth Potential, this issue). These impacts accrue from the change in those climate variables governing the distribution of species and from those variables that have molded the clines within varieties. Because limits of distribution and climatic clines are controlled by different sets of climate variables, they will act together to determine the total impact on the varieties of these species. Contributing to the disparate impacts of Table 1 is cline steepness which varies between species and varieties within species. As presented and discussed in PART 2, clines tend to be steeper, that is, evidence of stronger local adaptation, in the varieties of *P. menziesii* than those in *P. ponderosa* and in inland varieties rather than coastal varieties.

2.2.1. Contemporary niche space

Potential impacts portend large but disparate consequences to the climatic niche (Table 1). By 2060, the area climatically suited to *P. p* var. *ponderosa* is projected to be 14% smaller than it is today. At the trailing edge, nearly 45% of the contemporary niche is projected to be climates in which this taxon does not occur today. This means that 55% of the area now inhabited should continue to be suitable for this taxon through 2060. While severe, these impacts on *P. p* var. *ponderosa* are considerably less than those for *P. p.* var. *scopulorum*. For the latter, suitable climate space in 2060 should be only one-half that of today, with 77% of the contemporary niche space being lost at the trailing edge. In neither variety would gains at the leading edge offset the losses at the trailing edge, but this is especially so in var. *scopulorum*.

Projected impacts for the varieties of *P. menziesii* are moderate in var. *menziesii*, severe in var. *glauca,* and dire in Mexico's unnamed southernmost variety (Table 1). For var. *menziesii,* 82% of the current niche should remain suitable through 2060. Losses at the trailing edge should be offset by gains at the leading edge such that the climatically suitable area in 2060 should be about the same as today. For var. *glauca*, niche area of the future should be only slightly smaller than that of today, but only because large gains at the leading edge would tend to offset the 35% loss at the trailing edge. This would mean that 65% of the contemporary niche should remain climatically suitable through 2060. For the variety of southern Mexico, however, 98% of the contemporary climate niche is projected to be lost, but little new niche space would be added. Area of the climatic niche would be reduced by 94%.

The statistics of Table 1 are clearly suggestive of widespread changes in the distribution of the species and their varieties. A high proportion of today's climatic niche is projected to have future climates in which these taxa do not occur today. Although rates of demise, mortality, and disturbance are problematic, the implication is that these lands will be occupied eventually by species other than *P. ponderosa* and *P. menziesii.*

2.2.2. Niche space of 2060

The statistics of Table 1 shows for *P. p.* var. *ponderosa* that 64% of the 2060 climate niche should be a remnant of today's climatic niche, that is, the area where the taxa would persist. That means 36% of the future distribution would result from immigration at the leading edge. However, in the area where this variety should be persistent, only 39% of the future area is inhabited today by a climatype expected to be suitable for the 2060 climate. Together, these statistics would mean that only 25% of the future niche space is inhabited today by a suitable climatype. If var. *ponderosa* is to fully occupy its 2060 climatic niche with individuals that approach the level of adaptedness that we see today, an unfathomable 75% of the future distribution would need conversion to either or both species and climatypes different from those living there today. Comparable statistics for the other taxa are equally incredible. For *P. m.* var. *glauca*, for instance, the taxon with the steepest clines (Table 4, PART 2 (Comparative Genetic Responses to Climate in the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Clines in

Table 1
Statistics describing projected impacts of climate change on the area of contemporary and 2060 niche space for two varieties of *Pinus ponderosa* and three varieties of *Pseudotsuga menziesii* according to an ensemble of 17 general circulation models.

Taxon	Contemporary niche space				2060 Niche space		
	Grid cells[a] (thousands)	Change between 2060 and present (%)	Lost by 2060 (%)	Remaining suitable through 2060 (%)	Remaining suitable from today (%)	Emergent habitat (%)	Current climatype suitable through 2060 (%)
Pinus ponderosa							
var. *ponderosa*	455	−14	45	55	64	36	25
var. *scopulorum*	215	−50	77	23	47	53	8
Pseudotsuga menziesii							
var. *menziesii*	387	0	18	82	82	18	58
var. *glauca*	889	−5	35	65	68	32	1
Mexican	3	−94	98	2	38	62	–

[a] 0.0083° resolution.

Growth Potential, this issue)), 99% of the future forest area would require conversion to either or both the proper variety or adapted genotypes. For *P. m.* var. *menziesii*, the least impacted taxon, conversion would still be required on 42% of the future landscapes. Comparable statistics for the variety of *P. menziesii* in southern Mexico are meaningless because projected impacts are so dire (Table 1) that conservation would be the only practical recourse (see PART 2).

The statistics of Table 1 convey new insight for the concept of species persistence during climate change. While the area between leading and trailing edges may be remaining climatically suited for a species as a whole, the adaptedness of populations within the area can be in turmoil nonetheless. Assessing impacts of climate change to the vegetation are only rudimentary if genetic considerations are not taken into account.

Having high proportions of the 2060 climatic niche being inhabited today with species and populations not expected to be suited to the future climate portends enormous challenges for land managers, if healthy, productive forests are to be maintained. The extent of the challenge is illustrated in Figs. 2 and 3. These figures show the projected 2060 climatic niche (PART 1) for the two varieties of *P. ponderosa* and the two northernmost varieties of *P. menziesii*. The darkest shades show the area for which the contemporary climatype should remain suitable for the 2060 climate. The brightest shades color the area for which the contemporary taxon should still be suited in the 2060 climate but the contemporary climatype would be unsuitable; these lands, therefore, would need conversion to a proper climatype. The lightest colors map new niche space into which is needed either immigration from proximal populations or introduction.

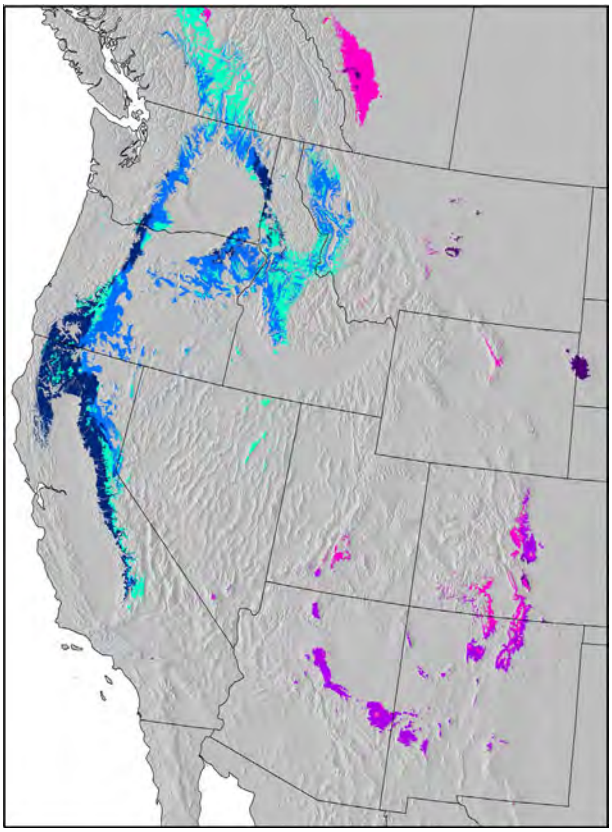

Fig. 2. Projected 2060 climate niche for two varieties of *Pinus ponderosa*. Blue colorpath, var. *ponderosa*; magenta colorpath, var. *scopulorum*. Darkest tones, current climatype suitable for 2060 climate; medium tones, current climatype unsuited for future climate; lightest tones, emergent habitat.

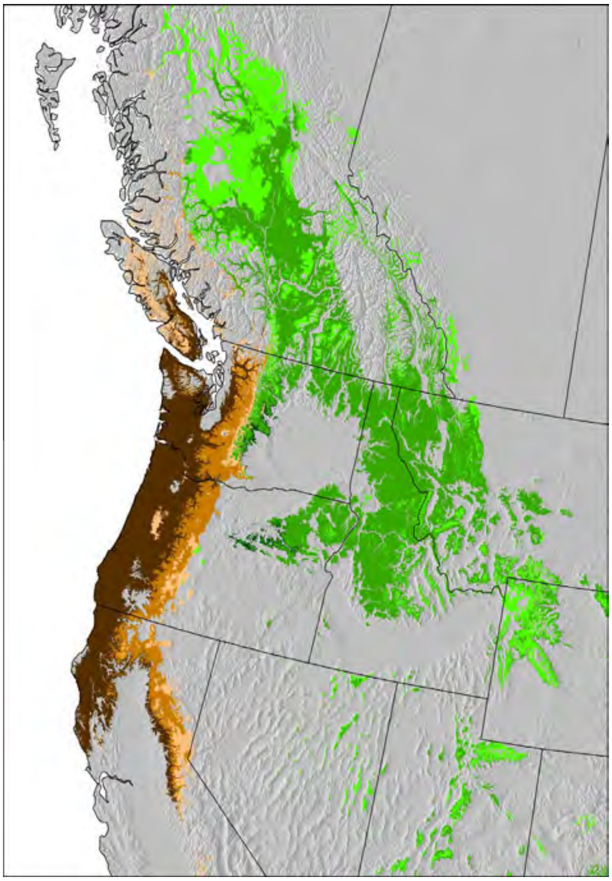

Fig. 3. Projected 2060 climatic niche for two varieties of *Pseudotsuga menziesii*. Brown colorpath, var. *menziesii*; green colorpath, var. *glauca*. Darkest tones, current climatype suitable for 2060 climate; medium tones, current climatype unsuited for future climate; lightest tone, emergent habitat.

The maps (Figs. 2 and 3) illustrate that land managers in the coastal ranges and low elevations of the Sierra Nevada and Cascade Range would face the least challenge, largely because the contemporary inhabitants should still be adapted to the 2060 climate. Yet, at the middle and higher elevations in these same mountains, conversion to better adapted climatypes would be appropriate. In the interior West, however, potential impacts are astounding; few contemporary populations would be suited genetically for the future climates at sites where they occur today; nearly all of the persistent niche space would require climatype conversion for adaptedness to be maintained.

2.3. Reforestation options and strategies

Regeneration options available to managers center on the statistics of Table 1. To us, the future area projected to have either maladapted genotypes or inappropriate species is staggering. For western North American landscapes as a whole, moreover, there is little reason to believe that these projections for *P. ponderosa* and *P. menziesii* are anomalous (see Rehfeldt et al., 2012). The magnitude of climate change impacts portends catastrophic ecological disruption on range-wide scales. Managers obviously will not be able to avert the ecological consequences across the entire landscape. In most jurisdictions, therefore, natural reproduction by default will be the most widespread approach to landscape management and forest renewal. While this option may be fitting for those lands inhabited today by climatypes suited for the future climate, the contingencies of seed production, seed dispersal (see

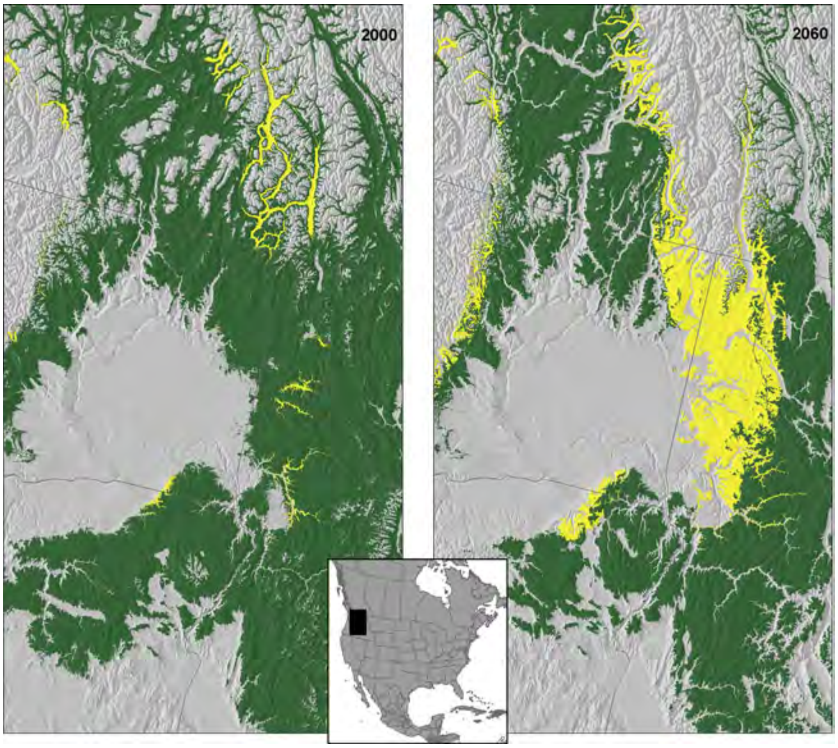

Fig. 4. Climatype of *Pseudotsuga menziesii* var. *glauca* (yellow) today (left) and projected for the decade surrounding 2060 (right) within the predicted (left) and projected (right) climate niche (dark green).

Clark et al., 1998; Solomon and Kirilenko, 1997; Davis, 1989), and seedling establishment make immigration on the leading edge problematic, particularly with timeliness and optimal stocking. Likewise, natural reproduction followed by natural selection likely will require multiple generations to convert maladapted climatypes into ones suited to the new climates within the area of persistence (see Rehfeldt et al., 1999, 2001, 2002, 2004). Phenotypic plasticity can be effective only in the short term, as directional shifts in climate will eventually outstrip the plastic capacity of individual genotypes (see Leites et al., 2012a, b). Whether natural systems can provide the amenities humans expect from forested lands within an acceptable time frame is questionable.

The need for comprehensive artificial reforestation programs seems unequivocal. At the trailing edge, conversion of species should be the management objective; at the leading edge, rapid colonization of emergent habitat. Fostering adaptation within the climate niche with shortened intervals of forest renewal can be accomplished only with iterative shifts in seed transfer guidelines as a foundation for widespread artificial reforestation. Yet, programs of extraordinary scope would be needed to rehabilitate all those lands Table 1 would suggest as being in need. Managers obviously will be faced with difficult decisions in setting priorities regarding goals and species. Yet, as advocated by McLachlan et al. (2007), the time is ripe for policies to be established and implemented.

The intent of our modeling (PARTS 1 and 2) was to provide managers avenues for informed actions on two fronts. The first concerns the conservation of genetic diversity of species and climatypes before impending crises make action problematic, that is, while enough healthy trees exist for producing a sufficient number of outcrossed seeds for stocking seed banks. The second concerns the reforestation guidelines needed to accommodate the changing climate such that ecosystem resilience and productivity can be maintained. Natural reproduction, despite problematic timeliness and stocking, might be suitable for lands inhabited today by climatypes suited for the future climates (see also Kremer et al., 2012). Artificial reforestation is particularly suited for introductions into emergent habitat, conversion of maladapted climatypes into productive forests, and conservation programs. Regardless, management objectives concentrating on the maintenance of forest health, wood production, or conservation are likely to emerge at the forefront over those addressing road networks, watershed effects, and wildlife that often drive contemporary reforestation practices (see Keiter et al., 1999).

3. Seed transfer guidelines, seed planning zones and breeding zones

Seed transfer guidelines and seed planting zones have been in widespread use to assure that regeneration would be adapted to site environment (see Lester et al., 1990; Morgenstern, 1996; Ying and Yanchuk, 2006; White et al., 2007). Tree breeding zones define the area in which trees bred for wood production can be safely deployed. We consider two approaches under which these concepts can be adapted to the changing climate. The approaches are linked to management objectives of either or both safeguarding forest landscapes or production of wood.

3.1. Climate-based zones

Climatypes developed by classifying genetic variation are directly applicable to fixed-zone concepts. For Figs. 4 and 5 of PART 2 (Comparative Genetic Responses to Climate in the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Clines in Growth Potential, this issue), genecology models were used to predict growth potential from current climate; predictions were classified by setting the breadth of a class to one-half the amount of genetic distance required for being reasonably assured that observations in different classes would be genetically different; and half-units were used to better display the genetic variation. Climatypes, therefore, can be delineated by combining any two adjacent classes. Because climatypes are defined climatically, they are readily mapped for future climates. In Fig. 4 (herein), the left panel shows in yellow the geographic distribution of a climatype of *P. m.* var. *glauca* within the contemporary climate niche (dark green). This climatype currently occupies mild and relatively moist valleys in northern Idaho and south central British Columbia. As shown in the right panel, the climate suited for this climatype should mushroom by 2060, eventually dominating future forest lands in much of northern Idaho. Current populations of this climatype (left panel) should be a primary source of seeds for the future forests of the region (right panel), that is, seeds from the area colored yellow in the left panel presumably would be suited to the 2060 climates of the same color in the right panel.

The advantage of discrete zones is in their simplicity, but the disadvantage is that climatypes are assembled by classifying continuous genetic variation. Clines are continuous across a climatype. While all populations within a climatype should be adequately suited for the future climate suitable for the climatype as a whole, all populations will not be optimally suited. Nonetheless, the climatype concept for delineating discrete zones is well established and well suited to the maintenance of forest health, safeguarding the forest resource, and expediting immigration into new habitat. The approach, however, is less well suited for optimizing productivity.

3.2. Continuous systems

An alternative to discrete zones are flexible guidelines that use to advantage clinal relationships. Their advantage over discrete zones is in recognizing that the cline exists within zones as well as between zones. Guidelines based on continuous variation, therefore, are suited to locating sources of seed best able to take advantage of the climate at a targeted site, that is, the optimal source. The approach we illustrate follows the imagination of Campbell, 1974, (but see also Mátýas and Yeatman, 1992), has been used in species introductions (Booth, 1990; Booth et al., 1989a) and seed source selections (Booth et al., 1989b; Rehfeldt, 1991; Parker and van Niejenhuis, 1996), and is illustrated in seed transfer guidelines for accommodating climate change in *Larix occidentalis* (Rehfeldt and Jaquish, 2010).

For illustration (Figs. 5 and 6), a site is targeted for reforestation with the goal of establishing trees today that should be suited to the 2060 climate. The climate profile models (PART 1) are used to determine the taxon suited to the future climate; and the genecological model (PART 2) appropriated for that taxon is used to determine a growth potential supportable by the target's future climate. This growth potential is viewed as the optimal for the 2060 climate; deviations in either direction would be of increasing risk of maladaptation (see Leites et al., 2012a, b) in the future climate. Contemporary populations then can be identified that lie within a climatype centered on the optimum growth potential for the 2060 climate. The contemporary populations within this climatype can be ordered according to their distance in climate space from the future climate of the targeted site, but for simplicity, we use the absolute value of the difference in growth potential between the contemporary populations and the 2060 optimum. Seed transfer guidelines of this type are particularly suited for management objectives stressing wood production.

Target sites are identified in the panels of Figs. 5 and 6, and statistics on minimum geographic transfer distances for optimal sources of seed to the targeted site are supported in Table 2. In all cases, transfer distances are consistent with the geographic clines of Table 4, PART 2 (Comparative Genetic Responses to Climate in the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Clines in Growth Potential, this issue).

For *P. ponderosa* in Fig. 5:

- Panel A targets a site at an elevation of 573 m in northern California that is within the contemporary distribution of var. *ponderosa* (Table 2). Even though the trees occupying the site today are of a climatype expected to be suited to the target's 2060 climate, the optimal source of seeds would be from a population about 10 km distant and 270 m lower in elevation.
- Panel B targets a northern Washington site occupied today with a var. *ponderosa* population not expected to be suitable for the 2060 climate. An optimal source for the 2060 climate would be geographically close (5 km) but lower in elevation by about 500 m.
- Panel C targets a central Idaho site for which the population of var. *ponderosa* population occurring there today should not be suited for the 2060 climate. Optimal sources of seed for the 2060 climate would be 23 km distant and at a far lower elevation (−550 m).
- Panel D targets a site in the Black Hills of South Dakota where clines in *P. p.* var. *scopulorum* are relatively flat. The climatype of the population currently inhabiting the site still should be suited to the 2060 climate, and the optimal source of seed would be only 150 m lower in elevation.
- Panel E targets a site in Alberta that is expected to be suited for var. *scopulorum* by 2060 but is north of the current *P. ponderosa* distribution. Contemporary populations geographically closest to the target are of var. *ponderosa,* lying to the west but across the Rocky Mountains, and, therefore, deemed not suitable for the target's future climate. While seeds from the proper variety and climatype might be available from the small, isolated populations in eastern Montana 300 km to the southeast, ostensibly more reliable sources of seed would be at distances of 1200–1400 km (inserts) or even greater distances to the south (circled area). These potential sources include the Sandhills of Nebraska (upper insert) where the species is projected to disappear by 2060 (Fig. 5, PART 1 (Comparative Genetic Responses to Climate for the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Realized Climate Niches, this issue)).
- Panel F illustrates projections typical for var. *scopulorum* throughout much of the central and southern Rocky Mountains: contemporary populations are expected to become maladapted by 2060. Sources of seed optimal for the future climate tend to be geographically close but at considerably lower elevations, especially in the southwest where clines are the steepest (Table 4, PART 2 (Comparative Genetic Responses to Climate in the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Clines in Growth Potential, this issue)).

Implications for *P. menziesii* are similar (Fig. 6) to those for *P. ponderosa*, but because of the steeper clines (see PART 2), seed transfers from populations providing the optimal growth potential for the 2060 climate of a targeted site tend to be more distant geographically (Table 2). For *P. m.* var. *menziesii*, panels A–C (Fig. 6) locate a site for which the contemporary population should no longer be suited to the 2060 climate; sources of seed expected to be optimal for the future are within 50 km but 550–775 m lower in elevation (Table 2). Panel D targets a site at 289 m in the Coastal Mountains where the population occurring there today still should be suited to the 2060 climate; seed sources with growth potentials that should be optimal for future climates currently occur along the coast 70 km to the west at elevations of about 140 m.

For *P. m.* var. *glauca,* few sites within the 2060 niche space appear to be inhabited today with a climatype suitable for the future climate (Fig. 2, Table 1). Panel E and F of Fig. 6, for instance,

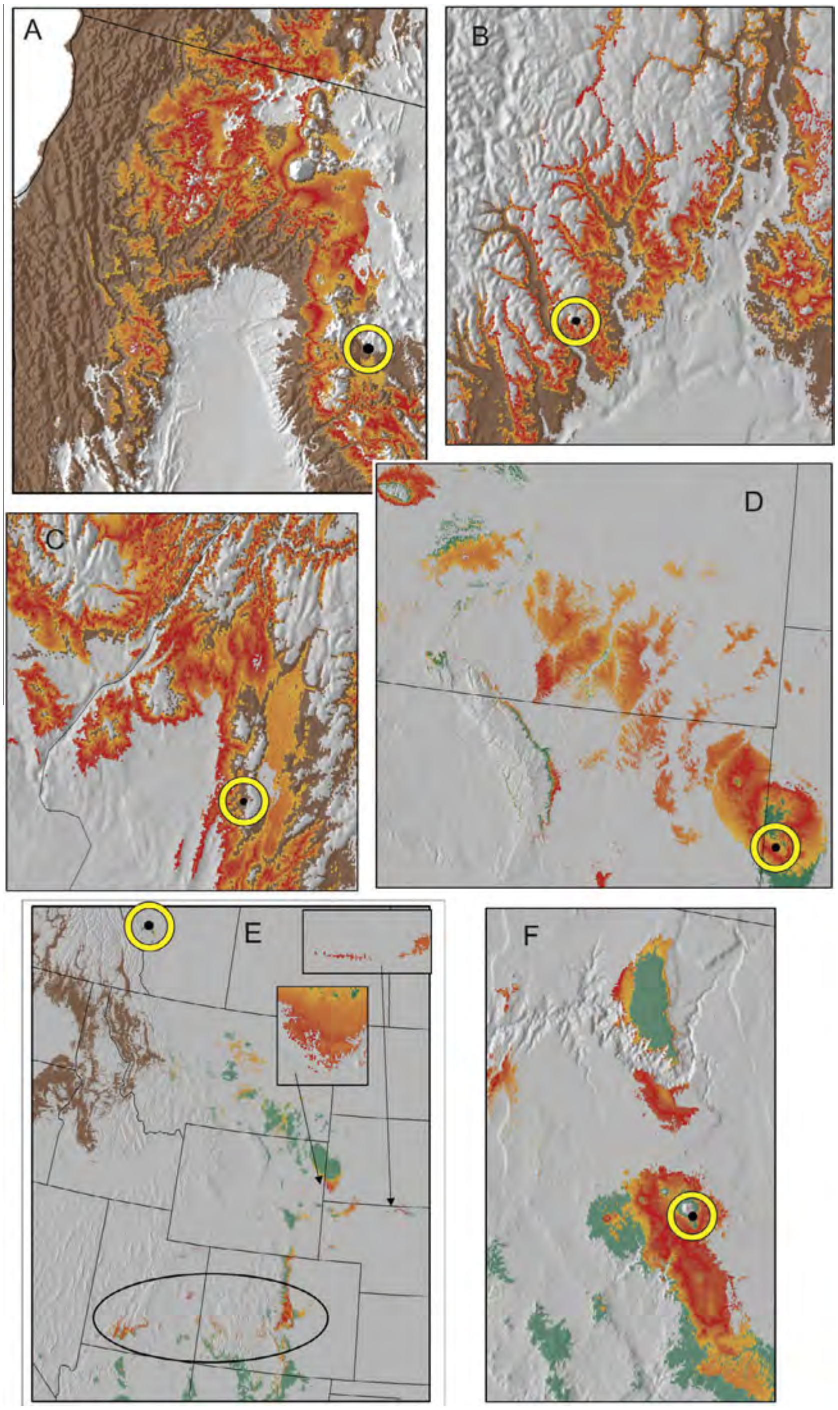

Fig. 5. Six panels located geographically in Fig. 1 (left) with the corresponding letters illustrating seed transfer guidelines for *Pinus ponderosa* var. *ponderosa* (Panels A–C) and var. *scopulorum* (Panels D–F). Dots centered in a yellow circle locate a site (Table 2) to be planted with seedlings suited to the 2060 climate. Dark brown and dark green code the present location of seed sources of *P. p.* var. *ponderosa* and *scopulorum*, respectively, not suited to the future climate of the target site. Contemporary populations suited to the future climate are colored according to suitability: light orange, lowest; orange–red, medium; bright red, highest.

target sites in northern Idaho. The former is at a middle elevation for which the seed sources deemed best suited to the 2060 climates currently occupy valley positions 500 m lower in elevation and 30–100 km distant. In F, the contemporary seed sources projected to be optimal for the 2060 climate currently are 700 m lower in elevation and 25–80 km to the northwest. Panel G targets a site in southwest Montana for which the seed sources expected to be optimal for the 2060 climate are concentrated 130 km to the north at elevations 500 m lower than the site itself. Panel H illustrates introduction of the taxon to a site in British Columbia north of the current distribution. Sources of seed deemed suitable for the 2060 climate originate nearly 1000 km to the southeast instead of the geographically closest population of today (insert in panel).

For *P. m.* var. *glauca* south of 40° N latitude and for the unnamed variety of Mexico, a lack of adequate provenance test data precludes assessing genetic responses to climate. Our analyses suggest that seed sources at elevations 300–500 m lower than a targeted site should be appropriate for var. *glauca*, but for the Mexican variety, locating suitable sites for cultivation may become the overriding priority (see PART 1).

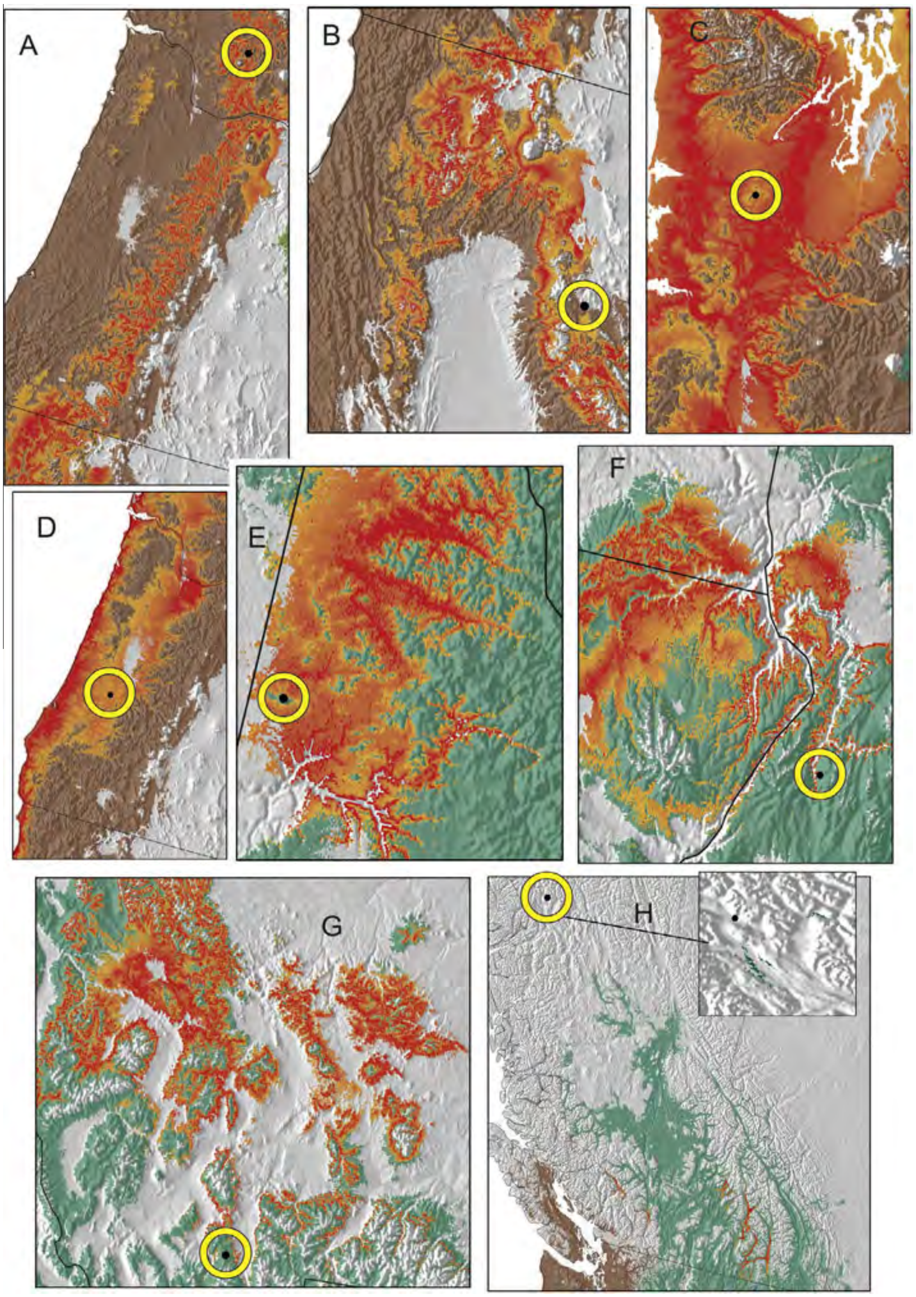

Fig. 6. Eight panels located geographically in Fig. 1 (right) with the corresponding letters illustrating seed transfer guidelines for *Pseudotsuga menziesii* var. *menziesii* (Panels A–D) and var. *glauca* (Panels E–H). Dots centered in a yellow circle locate a site (Table 2) to be planted with seedlings suited to the 2060 climate. Dark brown and dark green code the present location seed sources of *P. m.* var. *menziesii* and *glauca*, respectively, not suited to the future climate of the target site. Contemporary populations suited to the future climate are colored according to suitability: light orange, lowest; orange–red, medium; bright red, highest.

3.3. Conservation of genetic diversity

The status of the unnamed variety of southern Mexico seems particularly dire (see PART 1). While conservation efforts by necessity will involve establishing and managing refugia at locations where future climates may be suitable, the protection of contemporary populations from grazing, illegal logging and pests must not be neglected (Vargas-Hernández et al., 2003). Establishing seed banks and broad-based genetic archives of the southernmost populations of Oaxaca and Puebla are urgently needed; possible locations for such refugia would be along the Neovolcanic axis where suitable 2060 climates were identified previously (panel E, Fig. 7, PART 1 (Comparative Genetic Responses to Climate for the Varieties of Pinus ponderosa and Pseudotsuga menziesii: Realized Climate Niches, this issue)). Also desirable might be programs to actively alleviate effects of inbreeding (see Cruz-Nicolás et al., 2011) in Central Mexico populations by promoting gene flow (see Aitken and Whitlock, 2013) among neighboring populations with the subsequent establishment of managed refugia.

Issues concerning conservation of genetic diversity also encompass climatypes of both species currently adapted to the high elevations of the Sierra Nevada, Cascade Range, and central and southern Rocky Mountains. As noted in PART 2, the climate for which these climatypes are adapted is moving upwards, eventually disappearing off the tops of the mountain ranges. Projections do not suggest that these montane climates will arise anew in the north.

Table 2
Minimum distance in kilometers and elevation of contemporary seed sources best suited to the 2060 climate of several targeted sites (Fig. 1) as illustrated in the panels of Fig. 5 for *Pinus ponderosa* and of Fig. 6 for *Pseudotsuga menziesii*.

Targeted site			Minimum distance to contemporary sources optimal for the 2060 climate	
Panel[a]	Elevation (m)	Contemporary population suited to future climate	Kilometers	Δ Elevation
Pinus ponderosa				
A	573	Yes	10	−270
B	2087	No	5	−550
C	1965	No	23	−550
D	2041	Yes	12	−150
E[b]	1253	No	1200	–
F	2671	No	20	−470
Pseudotsuga menziesii				
A	1376	No	11	−620
B	1823	No	50	−775
C	561	No	26	−542
D	289	Yes	67	−152
E	1173	No	18	−525
F	1965	No	23	−700
G	2305	No	33	−350
H[b]	425	No	1000	–

[a] Figs. 5 or 6.
[b] Species not present in contemporary climate.

4. Caveats and other considerations

The philosophy driving the approach we outline has been guiding reforestation for decades, if not centuries: regenerate with the proper species, using a climatype genetically suited to the environment of the planting site. Our approach assimilates the best available information to reduce the uncertainties of targeting climates that are in transit. Prime candidates for invalidating this approach would be (a) an inability to predict future climates with suitable accuracy, and (b) the future occurrence of climates without contemporary analogs. For the former, we view the various combinations of GCMs, scenarios and time slices as a continuous range of timing options; uncertainties then revolve around when impacts will occur rather than if they will occur (discussion in PART 1); uncertainties, therefore, become the most critical for long-term targets. The potential occurrence of no-analog climates increases toward the end of the century but seems of little consequence for the period we consider (see PART 1). Our approach is consistent with the 'assisted gene flow' of Aitken and Whitlock (2013) and the 'assisted range expansion' and 'assisted population migration' of Winder et al. (2011).

The potential impacts of Table 1 range from pronounced to dire. Yet, the persistence of trees whose adaptedness is deteriorating is not fully understood. To be sure, provenance testing has demonstrated the process: environmental stresses and loss of vigor followed by mortality from a variety of biotic or abiotic agents (PART 2). Yet, dire predictions might be an exaggerated result of procedures that do not properly account for the resiliency of natural systems. Mátyás et al. (2010), for instance, considered plasticity and natural selection as sources of resiliency. Plasticity undoubtedly will contribute to persistence in the short term, but, as we note in Section 2.1, in the long term, and especially at the trailing edge, plasticity will be largely ineffectual. Natural selection indeed could occur at rates faster than commonly attributed to evolutionary processes, but its role undoubtedly will be focused on maintaining the clines, that is, population adaptation. There seems little doubt that by far the most effective mitigation strategy available will be careful and prudent actions by humans (Mátyás et al., 2010). The conclusion seems inescapable that strategic adjustments of forest management and conservation practices are both urgent and inevitable (see Czúcz et al., 2011).

We advocate a robust artificial regeneration program as the single most important management tool for mitigating ecological impacts from climate change. This makes us ripe for criticism from those who object to 'assisted migration' (e.g., Ricciardi and Simberloff, 2009; Webber et al., 2011; Van der Putten, 2012) largely because of the demonstrated abilities of humans to create ecological havoc, centered primarily on the concept of invasiveness (see Mueller and Hellmann, 2008). Yet, careful analyses (e.g., Davis, 1989; Davis and Shaw, 2001; Davis et al., 2005) repeatedly have led to the conclusion that projected rates of climate change are faster than rates of response in natural systems (although see Kremer et al., 2012). As a result, adaptation and migration lags are to be expected, leading, in turn, to the impoverished flora and loss of biodiversity evidenced in the climate change impacts recorded in packrat middens (Betancourt, 1990). Impacts summarize in Table 1, moreover, can, themselves, be viewed as fostering ecological havoc. For humans, the choice between action and inaction becomes an exercise in risk assessment (McLachlan et al., 2007). In our view, management objectives solely dependent on natural processes will be hopelessly ineffectual for supplying the amenities that humans expect from natural ecosystems within acceptable time frames. As indicated clearly by this series, perceived risks of inaction greatly outweigh the risks of action.

Developing the framework on which comprehensive planting programs depend undoubtedly will take time and resources, particularly in regions lacking adequate reforestation experience and forest nursery infrastructure. Nevertheless, the extent of projected impacts suggests urgency, particularly for developing and maintaining seed banks sufficient for supporting robust planting programs. As the climate changes, reliance on seed collections from natural stands will become problematic. This, coupled with the magnitude of geographic shifts in climate suitable to individual climatypes, suggests that interagency, interregional, and even international cooperation on a range-wide scale will be an essential attribute of effective seed bank management (see Ledig et al., 2012). Programs involving gene resource management, seed orchards, or tree breeding must retain the flexibility necessary to accommodate shifting niche space.

Recommendations drawn from our results are dependent on the clines in growth potential that have developed in relation to climate. Yet, provenance tests of these species have shown repeatedly that populations differ for additional adaptive traits, some of which may have relationships with climate that are independent of growth potential (see St Clair et al., 2005). Techniques exist, moreover, for incorporating multiple traits into climate-based seed transfer guidelines (see Rehfeldt and Jaquish, 2010). Growth potential, however, integrates many adaptive responses by means of strong negative correlations with cold hardiness and positive correlations with developmental events (e.g., Rehfeldt, 1989, 1991; Rehfeldt et al., 2004). This intercorrelated network customarily exhibits the strongest relationships with climate (e.g., Rehfeldt et al., 2004; St Clair et al., 2005). Nonetheless, reliance on growth potential alone imposes the risk of unrealistically simplifying patterns of genetic variation. We alleviate these risks with a conservative practical application that couches seed transfer within varieties and minimizes geographic distances when selecting among sources deemed equally suitable for a targeted site.

While we have used 2060 for illustration, climate change is expected to continue at accelerating rates. We acknowledge that modifying seed transfer guidelines such that climatypes are assorted into 2060 climate space is simplistic. Realizing expected growth potentials in targeting future climates requires adaptation to interim climates such that innate growth potentials can be expressed. Maladaptations to interim climates undoubtedly will constrain transfer distances (see Ukrainetz et al., 2011; Pedlar et al., 2011). The managerial solution to this dilemma would be a staged program of shifting seed transfer rules, aimed at optimizing climatype adaptedness over the anticipated life of a stand (Loya-Rebollar et al., 2013).

Abbreviated cycles of forest renewal undoubtedly will become the future norm. Silviculturists, therefore, will be facing 30- to 40-yr rotations in commercial forests regardless of the amount of wood that can be produced during that time. With managers reconciled to shortened rotations, proactive programs can be devised such that optimal sources transferred today can survive to reach the targeted future climate.

Our treatment of reforestation issues considers the coming generation. However, because the climate is continuing to change, climate niches will continue to shift geographically. Ecosystem resiliency, therefore, will be dependent on the maintenance of adaptedness and fitness in an ever changing environment. Effective multi-generation management strategies must reconcile adaptedness of populations with shifting deployment zones if forest health and productivity are to be maintained. Monitoring of the actual climate change, impacts, and regeneration responses are inherent components of flexible mitigation strategy.

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