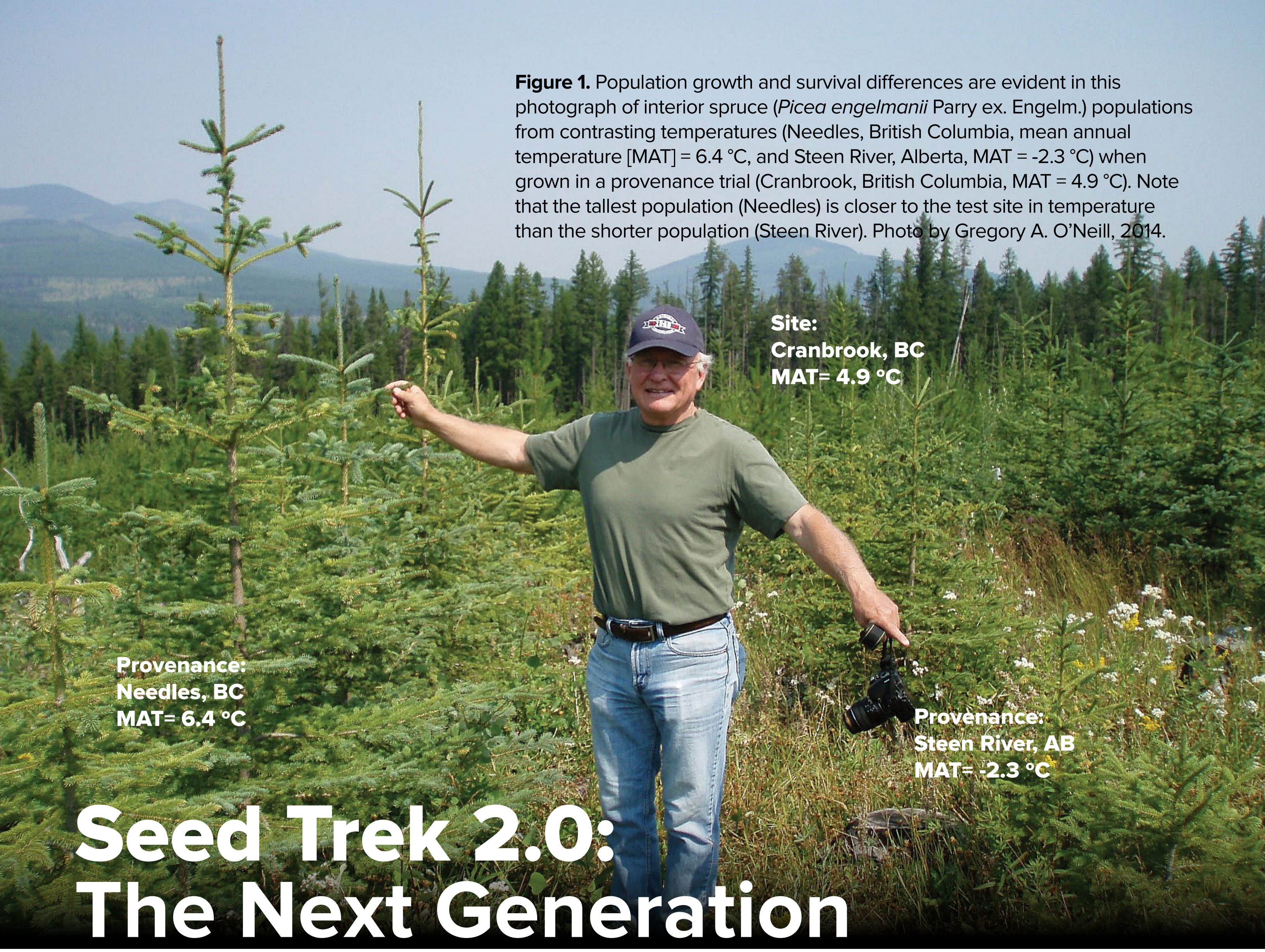

Figure 1. Population growth and survival differences are evident in this photograph of interior spruce (*Picea engelmanii* Parry ex. Engelm.) populations from contrasting temperatures (Needles, British Columbia, mean annual temperature [MAT] = 6.4 °C, and Steen River, Alberta, MAT = -2.3 °C) when grown in a provenance trial (Cranbrook, British Columbia, MAT = 4.9 °C). Note that the tallest population (Needles) is closer to the test site in temperature than the shorter population (Steen River). Photo by Gregory A. O'Neill, 2014.

Seed Trek 2.0: The Next Generation of Seed-Transfer Systems

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Abstract

The intention of this article is to make a case for foresters to "boldly go where no forester has gone before," thereby deconstructing the 100-year-old paradigm of planting with local seed sources (Thrupp 1927). Using the concepts of safe seed-transfer distance and migration distance, foresters can incorporate assisted migration into a climate-based seed-transfer system that matches a seed lot's historical climate with the planting site's future climate. Methods proposed here are low risk, low cost, easily implemented, transparent, and can help ensure that plantations are established with seed sources that will be well-adapted throughout the life of the plantation. This paper was presented at Growing Pains: Scaling up the Reforestation Pipeline—Joint Annual Meeting of the Western Forest and Conservation Nursery Association and the Forest Nursery Association of British Columbia (Portland, OR, September 19–21, 2023).

Historical Seed-Sourcing Methods

In the days before replanting seedlings after harvest was common practice in North America, the forest immediately surrounding a logged area or the seedbed laying dormant in the soil was relied upon to naturally provide the next generation of trees. In addition to being the cheapest option for reforestation, reliance on natural regeneration also built on the assumption that "local is best," i.e., the trees growing in a particular area are best adapted to the climate, pests, and soils of that area.

As the scale of industrial logging accelerated throughout the 20th century, foresters were forced to acknowledge that their timber base was ultimately finite, and that rotational forestry and sustained yield harvest were required to manage timber resources in the long term. This recognition led to increasing criticism of the slow and inconsistent regeneration provided by nature and a shift to plantation forestry. Planting seedlings after harvest is now ubiquitous throughout the United States and Canada and is legally required in many jurisdictions.

These widespread replanting programs necessitated efficient seed-collection programs, which ultimately led to a new question in reforestation: "If local is best, then how 'local' is local?" For many important timber species, seed zones were established to ensure that seedlings would be similarly adapted to the areas where they were planted. Seed-zone boundaries were often drawn along major geographic barriers or latitudes to group regions based on similar temperature and precipitation regimes. This system is referred to as geographic-based seed transfer, whereby the physical location of seed collection dictates the broader area in which it can be replanted.

To further inform and refine these seed zones, forestry researchers established provenance tests in which seed sources from various locations are planted side by side in recently harvested areas (figure 1). With many of these experiments replicated in multiple environments across or even outside a species' range, growth and survival data can be used to identify regions where trees will grow similarly, how far seed can be moved before trees start to become maladapted (figure 2), and whether certain regions produce particularly vigorous trees.

Climate Change Impacts on Forests

Numerous reports have already linked large-scale forest disturbance with climate change during the 20th and 21st centuries (Seidl et al. 2017). Collectively, these reports indicate that climate change is already impacting forests (as opposed to something that might impact forests in the future). The mountain pine beetle epidemic that devastated lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests of western Canada (Sambaraju et al. 2012), powdery mildew infection of oaks (*Quercus* spp.) in Europe (Marçais and Desprez-Loustau 2014), mortality of savanna parkland tree species in the African Sahel (Maranz 2009), and declines of aspen (*Populus* spp.) in western North America (Worrall et al. 2013), yellow cypress (*Callitropsis nootkatensis* [D. Don] Oerst. Ex D.P. Little) in Alaska (Hennon et al. 2006), and Scots pine (*Pinus sylvestris* L.) in Switzerland (Rebetez and Dobbertin 2004) are just a handful of species that have been impacted, at least in part, by climate change.

Provenance tests have emerged serendipitously as climate change laboratories (Carter 1996, Mátyás 1994). By testing populations from a range of source climates across a range of plantation climates, provenance tests show the real, on-the-ground impacts of climate change and seed transfer on tree growth and survival (figure 2). When these tests are conducted for many years, they sample the range of climatic extremes present at a plantation while integrating

Figure 2. Climate change impacts on tree growth and form can be assessed in provenance trials when the same populations are planted in differing climates. In these photographs, the same lodgepole pine (*Pinus contorta* Douglas ex Loudon) population from a cold northern British Columbia provenance was planted at a site with the same mean annual temperature (MAT) as its source (-1.3 °C) (left) and at a site with a MAT of 2.9 °C (i.e., 4.2 °C warmer MAT than the provenance climate) (right). Growth and form are excellent when populations are planted in a climate similar to that of their origin but are poor when planted in climates considerably warmer than that of the population origin. Photos by Gregory A. O'Neill, 2010.

diverse effects of biotic and abiotic stressors. Provenance tests reveal that, in the short term, a small amount of climate change may benefit growth rates. In the long term, however, productivity of naturally regenerated forests or plantations established with local seed sources is expected to decline substantially. For example, in central British Columbia, productivity of natural stands of lodgepole pine, the Province's primary lumber species, is expected to decline 30 to 60 percent (relative to 1975 productivity levels) by 2085 due to climate change (O'Neill et al. 2008).

Climate is changing too quickly for populations to follow their optimal climate through natural migration (Ash et al. 2017, Lenoir et al. 2020) or for natural selection to allow them to thrive under new climates (Davis and Shaw 2001, Rehfeldt et al. 2002) (figure 3). This rapid change creates an evolutionary lag, in which trees' annual life cycles become desynchronized from seasonal environmental cues and the pests they have evolved to tolerate. Together, these factors can contribute to reduced tree and stand productivity and increased pest damage. Many large shifts in climate have occurred in the geologic past, but forests survived. The unprecedented rate of current warming, however, requires innovative forest management strategies to avoid large-scale disturbance. Fortunately, foresters are positioned to respond proactively to climate change.

Figure 3. The rate of climate change is vastly outpacing the rate at which trees can migrate from one generation to the next, thereby creating an evolutionary lag that predisposes trees to poor growth and health. In this comic sketch, the tree's "climate home" is speeding northward much faster than the tree can keep pace. Image courtesy of Peter Strother, artist.

Rationale for Assisted Migration

To the extent that tree populations are locally adapted to biotic or abiotic disturbance agents, it may be possible to mitigate future disturbances through forestry-assisted migration—the establishment of plantations with seed sources from climates slightly warmer than that of the plantation. Forestry-assisted migration, as discussed in North America (Pedlar et al. 2012), includes both assisted population migration (movement of populations within the species' current natural distribution) and assisted range expansion (movement of populations slightly outside the species' current natural distribution). Exotic translocation (movement of populations to locations far outside the species' natural distribution where they are not expected to establish naturally in the foreseeable future) is not commonly considered within the rubric of forestry-assisted migration (Ste-Marie et al. 2011).

Plant biologists have migrated plant hardiness zones to facilitate selection of horticultural species and cultivars appropriate for a changed climate (McKenney et al. 2014) (figure 4). In agriculture, retrospective analyses of productivity and crop area for maize, wheat, and rice—three of the world's most important agricultural crops—show a poleward shift in their use, a response thought to have substantially moderated climate change impacts to these crops (Sloat et al. 2020). Forestry is usually a longer term proposition than horticulture or agriculture, and fewer interventions are available to protect forest plantations compared with horticulture plantings. Thus, a more considered approach to assisted migration is warranted in forestry.

Safe Seed-Transfer Distance and Migration Distance

When discussing forestry-assisted migration, two key concepts must be distinguished—safe seed-transfer distance (SSTD, a.k.a. critical seed-transfer distance) (Ukrainetz et al. 2011) and migration distance (O'Neill et al. 2017). SSTDs are the climate or geographic distances seed may be moved to provide some operational flexibility in the seed source selection process without displaying unacceptable declines in productivity. Migration distance is the climatic difference between a seed source and a plantation that seed should be migrated to optimize adaptation through the life of a plantation (Ukrainetz et al. 2011).

SSTDs are derived from trends relating population transfer distance to population growth, survival, or health traits using provenance test data (Raymond and Lindgren 1990) and are used to help determine seed-zone sizes and seed-transfer limits (figure 5). As the number of planted tree species vastly exceeds the number of species with

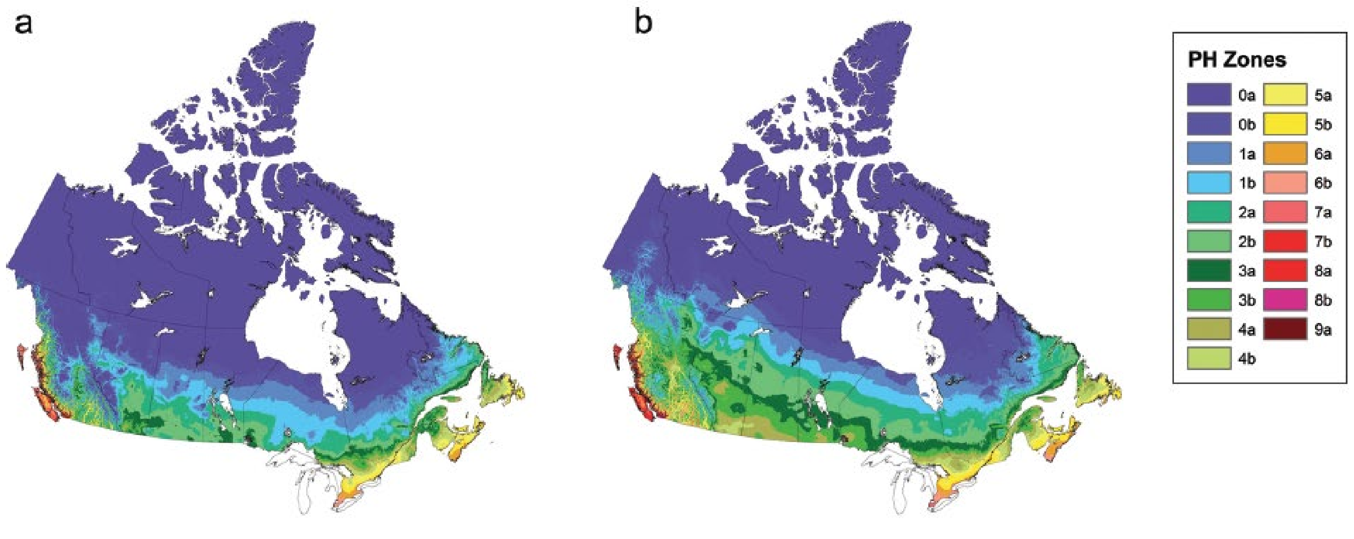

Figure 4. Canadian plant hardiness (PH) zone maps for 1931–1960 (a) and 1981–2010 (b) show substantial northward movement of plant hardiness zones. Source: McKenney et al. (2014).

good, long-term provenance tests, seed-transfer systems are often developed using SSTD estimates inferred from other species or from local practitioners. Therefore, in the absence of provenance test data, SSTDs for climatic variables can be inferred from the maximum climatic range present within existing geographic seed zones, assuming that maladaptation is rare for plantations within those zones. Climatic SSTDs used in British Columbia's climate-based seed-transfer (CBST) system are approximately +/- 3 °C mean annual temperature, +/- 4 °C mean coldest month temperature, +/- 3 °C continentality (difference between the temperatures of the warmest and coldest months), and +/- 40 percent of mean annual precipitation or mean summer precipitation, although these values differ slightly among species. Switching from a geographic-based seed-transfer system to a CBST system and incorporating assisted migration into a seed-transfer system does not alter maximum SSTDs. Consequently, the establishment of new provenance tests is not necessary when converting to a climate-based system if existing SSTDs in geographic-based systems result in acceptable plantation growth and health.

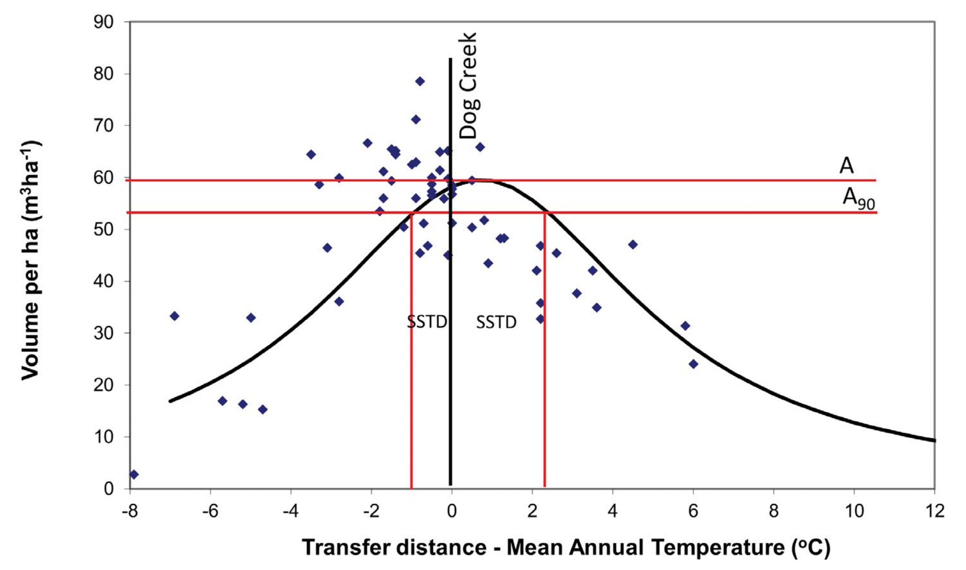

Figure 5. Calculation of safe seed-transfer distance (SSTD) is illustrated in this transfer function from a lodgepole pine (*Pinus contorta* Douglas ex Loudon) provenance trial at Dog Creek, British Columbia. A peaked function is fitted to relate population mean growth (volume per ha) as a function of population climate-transfer distance (the site climate minus the population climate; mean annual temperature transfer in this figure). Upper and lower SSTDs are obtained by interpreting the transfer distance at 90 percent of the maximum fitted value.

While evidence mounts in support of forestry-assisted migration (Nigh 2014, Pedlar et al. 2012, Williams and Dumroese 2013), there has been little discussion regarding migration distance. Migration distances that are too long can predispose plantations to frost damage or new pests, whereas migration distances that are too short may be ineffective at helping plantations escape drought and heat damage in the hot and dry parts of planted species' ranges (Mátyás 2010). Given the relative stability of climate in the millennium prior to the Anthropocene and the rapid rate of anthropogenic climate change, it may be assumed that populations best adapted to the present climate of a plantation are more likely to be found where a plantation's current climate existed a century ago, rather than locally. Even if populations selected for reforestation are optimally adapted to the present climate of a plantation they will likely be substantially maladapted at harvest. Furthermore, populations optimally adapted to the climate at harvest may not perform well during establishment when trees are most sensitive. Weighing the risk of maladaptation during seedling establishment versus the risk of maladaptation as a stand approaches maturity, British Columbia elected to use a migration distance that matches seed source climate during the period 1931 to 1960 (i.e., prior to significant Anthropogenic climate change) with the climate expected for the plantation at a quarter of the rotation age (approximately 15 years after planting in British Columbia) (O'Neill et al. 2017, Ukrainetz et al. 2011) (figure 6).

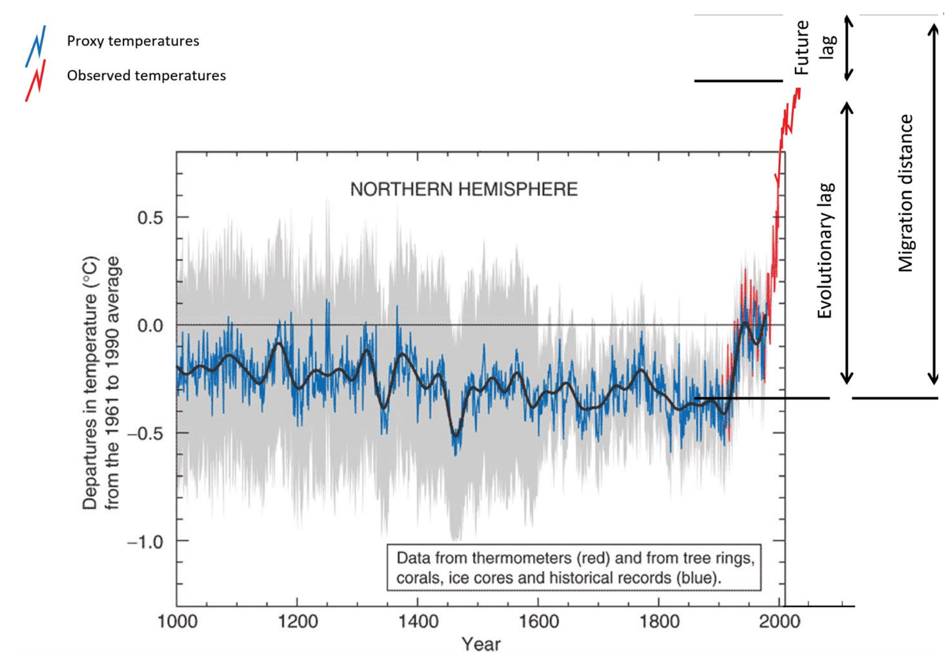

Figure 6. Migration distance is the climate distance seed is moved to account for climate change during the Anthropocene (evolutionary lag) and during the first fourth of a plantation's lifespan (future lag). Here, migration distance is illustrated for mean annual temperature (MAT) in this line chart of MAT (expressed as the annual deviation from the 1961 to 1990 MAT) for the Northern Hemisphere over the 20th century. Evolutionary lag is the difference in MAT between current and historical MAT (where historical is the most recent period when adaptation lag is presumed to be least). Future lag is the difference in MAT between current and future MAT. Migration distances are calculated for each SSTD variable. Climate deviations are from Houghton et al. (2001).

Devising a Climate-Based Seed-Transfer System

While fixed-zone, geographic-based seed-transfer systems around the world are straightforward (seed must stay within its zone of origin), they do not lend themselves to assisted migration, and SSTDs based on geography may over- or under-transfer seed, as geography is only a surrogate for climatic adaptation of plants. Therefore, converting to a climate-based system could facilitate adoption of assisted population and assisted range expansion and capitalizes upon widely available climate models (Wang et al. 2016). In CBST, seed sources suitable for use at a plantation are identified by first predicting the climate of the plantation in the future (e.g., 15 years) based on a specified migration distance. For all the climate variables determined to be relevant for adaptation, seed sources that are within the SSTD above or below this new climate can be examined (figure 7). If a seed source is within the SSTD for all variables, it can be used for reforestation. This system can also be used to determine how broadly a particular seed source can be planted. Including a minimum of four SSTD variables is recommended, with at least one being a precipitation-related variable.

Additional Criteria

Provenance tests generally consist of a handful of plantations located within the species' natural distribution, so they are not useful in determining the climatic limits of a species' range, now or in the future. Consequently, prior to choosing a seed source, species' future climate niche distribution models are needed to confirm that a plantation's future climate is within the intended species' fundamental future climate niche, thus ensuring the intended species is appropriate for current and future climates at the plantation.

Species' future climatic niche distributions are particularly important when planting beyond the species' cold limit (to ensure that the species' climate niche will include the plantation shortly after planting) or at the trailing (warm) edge (to ensure that the species' climate niche will continue to include the plantation throughout most of the rotation). Species selection for future climates must also continue to adhere to species' edaphic (soil nutrient and moisture) requirements (Mackenzie and Mahony 2021).

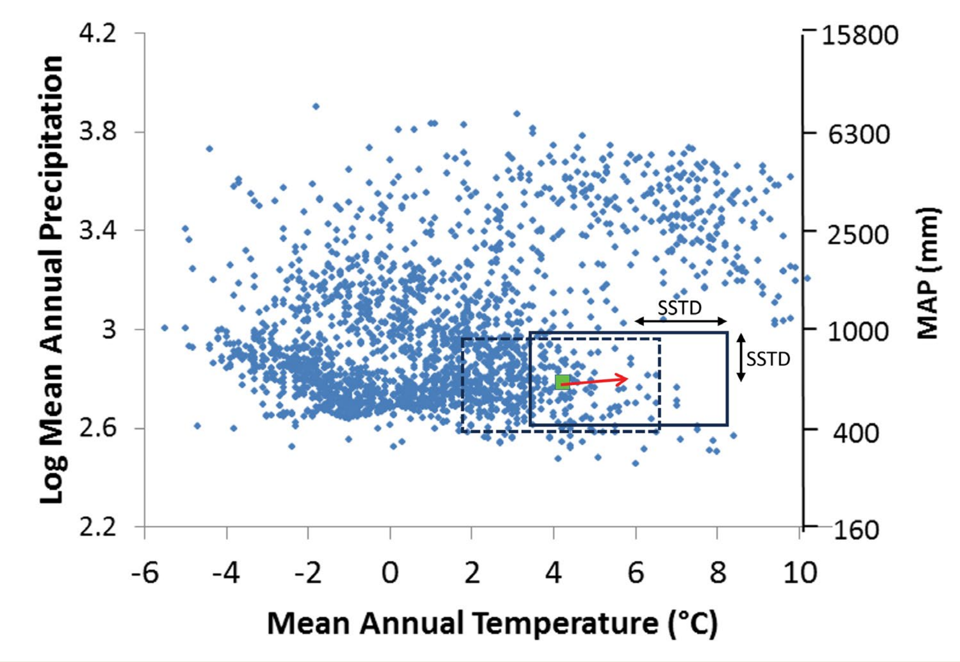

Figure 7. This two-climate variable schematic illustration shows the climates where seed can be obtained for a reforestation site using a climate-based seed-transfer (CBST) system. The migration distance (red arrow) is added to the climate of the reforestation site (green square) to identify the climate of the focal point at the head of the arrow. The seed procurement area (solid black box), where seed suitable for a reforestation site can be obtained, is defined by the safe seed-transfer distance (SSTD) on either side of the focal point. Without assisted migration, the seed procurement area is shown as the dashed black box centered on the plantation climate.

Risks

Assisted migration implemented without a CBST tool in place can pose risks. Seed sources transferred beyond their safe transfer distances can fail due to maladaptation. Alternatively, species introduced intentionally (e.g., cane toads in Australia and kudzu in the United States) or unintentionally (e.g., spotted knapweed, zebra mussels, blister rust, and Dutch elm disease in North America) (https://www.invasivespeciescentre.ca/) can become invasive, wreaking havoc on the recipient ecosystem by disrupting or displacing local species, particularly when an introduced species reproduces readily and escapes controls imposed by other organisms in its native habitat. The risk of a species failing or becoming invasive is negligible in forestry-assisted migration when a CBST system is in place to constrain the procurement of seed sources to within common SSTDs and migration distances. Likewise, the risk of acquiring a hitchhiking pest that becomes invasive is also minimal in forestry-assisted migration because climate migration distances used in CBST are associated with short geographic transfer distances, usually in the order of 200 to 300 m upward elevation transfer or 200 to 400 km poleward transfer, and do not require transcontinental or intercontinental transfers that are commonly associated with species invasions (Mueller and Hellmann 2008). Considering risks associated with species invasion, abundant provenance testing confirms that restoring seed sources into their historical climates of last century entails considerably less risk than planting local seed sources that will experience climates 4 °C warmer than their historical climate by the time of harvest.

Other Climate Change Adaptation Strategies

Assisted migration as a climate change adaptation strategy in forestry is low cost (seed from a location slightly warmer than the plantation compared with local seed are generally comparable in cost), low risk, easily implemented, and transparent. However, other valuable climate change adaptation strategies also warrant consideration. Genetic diversification may also mitigate climate change impacts to forests by buffering some of the uncertainty in climate and pest predictions. Planting multiple (climatically appropriate) seed sources from slightly different climates in each plantation (Looney et al. 2023) or employing a wider range of reforestation species (Mason et al. 2012) could help ensure that a harvestable crop is achieved should extreme climate events or pest outbreaks result in significant mortality.

In genetic-selection programs, selecting or breeding for pest resistance or testing and selecting for wide climate tolerance are proactive strategies to address potential pest and climate disturbances. Greater use of silviculture methods that provide more overstory and structural diversity (Gustafson et al. 2020), careful attention to matching stock type to plantation environment (Christiansen et al. 2023), careful microsite planting, and use of nurse plants (Carbajal-Navarro et al. 2019) can also reduce mortality risks at establishment.

Next Steps

As assisted migration shifts seed procurement to slightly warmer climates, some operators may find that suitable seed sources are unavailable locally (O'Neill and Gómez-Pineda 2021), forcing them to search for seed lots in neighboring jurisdictions. Seed lot owners may be unwilling to sell seed if they also have concerns regarding obtaining seed from their neighbors. To reverse this cycle of stagnation, seed lot databases from across jurisdictions should be shared, to provide wider markets for seed collectors and producers, an economy of scale for seed marketing, and, importantly, facilitation of the use of nonlocal seed lot databases, thereby assisting the migration of climatically suitable seed sources (Williams and Dumroese 2013). As stated by Erickson and Halford (2020), "A [common] seed zone framework greatly facilitates seed use planning and creates opportunities for sharing and exchange of plant material among landowners and seed banking programs and partners." By expanding the scale, seed demand can be aggregated, supporting investments in expanded databases and a willingness to supply a wider market for the next generation of forests.

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