REVIEW ARTICLE

J. For. 111(4):287–297
http://dx.doi.org/10.5849/jof.13-016

forest ecology

Preparing for Climate Change: Forestry and Assisted Migration

Mary I. Williams and R. Kasten Dumroese

Although plants have moved across the landscape in response to changing climate for millennia, projections of contemporary climate change suggest that forest tree species and populations will need to migrate faster than their natural ability. Therefore, climate change adaptation strategies, such as assisted migration, have gained attention since 2007. Effective implementation of assisted migration can only occur if target transfer guidelines are developed because our current seed transfer guidelines, established to guide the movement of plant materials, lack inherent spatial and temporal dynamics associated with climate change. This limitation restrains reforestation practitioners from making decisions about assisted migration. Lack of operating procedures, uncertainties about future climate conditions, risks associated with moving plants outside their current ranges, and existing policies have hampered formal actions in forest management and conservation. We review the current thinking on assisted migration of forest tree species and provide information that could facilitate implementation.

Keywords: assisted migration, climate change, forest management, seed transfer, seed zones

Climate has played a major role in shaping vegetative growth, composition, and genetic variation across landscapes (Jansen et al. 2007). Contemporary changes in our atmosphere have caused global mean temperatures to increase at rates not previously experienced in geologic time (Intergovernmental Panel on Climate Change [IPCC] 2007) such that climate appears to be changing faster than plants can adapt or migrate (Zhu et al. 2012, Gray and Hamann 2013). Current climate projections require plants, in general, to annually migrate 9,842−16,404 ft (3,000−5,000 m), which far exceeds their observed rates of less than 1,640 ft (500 m) (Davis and Shaw 2001, Aitken et al. 2008, Lempriere et al. 2008). Long-lived species, such as trees, will lag behind short-lived species in their ability to adapt and track suitable climate conditions (Jump and Penuelas 2005, Lenoir et al. 2008, Vitt et al. 2010). It may take several generations (centuries to millennia) for a tree population to become adapted through evolution to a new climate (Beaulieu and Rainville 2005, Ledig et al. 2012).

The mismatch in rates between climate change and tree adaptation will have serious impacts on forest growth and composition and, subsequently, important consequences for management and conservation (McKenney et al. 2009, Chmura et al. 2011, Lo et al. 2011). Synchronization of tree growth with seasonal cycles plays a major role in adaption and patterns of genetic variation within and among populations (Campbell 1974, 1979, Morgenstern 1996). Growing season length (i.e., frost-free season) has increased and will continue to lengthen under contemporary climate change (US Environmental Protection Agency 2010, Walsh et al. 2013). Although a longer growing season may cause an increase in forest productivity, it will probably be offset by increased evaporation, transpiration, and soil drying, thus making forest systems vulnerable to earlier and longer fire seasons (Trenberth 2011, Joyce et al. 2013, Walsh et al. 2013). Furthermore, because initiation and cessation of growth are influenced by temperature, precipitation, and light (Morgenstern 1996), forest systems are likely to experience phenological imbalances with longer growing seasons such that bud break may occur earlier in the spring, making those individual trees susceptible to weather events (e.g., freezing temperatures and snowfall) and pest damage (Parmesan 2007, Groffman et al. 2013, Joyce et al. 2013). The expected impacts on forests are not unlike what we have already observed, such as landscape-scale tree mortality due to mountain pine beetle outbreaks in the Rocky Mountains (Bentz et al. 2010) and prolonged drought and high temperatures in the southwestern United States

Received February 18, 2013; accepted May 31, 2013; published online July 4, 2013.

Affiliations: *Mary I. Williams (miwillia@mtu.edu), Michigan Technological University, School of Forest Resources and Environmental Science, USDA Forest Service, Rocky Mountain Research Station, Moscow, ID. R. Kasten Dumroese (kdumroese@fs.fed.us), USDA Forest Service, Rocky Mountain Research Station.*

Acknowledgments: *This collaborative work between Michigan Technological University, School of Forest Resources and Environmental Science and the USDA Forest Service, Rocky Mountain Research Station, Grassland, Shrubland, and Desert Ecosystems Program is accomplished through Joint Venture Agreement 11-JV-11221632-130, partially funded by the National Center for Reforestation, Nurseries, and Genetics Resources. We thank Dr. Martin Jurgensen for his contributions to this work . We also thank Randy Johnson, Bryce Richardson, Jerry Rehfeldt, and three anonymous individuals for reviewing this manuscript.*

(Breshears et al. 2005) and Canadian boreal forests (Michaelian et al. 2011). The impacts will intensify during the latter half of this century with forest systems continuing to experience shifts in phenology (Chuine 2010) and range (Zhu et al. 2012, Gray and Hamann 2013) and plants becoming poorly adapted to the local climate where they are growing (Aitken et al. 2008). For example, suitable climate conditions for western larch (*Larix occidentalis*) will shift northward and upward in elevation during the next 90 years at a rate that exceeds its natural migration (Rehfeldt and Jaquish 2010). Without human assistance, some plant species will be unable to adapt or migrate fast enough to track projected changes in climate.

During the past 30 years, climate change adaptation strategies have been proposed. One strategy is assisted migration (Peters and Darling 1985), defined as the movement of species and populations to facilitate natural range expansion in direct management response to climate change (Vitt et al. 2010). Drawing from conventional reforestation practices and proposed adaptation strategies, we review the current thinking on assisted migration of forest tree species and provide information for nursery managers, land managers, and restorationists to consider in management planning. Unlike recent reviews covering assisted migration, we expand implementation and provide options, resources, and tools to move forward. Our primary focus is on forest tree species and populations, but the information we provide is relevant to other native plant species.

An Adaptive Strategy

The climate will change more rapidly than some populations can adapt, and many landscapes are so fragmented that natural migration is limited (Crowe and Parker 2008, Hannah 2008). Humans have been moving plants for millennia, but the intentional movement as an adaptive strategy to climate change has only recently attracted attention (Aubin et al. 2011, Hewitt et al. 2011, Ste-Marie et al. 2011). Assisted migration can fulfill diverse goals, such as preventing species extinction, minimizing economic loss, and sustaining ecosystem services and biodiversity (Figure 1) (Aubin et al. 2011, Ste-Marie et al. 2011, Winder et al. 2011, Schwartz et al. 2012). For example, to avoid economic loss (e.g., wood volume) in the timber industry, seed sources and populations (group of intermating individuals in a geographic region having similar genetic traits and climate adaptive ability) of commercial trees could be moved within their current range (i.e., assisted population migration) or from their current range to suitable areas just outside to keep pace with changing climatic conditions (i.e., assisted range expansion; Figure 1A and B). Movement to locations far outside a species' current range is an option to prevent species extinction (i.e., assisted species migration; Figure 1C). For example, the rare tree Florida torreya (*Torreya taxifolia*) has been planted on private lands in five US states outside its current and historic range in an effort to curtail extinction (Torreya Guardians 2012).

Economic costs and ecological risks (e.g., establishment failure or invasion) can vary widely across the forms and goals of assisted migration (Figure 1) but will probably increase with migration distance (Mueller and Hellmann 2008, Vitt et al. 2010, Pedlar et al. 2012). Moving the species or population before the recipient site is suitable and inappropriate matching of the seed source with the outplanting site in a projected area could increase establishment failure (Vitt et al. 2010). Assisted migration to areas far outside the current range of a species (e.g., Florida torreya) would carry greater financial responsibilities and ecological risks than assisted population migration and assisted range expansion (Winder et al. 2011). Principle to in reforestation success is using locally adapted plant materials; thus, the greater the difference between seed origin and outplanting site, the greater the risk in maladaptation. In other words, an increase in distance (either geographic or climatic) is usually associated with loss in productivity, decrease in fitness, or mortality (Rehfeldt 1983, Campbell 1986, Lindgren and Ying 2000).

The intentional movement of species in response to climate change does not come without ethical, economical, legal, political, and ecological issues (Schwartz et al. 2012). Assisted migration is a sensitive strategy because it disrupts conservation objectives and paradigms and raises scientific, policy, and ethical questions (McLachlan et al. 2007). Adoption requires us to balance extinction or preservation of species against risks posed by introduced species (e.g., invasion) (Schwartz 1994). The debate, discussed thoroughly elsewhere, is largely focused on the assessment of risks and benefits (e.g., Ricciardi and Simberloff 2009, Aubin et al. 2011, Hewitt et al. 2011, Lawler and Olden 2011). Uncertainty about future climate conditions and risks, such as genetic pollution, hybridization, impairment of ecological function and structure, introduction of pathogens, and bringing on invasive species are major constraints to consensus and implementation (Gunn et al. 2009, Aubin et al. 2011).

Forestry and Assisted Migration

In the literature discussing assisted migration of plants, forest tree species are highlighted most often because of their economic value and focus in climate change research; however, assisted migration conducted for economic rather than conservation reasons is also cited as a major barrier to implementation (Hewitt et al. 2011), meaning that economic benefit may be an insufficient justification. We must recall, though, that the need for good timber resources played a significant role in the advancement of natural sciences, such as genecology (the study of genetic variation in relation to the

Management and Policy Implications

Climate is changing at a faster pace than natural plant migration, which poses a major challenge to forest management and conservation. We can draw from a century of forest research and management to curtail losses in forest growth, productivity, and conservation by implementing strategies, such as assisted migration. Even though we have seed transfer guidelines and seed zones for many commercial tree species, we lack clear, standard operating procedures to determine how, when, and where to implement movement. Movements outside current guidelines and zones may run afoul of legal restrictions and state and federal directives, but facilitating climatic adaptation through assisted migration has the potential to preserve forest health and productivity, subsequently maintaining ecosystem services, such as carbon sequestration, soil and water conservation, timber, and wildlife habitat. Our review and presentation of current information for researchers, foresters, landowners, and nurseries provides components to consider in their climate change adaptation plans.

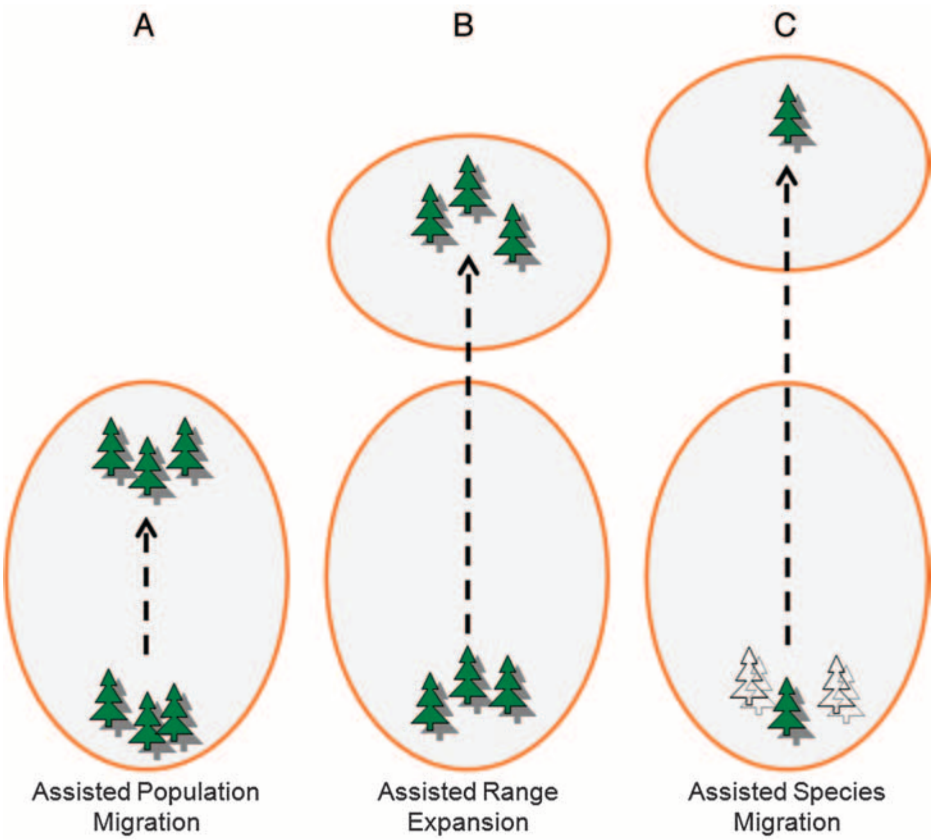

Figure 1. Assisted migration can occur in a variety of forms to fulfill diverse goals (Ste-Marie et al. 2011, Winder et al. 2011). To avoid economic loss in the timber industry, seed sources and populations (e.g., genotypes) of commercial trees could be moved within their current range (A) or from their current range to suitable areas just outside (B) to keep pace with changing conditions (e.g., warmer climates). Movement to locations far outside current ranges is an option to prevent species extinction (C). Risks can vary widely across the forms of assisted migration but would probably increase with migration distance (Mueller and Hellmann 2008, Vitt et al. 2010, Pedlar et al. 2012). For example, assisted migration to areas far outside its current range (e.g., C) would carry greater financial responsibilities and ecological risks (Winder et al. 2011).

environment) (Langlet 1971). Given its long tradition of research, development, and application of moving genetic resources through silvicultural operations, the forestry profession is well suited to evaluate, test, and use an assisted migration strategy (Beaulieu and Rainville 2005, Anderson and Chmura 2009, McKenney et al. 2009, Winder et al. 2011). For commercial forestry, assisted migration can address the maintenance of productivity and health in the coming decades (Gray et al. 2011) and would pose fewer ecological risks and economic costs because operational frameworks already exist and require only slight modifications (Pedlar et al. 2012).

Forest management policy drafts to encourage assisted migration and trials of assisted migration are currently underway in North America. The Assisted Migration Adaptation Trial (AMAT) is a large collective of long-term experiments undertaken by the British Columbia Ministry of Forests and several collaborators, including the US Department of Agriculture (USDA) Forest Service and timber companies, that tests assisted migration and climate warming (Marris 2009). The program evaluates the adaptive performance of 16 tree species collected from a range of sources in British Columbia, Washington, Oregon, and Idaho and planted on a variety of sites in British Columbia. Important components of the trial test how sources planted in northern latitudes perform as the climate changes and evaluate endurance of northern latitude sources to warmer conditions in southern latitudes. In the United States, movement has been practiced for decades in the southeast with southern pines (*Pinus* spp.), for which seed sources are moved one seed zone north to increase growth (Schmidtling 2001). Similarly, Douglas-fir (*Pseudotsuga menziesii*) has been planted around the Pacific Northwest to evaluate their growth response to climatic variation (Erickson et al. 2012).

In Canada, several provinces have modified policies or developed tools to enable assisted migration. Seed transfer guidelines for Alberta were revised to extend current guidelines northward by 2° latitude and upslope by 656 ft (200 m) (Natural Resources Canada 2013) and guidelines for some species were revised upslope by 656 ft (200 m) in British Columbia (O'Neill et al. 2008). Alberta is considering ponderosa pine (*Pinus ponderosa*) and Douglas-fir, now absent in the province, as replacements for lodgepole pine (*Pinus contorta*) because it is predicted to decline in productivity or suffer from extinction under climate change (Pedlar et al. 2011). Policy in British Columbia also allows the movement of western larch to suitable climatic locations just outside its current range (Natural Resources Canada 2013). To test species range limits in Quebec, northern sites are being planted with a mixture of seed sources from the southern portion of the province. Using seed transfer and provenance data of several commercial tree species, Quebec and Ontario have tools available that guide seed transfer decisions within their provinces (e.g., Optisource [Beaulieu 2009] and BioSim [Regniere and Saint-Amant 2008] in Quebec and Seed-Where in Ontario [McKenney et al. 1999]).

The lack of assisted migration projects in the United States does not suggest that natural resource agencies, managers, land owners, and stakeholders are not considering it as a climate change strategy; for examples, see Anderson and Chmura (2009), Erickson et al. (2012), Finch (2012), Gunn et al. (2009), and St. Clair and Howe (2009). The USDA Forest Service anticipates using assisted migration of species to suitable habitats to facilitate adaptation to climate change (USDA Forest Service 2008). However, these management statements imply that assisted migration should only be implemented in cases in which past research supports success (Johnson et al. 2013). Uncertainties about future climate conditions, risks associated with moving species and populations outside their current ranges, and existing policies have hampered preliminary studies and formal actions. Across federal, state, and private groups in the United States, very few adaptation and mitigation plans have been implemented or evaluated

Table 1. Resources related to native plant transfer guidelines, climate change, and assisted migration for the United States and Canada.

Resource or program	Description	Authorship
Center for Forest Provenance Data cenforgen.forestry.oregonstate.edu/index.php	Public users able to submit and retrieve tree provenance and genecological data	Oregon State University and USDA Forest Service
Centre for Forest Conservation Genetics www.genetics.forestry.ubc.ca/cfcg/	Portal for forest genetics and climate change research conducted in British Columbia, Canada	The University of British Columbia
Climate Change Resource Center www.fs.fed.us/ccrc/	Information and tools about climate change for land managers and decisionmakers	USDA Forest Service
Climate Change Tree Atlas www.nrs.fs.fed.us/atlas/tree/tree_atlas.html	An interactive database that maps current (2000) and potential status (2100) of eastern US tree species under different climate change scenarios	USDA Forest Service
Forest Seedling Network www.forestseedlingnetwork.com	Interactive website connecting forest landowners with seedling providers and forest management services and contractors; includes seed zone maps	Forest Seedling Network
Forest Tree Genetic Risk Assessment System (ForGRAS) www.forestthreats.org/research/projects/project-summaries/genetic-risk-assessment-system	Tool to identify tree species at risk of genetic degradation in the Pacific Northwest and Southeast	North Carolina State University and USDA Forest Service
MaxEnt (Maximum Entropy) www.cs.princeton.edu/~schapire/maxent/	Software that uses species occurrences and environmental and climate data to map potential habitat; can be used to develop seed collection areas	Phillips et al. (2006)
Native Seed Network www.nativeseednetwork.org/	Interactive database of native plant and seed information and guidelines for restoration, native plant propagation, and native seed procurement by ecoregion	Institute for Applied Ecology
Seed Zone Mapper www.fs.fed.us/wwetac/threat_map/SeedZones_Intro.html	An interactive seed zone map of western North America; user selects areas to identify provisional and empirical seed zones for grasses, forbs, shrubs, and conifers; map displays political and agency boundaries, topography, relief, streets, threats, and resource layers	USDA Forest Service
Seedlot Selection Tool sst.forestry.oregonstate.edu/index.html	An interactive mapping tool to help forest managers match seedlots with outplanting sites based on current climate or future climate change scenarios; maps current or future climates defined by temperature and precipitation	Oregon State University and USDA Forest Service
SeedWhere glfc.cfsnet.nfis.org/mapserver/seedwhere/seedwhere-about.php?lang=e	GIS tool to assist nursery stock and seed transfer decisions for forest restoration projects in Canada and the Great Lakes region; can identify geographic similarities between seed sources and outplanting sites	Natural Resources Canada, Canadian Forest Service
System for Assessing Species Vulnerability (SAVS) www.fs.fed.us/rm/grassland-shrubland-desert/products/species-vulnerability/	Software that identifies the relative vulnerability or resilience of vertebrate species to climate change; provides a framework for integrating new information into climate change assessments	USDA Forest Service

Most programs are easily located by searching their names in common web browsers. All URLs were valid as of June 21, 2013.

despite the increase in the amount of land management planning during the past 30 years (Bierbaum et al. 2013). Frameworks (e.g., Hoegh-Guldberg et al. 2008, Richardson et al. 2009, Vitt et al. 2010, McDonald-Madden et al. 2011), tools (e.g., McKenney et al. 1999, Howe et al. 2009, Lawler and Olden 2011), and implementations (e.g., Pedlar et al. 2011) have been introduced to make informed decisions about assisted migration (Table 1). Bioclimatic models coupled with species genetic information in a geographic information system (GIS) can be used to identify current and projected distributions (e.g., Rehfeldt and Jaquish 2010, McLane and Aitken 2012, Notaro et al. 2012). Although modeled projections have some uncertainty (i.e., in future climate predictions and tree responses, as discussed in Park and Talbot 2012), they provide an indication of how climatic conditions will change for a particular site. As foresters, we can gain considerable knowledge from past reintroductions, given our long history of moving and reestablishing species and from provenance trials established across a wide range of latitudes (Maschinski and Haskins 2012, Pedlar et al. 2012). Provenance studies, originating in France in 1745 (Langlet 1971), evaluate the performance and growth of populations from different geographic locations grown in common garden sites (Jump et al. 2009, Erickson et al. 2012).

In the following sections, we consult the current literature and address implementation of assisted migration. Albeit similar to conventional reforestation approaches that foresters have been practicing for more than a century, assisted migration will be fundamentally dictated by space, time, and, of course, available plant materials. In lieu of detailing specific, conventional instructions, we illustrate implementation from an assisted migration and climate change perspective and highlight some of the spatial and temporal challenges. The *Nursery Manual for Native Plants* (Dumroese et al. 2009), *Raising Native Plants in Nurseries: Basic Concepts* (Dumroese et al. 2012), volumes of *The Container Tree Nursery Manual* (Landis et al. 1989, 1998, 2010), The Society for Ecological Restoration *International Primer on Ecological Restoration* (Society for Ecological Restoration 2004), and the *Woody Plant Seed Manual* (Bonner et al. 2008) are some resources to consult for seed and plant collection, propagation, site selection and preparation, outplanting, and maintenance. Specifically, the Target Plant Concept (Landis et al. 2010), which is the culturing of stock types for specific outplanting goals and objectives, has been practiced in reforestation operations during the past 30 years and can be applied to assisted migration plans.

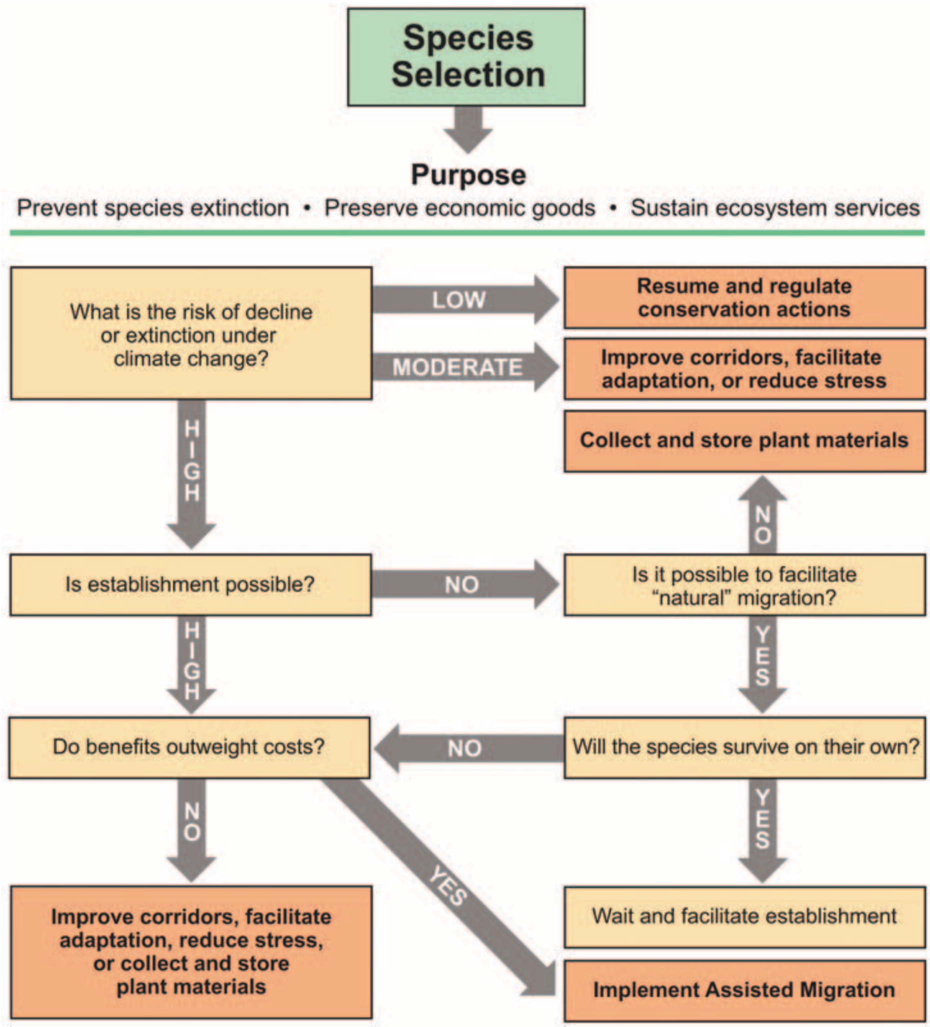

Figure 2. A decision framework from Hoegh-Guldberg et al. (2008) to determine adaption strategies for a plant species or population that has conservation, economic, or social value. Genetic information, bioclimatic models, historical records, and current assisted migration experiments can be consulted in navigating the framework (see Lawler and Olden 2011). Implementation of assisted migration is dependent on the species' risk of decline or extinction, establishment, and biological, economic, and social benefits and costs.

Implementation

Species Selection

Of the published frameworks, a decision matrix presented by Hoegh-Guldberg et al. (2008) helps to identify species risk and feasibility of migration under climate change (Figure 2). Species most vulnerable to climate change are rare, long-lived, locally adapted, geographically and genetically isolated, and threatened by fragmentation and insect and disease outbreaks (Erickson et al. 2012). Assisted migration can target commercial tree species that are predicted to decline in productivity due to changes in climate (O'Neill et al. 2008) or pests (Guerrant 2012). Listing tree species as candidates for assisted migration is a practical first step (Hunter 2007, Vitt et al. 2010, Pedlar et al. 2011) but requires a substantial amount of knowledge about the species and their current and projected distributions, including rotation lengths. The USDA Forest Service has begun to identify tree species at risk of genetic degradation in the Pacific Northwest and Southeast using the Forest Tree Genetic Risk Assessment System (ForGRAS). Provenance and distribution data exist for several commercial tree species and can be used to estimate their response to climate scenarios (e.g., Leites et al. 2012). The Center for Forest Provenance Data provides an online database of tree provenance information (St. Clair et al. 2013), and the Climate Change Tree Atlas is a spatial database containing the current and potential status of 134 eastern US tree species (Prasad et al. 2007) (Table 1).

Available habitat, endangered status, migration potential, and rotation length are considerations in the species selection process (McKenney et al. 2009, Vitt et al. 2010). Maintaining or improving conservation plans would be sufficient for species at low risk, whereas species at moderate or high risk require more involved actions. Assisted migration might be warranted if a species is at high risk of decline or extinction and can be established, and its migration provides more benefit than cost. Conservation and facilitating adaptation are alternative options to consider. Reducing fragmentation, increasing landscape connections, and creating suitable habitats could facilitate "natural" migration (Hoegh-Guldberg et al. 2008, St. Clair and Howe 2009, Ciccarese et al. 2012). Collecting and storing seed can also facilitate migration. For example, Alberta is collecting and storing limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*) seed for reintroduction into current ranges or relocation to ranges projected to have favorable climate conditions (Pedlar et al. 2011). Risk status will change over time as climatic and landscape conditions change. Existing tools and programs (described in detail in Beardmore and Winder 2011 and Friggens et al. 2012) such as the NatureServe Climate Change Vulnerability Index (NatureServe 2011), System for Assessing Species Vulnerability (SAVS) (Bagne et al. 2011), and Seeds of Success program (Byrne and Olwell 2008) are available to determine a species' risk to climate change (Table 1). Vulnerability assessments are often the first step in developing adaptation strategies for a species (Friggens et al. 2012).

Target Migration Distance

How far we move plant materials to facilitate migration will depend on goals (Figures 1 and 2), the target species and populations, location, projected climatic conditions, and time. Target migration distance is the distance that populations should be moved to address future climate change and ensure adaptation throughout a tree's lifetime (O'Neill et al. 2008). Target migration distance can be geographic (e.g., feet or meters along an elevation gradient), climatic (e.g., change in number of frost-free days along the same elevational gradient), and/or temporal (e.g., date when the current climate of the migrated population equals the future climate of the outplanting site). In current tree improvement programs, seed transfer guidelines and zones are used to determine the safest distance that a population can be moved to avoid maladaptation (Johnson et al. 2004). Transfer functions, derived from provenance trials, are used to determine safe seed transfer distances that are then used to delineate geographic boundaries or climatic bands of fixed and focal point seed zones (Raymond and Lindgren 1990, McKenney et al. 2009). Because genetic variation differs by species and location, safe seed transfer distances also vary. Douglas-fir has the largest north to south distribution of any commercial conifer in North America and subsequently much local adaptation within populations influenced by elevation, latitude, and longitude (Rehfeldt 1979). Across Washington and Oregon, the variation in Douglas-fir changes more rapidly along an elevational gradient than that of western redcedar (*Thuja plicata*). Thus, safe seed transfer distances, in general, will be much shorter for Douglas-fir than for western redcedar (Johnson et al. 2004). Further, seed zones can range from a few thousand acres (hectares) to many thousands of square miles (kilometers) depending on geographic features. In the western mountains of North America, the environment varies dramatically over very short distances. As a result, many narrow, species-specific seed transfer guidelines and seed zones exist in western North America relative to fewer, broader guidelines and zones in eastern North America (Randall and Berrang 2002). Growth and productivity of most southeastern pines, for example, are influenced by annual average minimum temperatures and can be transferred to outplanting sites along an east-west gradient and to sites within 5° F (−15° C) of their source location (Schmidtling 2001).

Paramount to any assisted migration effort will be the movement of populations to sites that are climatically suitable for growth and productivity at some point in the future (Pedlar et al. 2011). For a species or population, this may entail moving seed across seed-zone boundaries or beyond transfer guidelines (Ledig and Kitzmiller 1992). Assisted migration will be best implemented where seed transfer guidelines and zones are currently in place and most successful if based on climate conditions (McKenney et al. 2009). Provenance data, seed transfer guidelines, and seed zones can be used to ensure that trees being established today will be adapted to future climates (Pedlar et al. 2012). General tree seed transfer guidelines developed by the USDA (McCall et al. 1939) have since improved for commercial tree species through provenance trials, but most are not adjusted for the spatial and temporal dynamics associated with contemporary climate change. For reforestation practitioners, this is a major limitation in making informed decisions about assisted migration. Transfer research must factor in climate change scenarios because plant materials guided by current seed transfer guidelines and seed zones might be faced with unfavorable growing conditions by the end of this century. An overwhelming conundrum for assisted migration lies in the matching of existing plant materials (seed, nursery stock, or genetic material) with future ecosystems that have different climate conditions (Potter and Hargrove 2012).

Because long-lived tree species may take several decades to reach sexual reproductive maturity and many generations to produce locally adapted genotypes (Ledig et al. 2012, Potter and Hargrove 2012), target migration distances must be short enough to allow survival, but long enough to ensure adaptation toward the end of a rotation, or lifespan of a tree plantation (McKenney et al. 2009). Therefore, target migration distances are needed for short- and long-term planning efforts and will require adjustments as new climate change information comes to light. Methods using transfer functions and provenance data have been developed to guide seed movement under climate change (e.g., Beaulieu and Rainville 2005, Wang et al. 2006, Crowe and Parker 2008, Thomson et al. 2010, Ukrainetz et al. 2011). Online tools are available to assist forest managers and researchers in making decisions about matching seedlots with outplanting sites and seed transfer (Table 1). The Seedlot Selection Tool (Howe et al. 2009) is a mapping tool that matches seedlots with outplanting sites based on current or future climates for tree species such as Douglas-fir, ponderosa pine, and western redcedar, and SeedWhere (McKenney et al. 1999) can map out potential seed collection or outplanting sites based on climatic similarity of chosen sites to a region of interest. Bioclimatic models mapping current and projected seed zones have also been assessed for aspen (*Populus tremuloides*) (Gray et al. 2011); lodgepole (Wang et al. 2006), longleaf (*Pinus palustris*) (Potter and Hargrove 2012), and whitebark pines (McLane and Aitken 2012); dogwood (*Cornus florida*) (Potter and Hargrove 2012); and western larch (Rehfeldt and Jaquish 2010). Preliminary work in Canada on most commercial tree species demonstrates that target migration distances would be short, occurring within current ranges (O'Neill et al. 2008, Gray et al. 2011). For some tree species, target migration distances are >656,168 ft (200 km) north or >328 ft (100 m) up in elevation during the next 20 to 50 years (Beaulieu and Rainville 2005, O'Neill et al. 2008, Pedlar et al. 2012, Gray and Hamann 2013). The short-distance movements, however, may not be adapted to their climatic conditions at the end of this century (Gray and Hamann 2013). Given the uncertainty in global climate model predictions beyond 2050, it will be difficult to estimate migration distances for long-rotation tree species, but this is not evidence to counter the long-term management planning (Gray and Hamann 2011, Gray et al. 2011).

Deployment Strategies

When and where you plant a long-lived species in a rapidly changing climate may be one of the most significant and perplexing components of assisted migration (McDonald-Madden et al. 2011). Maladaptation may occur if a species is introduced too soon to its "new" environment, or a species may competitively interact with other species, causing loss of ecosystem function or structure (Aubin et al. 2011). Optimal timing will depend on the target population, cost, and carrying capacity of seed source and outplanting locations (McDonald-Madden et al. 2011). Assisted migration experiments coupled with projected climate change may help determine the best time to deploy plant materials (Lawler and Olden 2011). Outplanting at high densities can allow for natural and artificial selection by thinning, thereby removing the maladapted or slow-growing trees (St. Clair and Howe 2009), however with the downside of higher costs.

Existing reforestation guidelines focus on using local seed sources because they are best adapted to the local conditions (Kramer and Havens 2009). In the context of climate change, however, "local" becomes irrelevant. A key challenge in forestry is to develop an adaptive program that conserves the evolutionary potential of a tree species and/or population, which relates directly to seed selection, production, and collection (Crowe and Parker 2008). The goal is to select and deploy seed sources adapted to future climate conditions at target outplanting sites, i.e., seed sources that show the least amount of maladaptation and outbreeding and inbreeding depression over time (Breed et al. 2012). To alleviate concerns about suitability of local populations as seed sources, Breed et al. (2012) developed a seed source (provenance) decision framework, in which strategies (predictive, composite, and admixture provenancing) are selected based on climate change projections and level of genetic and environmental information about a population. Predictive provenancing (Sgrò et al. 2011) couples population growth data with climate change and bioclimatic models to identify genotypes adapted to future climatic conditions (e.g., Beaulieu and Rainville 2005, Crowe and Parker 2008, Rehfeldt and Jaquish 2010, Wang et al. 2010). When done correctly, predictive provenancing can reduce maladaptation, but there is high uncertainty in climate forecasts beyond 2050 such that if climate change predictions are incorrect, selected genotypes may fail to establish (Aubin et al. 2011, Breed et al. 2012). Gray and Hamann (2011) used bioclimatic modeling and multivariate approaches to identify the best matching seed sources for current and projected climates (2020, 2050, and 2080) in Alberta. Although they encourage the use of identified seed sources for current and 2020 projections, they discourage using seed sources identified for 2050 and 2080 because of the high uncertainty with climate modeling. Composite provenancing (Broadhurst et al. 2008) is the collection of seed near the outplanting site and from distant but climatically similar sites. It prescribes collecting from populations of increasing distance in an attempt to mimic gene flow patterns in the direction of predicted climate change (Breed et al. 2012). Both predictive and composite provenancing require population growth and genetic information coupled with climate change projections.

Where we lack genetic information and associated climatic model projections for target tree populations, admixture provenancing (Breed et al. 2012), climatic matching of outplanting site with seed source (McKenney et al. 2009), and broadening of collection guidelines to capture a diversity of genotypes from various environments (Broadhurst et al. 2008) can increase a population's chance for adaptation in assisted migration efforts. Admixture provenancing (Breed et al. 2012) is the collection of seed from a large population across different environments with no spatial bias to the outplanting site. Guidelines that focus on increasing the genetic diversity within the deployment population provide some long-term insurance that would counter against uncertainty in climate predictions and species reactions to climate change (Ledig and Kitzmiller 1992, St. Clair and Howe 2009, Vitt et al. 2010), although extremely high levels of diversity may swamp the few individuals in a collection that are adapted to either the current or future climate conditions (Falk et al. 2001). Therefore, the level of diversity should match the level of climate uncertainty. Seed from tree seed orchards might be favored over local and natural sources because these trees have been selected to produce offspring that perform well across a large geographic area (Randall and Berrang 2002), but it is not clear how climate change will affect seed production over time for each species (Pedlar et al. 2011). Provisional seed zones can also be used to select deployment areas for species and populations (Table 1). Tree improvement programs in North America can provide opportunities to breed and select for traits, such as drought tolerance (St. Clair and Howe 2009). Allowing for physiological or morphological variation in nursery stock might serve to facilitate natural selection to future climates, more so than planting stock that has uniformity in traits (Anderson and Chmura 2009).

Commercial tree species have a long history of human-assisted propagation; therefore, site selection will be largely determined by harvest and reforestation operations (and, by their very nature, produce outplanting sites) (Pedlar et al. 2011). Current and projected seed zones generated from bioclimatic models in GIS can identify suitable outplanting sites. SeedWhere (McKenney et al. 1999) and the Seedlot Selection Tool (Howe et al. 2009) operate a focal point seed zone system that rates climatic similarity between a planting site and a population's distribution across a region of interest in North America. Output maps allow users to view and choose desired levels of climatic conditions for seed collection or outplanting (McKenney et al. 2009). Creation of outplanting sites might be necessary for species and populations at moderate or high risk of decline (Hoegh-Guldberg et al. 2008, Aubin et al. 2011). Use of disturbed areas as outplanting sites to test assisted migration is another option, especially where a species or population is experiencing habitat loss (Jones and Monaco 2009, Aubin et al. 2011). Soil surveys and ecological site descriptions provide additional support in site selection (Herrick et al. 2006).

Maintenance and Monitoring

Throughout the entire assisted migration process, careful documentation is critical. All assisted migration efforts should start with species and provenance information—location and size of seed source and population, outplanting design (date and density), outplanting location (climate, aspect, slope, and site preparation), and assessment of survival and recruitment (Breed et al. 2012). Postestablishment maintenance, such as herbicide application and pest/predation control, can be used to help plants establish. Measures that determine success, such as growth standards, reproductive fitness or ability, ecosystem health assessments, and degree of invasiveness will be critical to assisted migration efforts (Aubin et al. 2011, Winder et al. 2011, Pedlar et al. 2012). Short-term (first few months to 1 year) and long-term (>3 years) monitoring of survival and growth will provide valuable feedback about target plant characteristics and measures for success to nursery and land managers (Landis et al. 2010). A lag in response time to both climate change and assisted migration will make it especially difficult to determine success, in addition to the fact that the ecological consequences of assisted migration on recipient ecosystems may be delayed and/or difficult to measure. Projects may need long-term intervention due to uncertainties about the impact of a species migration. Monitoring will provide valuable information about tree response and provide feedback to decision frameworks.

Additional Considerations

The biological, operational, and administrative tradeoffs are vital considerations in development of target migration distances for future climate scenarios. Cost will increase as the number of seed zones increases relative to seed and nursery production (stock, storage, and delivery), along with the increased burden of administrative regulations, and recordkeeping (Lindgren and Ying 2000). The lack of target migration distances is a major limitation in making informed decisions about assisted migration, given the uncertainty about which climate to prepare for. This brings to light the spatial and temporal challenges associated with assisted migration and climate change adaptation strategies in general. Managers should prepare for all climate scenarios (Park and Talbot 2012), but with several emissions scenarios (IPCC 2000) and many global climate models (IPCC 2007), this is an overwhelming task, even in light of new scenarios and models in the forthcoming IPCC Assessment Report (IPCC 2013). Climate change projections are developed at broader spatial and temporal scales than land management planning, but managers can refer to downscaled output scenarios specific to local regions to help understand the range of possibilities (Daniels et al. 2012). Further, projected scenarios can be combined into consensus maps showing agreements, which have been demonstrated for Brewer spruce (*Picea breweriana*) (Ledig et al. 2012) and Douglas-fir (Wang et al. 2012).

Small-scale experiments, such as outplanting of fast-growing trees adapted to projected climate in the next 15–30 years or randomly outplanting a variety of seed sources in one area and monitoring their adaptive response (similar to provenance trials) can provide valuable information and feedback to assisted migration frameworks (Pedlar et al. 2011, Park and Talbot 2012). A way to address uncertainty in climate change forecasts is to conserve and/or maximize genetic and geographic diversity in plant materials (Ledig and Kitzmiller 1992, Sgrò et al. 2011). Diversity is an insurance policy, providing populations with adaptive and evolutionary abilities to offset climate change (Lynch and Walsh 1998). Genetic diversity can be conserved by protecting natural reserves in heterogeneous landscapes, through provenance and seed source tests, and collecting seed from many populations across their geographic range for long-term storage (St. Clair and Howe 2009, Sgrò et al. 2011). A seed collection from high-elevation seed zones could also be supplemented with seeds from a lower-elevation seed zone, with the assumption that the higher-elevation sites will become warmer due to climate change (Friggens et al. 2012).

Assisted migration may not be appropriate for every species, population, or ecosystem. Changes in climate are increasing the likelihood, frequency, and intensity of extreme weather events, such as heat waves, floods, and drought (Walsh et al. 2013). Over most of the United States, heat waves will be a common occurrence (Karl et al. 2008), contributing to drought and wildfires (Trenberth 2011). Climate change effects might be so abrupt that assisted migration may not be an option, even within a species' current range. Reductions in fire frequency from 100 to 300 years to 30 years, for example, have the potential to quickly shift some forest systems to woodlands and grasslands (Westerling et al. 2011), thereby reducing the availability of genetic resources needed to move tree populations. By 2100, an estimated 55% of landscapes in the western United States may exhibit climates that are incompatible with vegetation ecosystems occurring there today (Rehfeldt et al. 2006). Evaluation of complementary actions, such as ecosystem engineering (e.g., using drastically disturbed areas as sites to test assisted migration) and landscape connectivity (e.g., reduce fragmentation) are warranted (Jones and Monaco 2009, Seddon 2010, Lawler and Olden 2011). Notwithstanding, plant survival may be more determined by availability of suitable recipient ecosystems (Aubin et al. 2011), existence of landscape connections needed for plants to move (Hannah 2008), and intensity of insect outbreaks (Logan et al. 2003, Bentz et al. 2010). The mountain pine beetle outbreaks in the Rocky Mountains on lodgepole pine populations, for example, are accelerated by warm temperatures and low precipitation to such an extent that even changes in management cannot curtail their impact (Regniere and Bentz 2008).

Conclusion

Forest management and conservation plans need to incorporate climate change research as it becomes available (Peters and Darling 1985). We can predict with some certainty how species, populations, and ecosystems will be affected by climate change (Chmura et al. 2011), and adaptive frameworks that lead to action are pertinent (McLachlan et al. 2007, Lawler and Olden 2011, Park and Talbot 2012). Ultimately our capacity to implement assisted migration will be limited by politics, cost, location, and time; however, synthesizing what we already know about plant adaptation and climate change is a necessary start. Target migration distances can be estimated with provenance data (e.g., adaptive traits and geographic and climatic characteristics) and modeling tools, but we need researchers to collaborate and incorporate data into a central warehouse (e.g., Center for Forest Provenance Data; Table 1). Most importantly, land managers testing new adaptation strategies must share their successes and failures across landscapes, regions, and agencies and provide feedback to adaptive management plans. The key to long-term success is the integration of current research with both short and long-term experiments.

Literature Cited

Aitken, S.N., S. Yeaman, J.A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evol. Appl.* 1:95–111.

Anderson, P.D., and D.J. Chmura. 2009. Silvicultural approaches to maintain forest health and productivity under current and future climates. *West. For.* 54(1):6–8.

Aubin, I., C.M. Garbe, S. Colombo, C.R. Drever, D.W. McKenney, C. Messier, J. Pedlar, et al. 2011. Why we disagree about assisted migration: Ethical implications of a key debate regarding the future of Canada's forests. *For. Chron.* 87:755–765.

Bagne, K.E., M.M. Friggens, and D.M. Finch. 2011. *A system for assessing vulnerability of species (SAVS) to climate change.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-257, Fort Collins, CO. 28 p.

Beardmore, T., and R. Winder. 2011. Review of science-based assessments of species vulnerability: Contributions to decision-making for assisted migration. *For. Chron.* 87:745–754.

Beaulieu, J. 2009. *Optisource: A tool for optimizing seed transfer.* Canadian Forest Service, Ottawa, ON, Canada. 2 p.

Beaulieu, J., and A. Rainville. 2005. Adaptation to climate change: Genetic variation is both a short- and a long-term solution. *For. Chron.* 81:704–709.

Bentz, B.J., J. Regniere, C.J. Fettig, E.M. Hansen, J.L. Hayes, J.A. Hicke, R.G. Kelsey, J.F. Negron, and S.J. Seybold. 2010. Climate change and bark beetles of the Western United States and Canada: Direct and indirect effects. *BioScience* 60:602–613.

Bierbaum, R., J.B. Smith, A. Lee, M. Blair, L. Carter, F.S. Chapin, P. Fleming, et al. 2013. A comprehensive review of climate adaptation in the United States: More than before, but less than needed. *Mitig. Adapt. Strateg. Global Change* 18:361–406.

Bonner, F.T., R.P. Karrfalt, and R.G. Nisley. 2008. *The woody plant seed manual.* USDA For. Serv., Agr. Handbk. 727, Washington, DC. 1223 p.

Breed, M.F., M.G. Stead, K.M. Ottewell, M.G. Gardner, and A.J. Lowe. 2012. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conserv. Genet.* 14:1–10.

Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, et al. 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. USA* 102:15144–15148.

Broadhurst, L.M., A. Lowe, D.J. Coates, S.A. Cunningham, M. McDonald, P.A. Vesk, and C. Yates. 2008. Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evol. Appl.* 1:587–597.

Byrne, M.K., and P. Olwell. 2008. Seeds of success: The national native seed collection program in the United States. *Publ. Gardens* 23:3–4.

Campbell, R.K. 1974. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. *J. Appl. Ecol.* 11:1069–1080.

Campbell, R.K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology* 60:1036–1050.

Campbell, R.K. 1986. Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. *Silv. Genet.* 35:2–3.

Chmura, D.J., P.D. Anderson, G.T. Howe, C.A. Harrington, J.E. Halofsky, D.L. Peterson, D.C. Shaw, and J.B. St. Clair. 2011. Forest responses to climate change in the northwestern United States: Ecophysiological foundations for adaptive management. *For. Ecol. Manage.* 261:1121–1142.

Chuine, I. 2010. Why does phenology drive species distribution? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365:3149–3160.

Ciccarese, L., A. Mattsson, and D. Pettenella. 2012. Ecosystem services from forest restoration: Thinking ahead. *New For.* 43:543–560.

Crowe, K.A., and W.H. Parker. 2008. Using portfolio theory to guide reforestation and restoration under climate change scenarios. *Climatic Change* 89:355–370.

Daniels, A.E., J.F. Morrison, L.A. Joyce, N.L. Crookston, S.C. Chen, and S.G. McNulty. 2012. *Climate projections FAQ.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-277, Fort Collins, CO. 32 p.

Davis, M.B., and R.G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292:673–679.

Dumroese, R.K., T.D. Landis, and T. Luna. 2012. *Raising native plants in nurseries: Basic concepts.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-274, Fort Collins, CO. 92 p.

Dumroese, R.K., T. Luna, and T.D. Landis. 2009. *Nursery manual for native plants: A guide for tribal nurseries.* USDA For. Serv., Agr. Handbk. 730, Washington, DC. 302 p.

Erickson, V.J., C. Aubry, P.C. Berrang, T. Blush, A.D. Bower, B.S. Crane, T. DeSpain, et al. 2012. *Genetic resource management and climate change: Genetic options for adapting national forests to climate change.* USDA For. Serv., Forest Management, Washington, DC. 24 p.

Falk, D.A., E.E. Knapp, and E.O. Guerrant Jr. 2001. *An introduction to restoration genetics.* Society for Ecological Restoration, Washington, DC. 33 p.

Finch, D.M. 2012. *Climate change in grasslands, shrublands, and deserts of the interior American West: A review and needs assessment.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-285, Fort Collins, CO. 139 p.

Friggens, M.M., J.R. Pinto, R.K. Dumroese, and N.L. Shaw. 2012. Decision support: Vulnerability, conservation, and restoration. P. 116–139 in *Climate change in grasslands, shrublands, and deserts of the interior American West: A review and needs assessment*, Finch, D.M. (ed.). USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-285, Fort Collins, CO.

Gray, L.K., T. Gylander, M.S. Mbogga, P. Chen, and A. Hamann. 2011. Assisted migration to address climate change: Recommendations for aspen reforestation in western Canada. *Ecol. Appl.* 21:1591–1603.

Gray, L.K., and A. Hamann. 2011. Strategies for reforestation under uncertain future climates: Guidelines for Alberta, Canada. *PLoS One* 6:1–9.

Gray, L.K., and A. Hamann. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change* 117:289–303.

Groffman, P.M., P. Kareiva, S. Carter, N.B. Grimm, J.J. Lawler, M. Mack, V. Matzek, and H. Tallis. 2013. Ecosystems. P. 291–330 in *NCADAC draft climate assessment report*. US Global Change Research Program, Washington, DC.

Guerrant, E.O. Jr. 2012. Characterizing two decades of rare plant reintroductions. P. 9–29 in *Plant reintroduction in a changing climate: Promises and perils*, Maschinski, J., and K.E. Haskins (eds.). Island Press, Washington, DC.

Gunn, J.S., J.M. Hagan, and A.A. Whitman. 2009. *Forestry adaptation and mitigation in a changing climate—A forest resource manager's guide for the northeastern United States.* Manomet Center for Conservation Sciences, Rep. NCI-2009-1, Brunswick, ME. 16 p.

Hannah, L. 2008. Protected areas and climate change. *Ann. N.Y. Acad. Sci.* 1134:201–212.

Herrick, J.E., G.E. Schuman, and A. Rangoa. 2006. Monitoring ecological processes for restoration projects. *J. Nat. Conserv.* 14:161–171.

Hewitt, N., N. Klenk, A.L. Smith, D.R. Bazely, N. Yan, S. Wood, J.I. Maclellan, C. Lipsig-Mumme, and I. Henriques. 2011. Taking stock of the assisted migration debate. *Bio. Conserv.* 144:2560–2572.

Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D.B. Lindenmayer, C. Parmesan, H.P. Possingham, and C.D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* 321:345–346.

Howe, G.T., J.B. St. Clair, and R. Beloin. 2009. *Seedlot Selection Tool.* Available online at sst.forestry.oregonstate.edu/contact_us.html; last accessed Jan. 3, 2013.

Hunter, M.L. Jr. 2007. Climate change and moving species: Furthering the debate on assisted colonization. *Conserv. Biol.* 21:1356–1358.

Intergovernmental Panel on Climate Change. 2000. *Special report emissions scenarios: Summary for policymakers.* Available online at www.grida.no/publications/other/ipcc_sr/?src=/climate/ipcc/emission/; last accessed June 24, 2013.

Intergovernmental Panel on Climate Change. 2007. *Climate change 2007: The physical science basis.* Available online at www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html; last accessed June 24, 2013.

Intergovernmental Panel on Climate Change. 2013. *Activities: Fifth assessment report.* Available online at www.ipcc.ch/activities/activities.shtml#.UZviqqLvvTo; last accessed June 24, 2013.

Jansen, E., J. Overpeck, K.R. Briffa, J.-C. Duplessy, F. Joos, V. Masson-Delmotte, D. Olago, et al. 2007. Palaeoclimate. P. 433–498 in *Climate change 2007: The physical science basis*, Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller (eds.). Cambridge University Press, Cambridge, UK.

Johnson, G.R., F.C. Sorensen, J.B. St. Clair, and R.C. Cronn. 2004. Pacific northwest forest tree seed zones: A template for native plants? *Native Plants J.* 131–140.

Johnson, R., S. Boyce, L. Brandt, V. Erickson, L. Iverson, G. Kujawa, L. Stritch, and B. Tkacz. 2013. Policy and strategy considerations for assisted migration on USDA Forest Service lands. *Proc. of the 60th Western international forest disease work conference (WIFDWC)*, Browing, J. (ed.). Lake Tahoe, CA. In press.

Jones, T.A., and T.A. Monaco. 2009. A role for assisted evolution in designing native plant materials for domesticated landscapes. *Front. Ecol. Environ.* 7:541–547.

Joyce, L.A., S.W. Running, D.D. Breshears, V.H. Dale, R.W. Malmsheimer, R.N. Sampson, B. Sohngen, and C.W. Woodall.

2013. Forestry. P. 263–289 in *NCADAC Draft Climate Assessment Report*. US Global Change Research Program, Washington, DC.
JUMP, A.S., AND J. PENUELAS. 2005. Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8:1010–1020.
JUMP, A.S., C. MATYAS, AND J. PENUELAS. 2009. The altitude-for-latitude disparity in the range retractions of woody species. *Trends Ecol. Evol.* 24(12):694–701.
KARL, T.R., G.A. MEEHL, T.C. PETERSON, K.E. KUNKEL, J.W.J. GUTOWSKI, AND D.R. EASTERLING. 2008. *Weather and climate extremes in a changing climate: North America, Hawaii, Caribbean, and US Pacific Islands*, Karl, T.R., G.A. Meehl, C.D. Miller, S.J. Hassol, A.M. Waple, and W.L. Murray (eds.). US Climate Change Science Program and the Subcommittee on Global Change Research, Washington, DC.
KRAMER, A.T., AND K. HAVENS. 2009. Plant conservation genetics in a changing world. *Trends Plant. Sci.* 14:599–607.
LANDIS, T.D., R.K. DUMROESE, AND D.L. HAASE. 2010. *The container tree nursery manual: Seedling processing, storage, and outplanting*, vol. 7. USDA For. Serv., Agr. Handbk. 674, Fort Collins, CO. 192 p.
LANDIS, T.D., R.W. TINUS, AND J.P. BARNETT. 1998. *The container tree nursery manual: Seedling propagation,* vol. 6. USDA For. Serv., Agr. Handbk. 674, Fort Collins, CO. 166 p.
LANDIS, T.D., R.W. TINUS, S.E. MCDONALD, AND J.P. BARNETT. 1989. *The container tree nursery manual: Seedling nutrition and irrigation*, vol. 4. USDA For. Serv., Agr. Handbk. 674, Fort Collins, CO. 119 p.
LANGLET, O. 1971. Two hundred years genecology. *Taxon* 20(5/6):653–721.
LAWLER, J.J., AND J.D. OLDEN. 2011. Reframing the debate over assisted colonization. *Front. Ecol. Environ.* 9:569–574.
LEDIG, F.T., AND J.H. KITZMILLER. 1992. Genetic strategies for reforestation in the face of global climate change. *For. Ecol. Manage.* 50: 153–169.
LEDIG, F.T., G.E. REHFELDT, AND B. JAQUISH. 2012. Projections of suitable habitat under climate change scenarios: Implications for transboundary assisted colonization. *Am. J. Bot.* 99: 1217–1230.
LEITES, L.P., A.P. ROBINSON, G.E. REHFELDT, J.D. MARSHALL, AND N.L. CROOKSTON. 2012. Height-growth response to climate changes differs among populations of Douglas-fir: A novel analysis of historic data. *Ecol. Appl.* 22: 154–165.
LEMPRIERE, T.C., P.Y. BERNIER, A.L. CARROLL, M.D. FLANNIGAN, R.P. GILSENAN, D.W. MCKENNEY, E.H. HOGG, J. PEDLAR, AND D. BLAIN. 2008. *The importance of forest sector adaptation to climate change.* North. For. Centre, Info. Rep. NOR-X-416E, Natural Resources Canada, Canadian Forest Service, Edmonton, AB, Canada. 78 p.
LENOIR, J., J.C. GEGOUT, P.A. MARQUET, P. DE RUFFRAY, AND H. BRISSE. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320: 1768–1771.
LINDGREN, D., AND C.C. YING. 2000. A model integrating seed source adaptation and seed use. *New For.* 20:87–104.
LO, Y., J.A. BLANCO, J.P. KIMMINS, B. SEELY, AND C. WELHAM. 2011. Linking climate change and forest ecophysiology to project future trends in tree growth: A review of forest models. P. 63–87 in *Climate change research and technology for adaptation and mitigation*, Blanco, J. (eds.). InTech, Rijeka, Croatia.
LOGAN, J.A., J. REGNIERE, AND J.A. POWELL. 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1:130–137.
LYNCH, M., AND B. WALSH. 1998. *Genetics and analysis of quantitative traits.* Sinauer Assoc., Inc., Sunderland, MA. 980 p.
MARRIS, E. 2009. Planting the forest for the future. *Nature* 459:906–908.
MASCHINSKI, J., AND K.E. HASKINS. 2012. *Plant reintroduction in a changing climate: Promises and perils.* Island Press, Washington, DC. 402 p.
MCCALL, M.A., F.A. SILCOX, D.S. MYER, AND H.A. WALLACE. 1939. Forest policy of US Department of Agriculture. *J. For.* 37:820–821.
MCDONALD-MADDEN, E., M.C. RUNGE, H.P. POSSINGHAM, AND T.G. MARTIN. 2011. Optimal timing for managed relocation of species faced with climate change. *Nat. Clim. Change* 1:261–265.
MCKENNEY, D.W., B.G. MACKEY, AND D. JOYCE. 1999. Seedwhere: A computer tool to support seed transfer and ecological restoration decisions. *Environ. Model.* 14:589–595.
MCKENNEY, D.W., J. PEDLAR, AND G.A. O'NEILL. 2009. Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *For. Chron.* 85:258–265.
MCLACHLAN, J.S., J.J. HELLMANN, AND M.W. SCHWARTZ. 2007. A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* 21:297–302.
MCLANE, S.C., AND S.N. AITKEN. 2012. Whitebark pine (*Pinus albicaulis*) assisted migration potential: Testing establishment north of the species range. *Ecol. Appl.* 22:142–153.
MICHAELIAN, M., E.H. HOGG, R.J. HALL, AND E. ARSENAULT. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biol.* 17:2084–2094.
MORGENSTERN, E.K. 1996. *Geographic variation in forest trees: Genetic basis and application of knowledge in silviculture.* UBC Press, Vancouver, BC, Canada. 206 p.
MUELLER, J.M., AND J.J. HELLMANN. 2008. An assessment of invasion risk from assisted migration. *Conserv. Biol.* 22:562–567.
NATURESERVE. 2011. *NatureServe mission.* Available online at www.natureserve.org/aboutUs/index.jsp; last accessed June 24, 2013.
NATURAL RESOURCES CANADA. 2013. *Assisted migration.* Available online at cfs.nrcan.gc.ca/pages/367; last accessed June 24, 2013.
NOTARO, M., A. MAUSS, AND J.W. WILLIAMS. 2012. Projected vegetation changes for the American Southwest: Combined dynamic modeling and bioclimatic-envelope approach. *Ecol. Appl.* 22:1365–1388.
O'NEILL, G.A., N.K. UKRAINETZ, M. CARLSON, C. CARTWRIGHT, B. JAQUISH, J. KING, J. KRAKOWSKI, ET AL. 2008. *Assisted migration to address climate change in British Columbia: Recommendations for interim seed transfer standards.* BC Ministry of Forestry and Range, Tech. Rep. 048, Victoria, BC, Canada. 38 p.
PARK, A., AND C. TALBOT. 2012. Assisted migration: Uncertainty, risk and opportunity. *For. Chron.* 88:412–419.
PARMESAN, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol.* 13(9):1860–1872.
PEDLAR, J., D.W. MCKENNEY, J. BEAULIEU, S. COLOMBO, J.S. MCLACHLAN, AND G.A. O'NEILL. 2011. The implementation of assisted migration in Canadian forests. *For. Chron.* 87:766–777.
PEDLAR, J., D.W. MCKENNEY, I. AUBIN, T. BEARDMORE, J. BEAULIEU, L.R. IVERSON, G.A. O'NEILL, R.S. WINDER, AND C. STE-MARIE. 2012. Placing forestry in the assisted migration debate. *BioScience* 62:835–842.
PETERS, R.L., AND J.D.S. DARLING. 1985. The greenhouse-effect and nature reserves. *BioScience* 35:707–717.
PHILLIPS, S.J., R.P. ANDERSON, AND R.E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190:231–259.
POTTER, K.M., AND W.W. HARGROVE. 2012. Determining suitable locations for seed transfer under climate change: A global quantitative method. *New For.* 43:581–599.
PRASAD, A.M., L.R. IVERSON, S. MATTHEWS, AND M. PETERS. 2007. *A climate change atlas for 134 forest tree species of the Eastern United States.* Available online at www.nrs.fs.fed.us/atlas/tree/tree_atlas.html; last accessed Feb. 1, 2013.
RANDALL, W.K., AND P.C. BERRANG. 2002. *Washington tree seed transfer zones.* Washington Department of Natural Resources, Olympia, WA. 84 p.
RAYMOND, C.A., AND D. LINDGREN. 1990. Genetic flexibility—A model for determining the range of suitable environments for a seed source. *Silv. Genet.* 39:112–120.
REGNIERE, J., AND B. BENTZ. 2008. Mountain pine beetle and climate change. P. 63–64 in *Proc. 19th US Department of Agriculture Interagency research forum on invasive species.* USDA For. Serv., Gen. Tech. Rep. NRS-P-36, Newtown Square, PA.
REGNIERE, J., AND R. SAINT-AMANT. 2008. *BioSIM 9—User's manual.* Laurentian For. Centre, Info. Rep. LAU-X-134:76, Natural Resources Canada, Canadian Forest Service.
REHFELDT, G.E. 1979. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *Glauca*) populations. I. North Idaho and North-East Washington. *Heredity* 43:383–397.

Rehfeldt, G.E. 1983. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *Glauca*) populations. III. Central Idaho. *Can. J. For. Res.* 13:626–632.

Rehfeldt, G.E., and B.C. Jaquish. 2010. Ecological impacts and management strategies for western larch in the face of climate-change. *Mitig. Adapt. Strat. Global Change* 15:283–306.

Rehfeldt, G.E., N.L. Crookston, M.V. Warwell, and J.S. Evans. 2006. Empirical analysis of plant-climate relationships for the western United States. *Int. J. Plant Sci.* 167:1123–1150.

Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. *Trends Ecol. Evol.* 24(5):248–253.

Richardson, D.M., J.J. Hellmann, J.S. Mclachlan, D.F. Sax, M.W. Schwartz, P. Gonzalez, E.J. Brennan, et al. 2009. Multidimensional evaluation of managed relocation. *Proc. Natl. Acad. Sci. USA* 106:9721–9724.

Schmidtling, R.C. 2001. *Southern pine seed sources.* USDA For. Serv., Gen. Tech. Rep. GTR-SRS-44, Asheville, NC. 35 p.

Schwartz, M.W. 1994. Conflicting goals for conserving biodiversity: Issues of scale and value. *Nat. Areas J.* 14:213–216.

Schwartz, M.W., J.J. Hellmann, J.M. Mclachlan, D.F. Sax, J.O. Borevitz, J. Brennan, A.E. Camacho, et al. 2012. Managed relocation: Integrating the scientific, regulatory, and ethical challenges. *BioScience* 62: 732–743.

Seddon, P.J. 2010. From reintroduction to assisted colonization: Moving along the conservation translocation spectrum. *Restor. Ecol.* 18: 796–802.

Society for Ecological Restoration. 2004. *The SER international primer on ecological restoration.* Society for Ecological Restoration Tucson, AZ. 15 p.

Sgro, C.M., A.J. Lowe, and A.A. Hoffmann. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* 4:326–337.

St. Clair, J.B., and G.T. Howe. 2009. Genetic options for adapting forests to climate change. *West. For.* January/February:9–11.

St. Clair, J.B., G.T. Howe, J. Wright, and R. Beloin. 2013. *Center for Forest Provenance Data.* Available online at cenforgen.forestry.oregonstate.edu/contact_us.php; last accessed June 24, 2013.

Ste-Marie, C., E.A. Nelson, A. Dabros, and M. Bonneau. 2011. Assisted migration: Introduction to a multifaceted concept. *For. Chron.* 87:724–730.

Trenberth, K.E. 2011. Changes in precipitation with climate change. *Climate Res.* 47:123.

Thomson, A.M., K.A. Crow, and W.H. Parker. 2010. Optimal white spruce breeding zones for Ontario under current and future climates. *Can. J. For. Res.* 40:1576–1587.

Torreya Guardians. 2012. *Assisted migration (assisted colonization, managed relocation) and rewilding of plants and animals in an era of global warming.* Available online at www.torreyaguardians.org/assisted-migration.html; last accessed June 24, 2013.

Ukrainetz, N.K., G.A. O'Neill, and B.C. Jaquish. 2011. Comparison of fixed and focal point seed transfer systems for reforestation and assisted migration: A case study for interior spruce in British Columbia. *Can. J. For. Res.* 41:1452–1464.

US Environmental Protection Agency. 2010. *Climate change indicators in the United States.* Available online at www.epa.gov/climatechange/indicators.html; last accessed June 24, 2013.

USDA Forest Service. 2008. *Forest Service strategic framework for responding to climate change.* Washington, DC. 21 p.

Vitt, P., K. Havens, A.T. Kramer, D. Sollenberger, and E. Yates. 2010. Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biol. Conserv.* 143:18–27.

Walsh, J., D. Wuebbles, K. Hayhoe, K. Kunkel, R. Somerville, G. Stephens, P. Thorne, et al. 2013. Our changing climate. P. 25–103 in *NCADAC draft climate assessment report*. US Global Change Research Program, Washington, DC.

Wang, T., G.A. O'Neill, and S.N. Aitken. 2010. Integrating environmental and genetic effects to predict responses to tree populations to climate. *Ecol. Appl.* 20:153–163.

Wang, T., E.M. Campbell, G.A. O'Neill, and S.N. Aitken. 2012. Projecting future distributions of ecosystem climate niches: Uncertainties and management applications. *For. Ecol. Manage.* 279:128–140.

Wang, T., A. Hamann, A. Yanchuk, G.A. O'Neill, and S.N. Aitken. 2006. Use of response functions in selecting lodgepole pine populations for future climates. *Global Change Biol.* 12:2404–2416.

Westerling, A.L., M.G. Turner, E.A.H. Smithwick, W.H. Romme, and M.G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proc. Natl. Acad. Sci. USA* 108(32): 13165–13170.

Winder, R., E.A. Nelson, and T. Beardmore. 2011. Ecological implications for assisted migration in Canadian forests. *For. Chron.* 87: 731–744.

Zhu, K., C.W. Woodall, and J.S. Clark. 2012. Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biol.* 18:1042–1052.