

Assisted migration: uncertainty, risk and opportunity

by Andrew Park^{1,2} and Carolyn Talbot¹

ABSTRACT

The recent *Forestry Chronicle* special section on the subject of Assisted Migration (AM) did a great service to the Canadian forestry community by summarizing the risks, opportunities and ecological aspects of this forest management strategy. In this paper, we expand on some aspects of AM that were discussed in the special section, as well as discussing additional dimensions of AM that should be considered and debated. We expand on the theme of scientific uncertainties around future warming, emphasizing the full extent of uncertainty in estimates of climate sensitivity. We also expand upon and summarize a number of recent ecophysiological results that have implications for the adaptation and acclimation of trees to climate change. We also discuss opportunities for innovative forest management, the influence of economic trends on the future of the Canadian forest industry, and limitations on public knowledge of climate change, all of which are factors that will influence the feasibility of AM schemes in the future.

Key words: assisted migration, managed relocation, climate change scenarios, uncertainty, ecophysiology, epigenetics

RÉSUMÉ

La section spéciale publiée dernièrement dans le *Forestry Chronicle* portant sur le sujet de la migration assistée (MA) a rendu un fier service à la communauté forestière canadienne en résumant les risques, les opportunités et les questions écologiques liés à cette stratégie d'aménagement forestier. Nous approfondissons dans cet article certains aspects de la MA qui ont été abordés dans la section spéciale et nous discutons également des dimensions additionnelles de la MA qui devraient être considérées et débattues. Nous nous attardons sur le thème portant sur les incertitudes scientifiques entourant le réchauffement climatique, mettant en évidence la portée complète de l'incertitude touchant les estimés de la sensibilité climatique. Nous résumons et nous discutons également de certains résultats écophysologiques récents qui ont des répercussions sur l'adaptation et l'acclimatation des arbres face aux changements climatiques. Nous discutons aussi des opportunités d'innovation en matière d'aménagement forestier, de l'influence des tendances économiques sur l'avenir de l'industrie forestière canadienne et des limites des connaissances du public sur les changements climatiques, tous constituant des facteurs qui influenceront la faisabilité des schémas de MA dans le futur.

Mots clés : migration assistée, relocalisation planifiée, scénarios de changements climatiques, incertitude, écophysologie, épigénétique

Introduction

Assisted migration (also called managed relocation or assisted colonization Ste-Marie *et al.* 2011) refers to the intentional movement of organisms (be they trees, animals or crops) to areas outside their historic range. A restricted form of assisted migration (AM) is made possible by the seed transfer guidelines that are used in several provinces (O'Neill *et al.* 2008) to optimize the matching of seed sources to sites in forestry. More extensive AM of provenances and species is being contemplated as an adaptive response to anthropogenic global warming (AGW). Assisted migration was originally contemplated as a conservation measure to address the possibility that existing tree populations may become maladapted to their local conditions as the climate shifts around them. More recently, it has been argued that AM could be used to pre-emptively adapt forests to the effects of AGW. Either goal



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would be accomplished by moving provenances and species from their current habitats to cooler regions that are anticipated to match their climatic niches in the future. Although practised for centuries, especially in Europe (Bolte *et al.* 2006), the wisdom of moving tree species across national and ecosystem boundaries is heavily debated in North America (McLachlan *et al.* 2007, Minter and Collins 2010).

The recent special section on AM of forest trees in *The Forestry Chronicle* (vol. 87/6, 2011) was a necessary and insightful contribution to the literature on this subject. The various articles summarized the ethical debates (Aubin *et al.* 2011), ecological considerations (Winder *et al.* 2011), and potential species vulnerabilities (Beardmore and Winder 2011) that come into play when AM is considered. Some existing AM trials and planning processes, as well as potential silvicultural actions were also outlined (Pedlar *et al.* 2011, Winder *et al.* 2011).

While the special section on AM was informative, there are additional dimensions to this subject that should be considered. These include: 1) the true extent of uncertainty around future climate and variability in tree responses to climate change requires more complete coverage; 2) opportunities for innovative forest management and adaptation that climate change may bring; 3) the influence of economic trends on potential futures for the Canadian forest industry; and 4) balancing public input to the AM debate against generally low levels of public knowledge about climate change. We consider these factors sequentially below.

Uncertainty in Future Climate and Tree Responses

Future climate

Recent reports by the Intergovernmental Panel on Climate Change (IPCC) emphasize increasing scientific confidence that some level of AGW will occur (IPCC 2007, Trenberth *et al.* 2007). However, a growing body of research acknowledges, and seeks to dissect, the considerable uncertainty that remains about the future magnitude of AGW.

At the heart of these deliberations are uncertainties about the feedback processes that influence climate sensitivity to carbon dioxide (CO₂). Climate sensitivity is defined as the global equilibrium surface warming that will occur following a doubling of atmospheric CO₂ concentration. This figure is subject to numerous positive and negative forcings, including changes in atmospheric water vapour, ocean temperature, ice cover, vegetation, and atmospheric aerosols, as well as changes in the spectral properties of water and clouds brought about by warming. The feedbacks are so complex that, in the words of one article on the subject, "The quest to determine climate sensitivity has now been going on for decades, with disturbingly little progress in narrowing the large uncertainty range" (Knutti and Hegerl 2008).

How large is the range of uncertainty? Depending on the policy scenario, IPCC projections result in warming of 1.1°C to 6.4°C by the year 2100. Studies employing comprehensive lists of feedback factors predict temperature increases of up to 8°C (Andreae *et al.* 2005, Meinshausen *et al.* 2009). But given the great uncertainties in feedback magnitude and variability, there is a low probability that temperature could rise by 10°C or more, or by 2°C or less (Roe and Baker 2005, Knutti and Hegerl 2008, Fig.1). Unfortunately, the latest generation of general circulation models (GCMs) currently being tested is

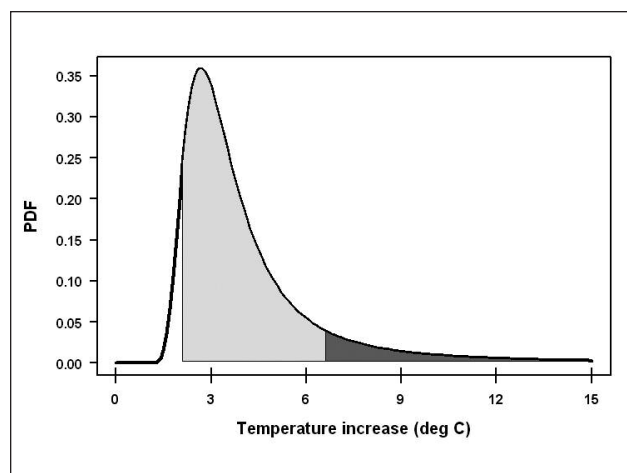


Fig. 1. Probability distribution of climate sensitivity to a doubling of CO₂. The distribution is skewed because the relationship between temperature increase and feedbacks (f) from the climate system is exponential (see Roe and Baker 2009 for details). The curve shown illustrates a mean f of 0.65, with a standard deviation (s) of 0.15, and is one of a whole family of curves whose shapes depend on the precise combination of f and s deployed. These estimates are, in turn, derived from model runs by Global Circulation Models (GCMs). The 10th to 80th probability percentiles are shown in light grey, and the 90th to 100th percentile in dark grey. Other lines of evidence yield similar results, but do not reduce the uncertainty in sensitivity estimates.

unlikely to reduce this uncertainty. Newer models are incorporating more sophisticated and complete representations of feedback mechanisms. Different models are constructed using a variety of techniques and guiding philosophies. These differences among models, together with the more complete representation of feedbacks, are likely to increase rather than reduce variations in the next generation of climate projections (Trenberth 2010).

By the end of this century, therefore, global warming may produce cumulative effects that vary from relatively mild inconvenience to major ecological and social disruption. But unfortunately, the current state of climate science provides a rather weak basis for predicting which version of the future is most likely to prevail.

Tree responses to climate

Projections from GCMs are frequently used to drive species distribution models (SDMs), whose purpose is to assess the effects of climate change on the distribution and health of trees. Until recently, ranges projected by SDMs would have been driven by a limited range of scenario/GCM combinations, thus sampling only a limited range of potential futures. To a degree, more recent distribution models have corrected this oversight. (Gray *et al.* 2011), for example, condition their aspen distribution model on an ensemble of 18 GCM/scenario combinations. Most SDMs also fail to include limitations on seed dispersal, disturbances, competition, and other determinants of species' realized niches. The incorporation of functional traits (as defined by Violle *et al.* 2007), local environmental variables and disturbance into model projections, has greatly reduced estimates of potential tree migration rates

compared to models lacking these variables. The use of traits, such as shade tolerance or disturbance sensitivity, has allowed tentative generalizations to be made about the potential of some tree species to adapt to the direct and indirect effects of AGW (Kienast *et al.* 2010, Matthews *et al.* 2011).

As with GCMs, increasing ecological realism in SDMs tends to produce divergence of potential future outcomes rather than convergence of expectations. SDMs that model future distributions of different provenances of maritime pine (*Pinus pinaster* Solan), Scots pine (*Pinus sylvestris* L.) (Garzón *et al.* 2011) and Canadian seed zones of trembling aspen (*Populus tremuloides* Michx.) (Gray *et al.* 2011) all illustrate this tendency. We therefore expect provenances within species to respond idiosyncratically to climate change, generating another source of uncertainty. Acknowledging this uncertainty has led to the development of a “bet-hedging” strategy for provenance selection that borrows from Portfolio theory for spreading risk in the stock market (Crowe and Parker 2008).

There is an emerging body of research on phenological and physiological acclimation to changing climate that has yet to be incorporated into SDMs. It is becoming clear that year to year changes in localized climate produce distinct responses in local genotypes. This appears to be an epigenetic phenomenon—a heritable change in gene expression with no change in DNA sequencing (Nicotra *et al.* 2010). Thus, progeny of full and half-sib families of Norway spruce experience delayed budset and increased susceptibility to freezing injury when the parent plants are exposed to warmer temperatures during embryogenesis (Johnsen *et al.* 2005b). The timing of bud set in this experiment was equivalent to that produced by 6° of latitude in seedlings whose embryos were exposed to cold versus warm conditions (Kvaalen and Johnsen 2008). Hybrid white spruce/Engelmann spruce (*Picea engelmannii* [Parry]) seedlings raised in warm days and cool nights had significantly lower spring and fall frost hardiness than those from a cool day regime (Webber *et al.* 2005). Day length during embryogenesis also modulates subsequent phenology in Norway spruce, with short day/warm temperature embryos being less frost hardy than those from other temperature/day length combinations (Johnsen *et al.* 2005a).

Trees may experience a transitory increase in respiration in response to rising temperatures, followed by a partial readjustment back towards pre-warming rates. This acclimation effect is observed in seedlings of paper birch (*Betula papyrifera* Marsh.), tamarack (*Larix laricina* [Du Roi] K. Koch), jack pine (*Pinus banksiana* Lamb) and black spruce (*Picea mariana* [Mill.] BSP) under ambient and elevated CO₂ (Tjoelker *et al.* 1999a,b), in three-year-old red and white oaks (*Quercus* spp.) (Bolstad *et al.* 2003), and latitudinally distinct provenances of sugar maple (*Acer saccharum* Marsh.) (Gunderson *et al.* 2000). Respiration also acclimated to higher temperatures in 20 climatically distinct jack pine provenances distributed among common gardens spanning a 7°C range in mean annual temperatures (Tjoelker *et al.* 2008).

How will epigenetic factors and acclimation of respiration factors affect the prospective results of AM? Climatically induced phenotypic plasticity (Jump and Peñuelas 2005) may buffer tree species that produce regular cohorts of seedlings against some of the effects of climate change. Longer growth periods but risky late-season budset in “warm-year” seedlings

might be offset by the less competitive but conservative early budset of “cold-year” phenotypes. In species whose establishment depends on periodic disturbance, however, the short window of establishment would likely allow only one or two epigenetic phenotypes to establish, depending on the climate of the year. Acclimation of respiration is likely to have positive effects, since any process that improves stomatal resistance in a warming climate will improve relative water economy. But the small species pool in which these processes have been demonstrated, and the fact that they are not included in models, inevitably contributes to our uncertainty about species response to climate change.

Negatives and Positives of Assisted Migration

How serious are negative impacts?

Many articles on AM have been written by conservation biologists, who have tended to generalize the risk of species becoming invasive across multiple taxonomic groups (Hunter Jr. 2007, Fazey and Fischer 2009, Ricciardi and Simberloff 2009). Whether an organism becomes invasive or not depends on functional traits whose character and behaviour will vary across taxonomic groups. Among plants, traits associated with invasiveness potential may also be silviculturally desirable. For example, an absence of identifiable natural enemies, which contributes to the severity of transcontinental invasions (Thompson and Davis 2011), may be a boon to species establishment in a planned silvicultural system.

According to some definitions, even native species that spread outside of their current range would be considered invasive (Niemi 2009). As Aubin *et al.* (2011) point out, however, the establishment of a translocated tree species would imply that it had been successfully naturalized, not that it was invasive. Furthermore, the inertia of intact forests against non-endemic tree species establishing themselves appears to be quite high (Hewitt and Kellman 1998). This may be one reason why Winder *et al.* (2011) found few examples of native North American species becoming invasive. Only one of these—the invasion of oak savannah by Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco)—appeared to be human-mediated. Others may not have been instances of invasion at all. For example, the increased dominance of beech over sugar maple in Québec may have been facilitated by factors related to natural succession and natural disturbance (Messier *et al.* 2009a), and the invasion of hardwood stands by eastern hemlock in upper Michigan may simply reflect an ongoing migration initiated in the early Holocene (Ste-Marie *et al.* 2011).

The available evidence therefore suggests that North American species translocated within the subcontinent have a low probability of becoming invasive. Set against this small probability are numerous advantages of pursuing well thought-out AM experiments and programs, with suitable controls to prevent the “migration” of pests along with the trees.

Different uses for AM

Constraints on species dispersal (Iverson *et al.* 2004, Araújo 2005, Svenning and Skov 2007) imply that large-scale natural migrations of tree species are unlikely. Under mid-range IPCC scenarios (about 3°C–6°C of warming), the translocation of provenances adapted to warm temperatures may therefore be the only way to ameliorate the effects of ongoing

climate change. "Off-site plantations" of seedlot provenances have been established historically (up to 50 years ago) in British Columbia, and have been remeasured to assess their long-term performance in the biogeographic zones to which they were moved (LePage and McCulloch n.d.). To adapt to more extreme climate change scenarios, however, managers may have to contemplate the establishment of no-analogue plantations composed of species imported from distant climate zones.

AM is also being contemplated for urban environments. In Chicago, trees characteristic of the southern US states, like swamp oak (e.g., *Quercus bicolor* Willd) and sweet gum (*Liquidambar styraciflua* L.), are being planted in anticipation of a warmer future. In Toronto, Kentucky coffee trees (*Gymnocladus dioica* [L.] K. Koch) are being planted for the same reason (Agrell 2011). AM could also be used to increase urban tree diversity, especially where existing boulevard trees are under threat from exotic pathogens such as Dutch elm disease (*Ophiostoma ulmi*) or emerald ash borer (*Agrilus planipennis*). Urban forests may also provide relatively low-risk environments for small-scale trials of non-endemic species from warm climates, whose survival at unfamiliar latitudes in cooler climate zones is not ensured.

Assisted migration may be co-opted to serve the goals and strategies for ecosystem restoration (ER), which are also likely to be affected by AGW. Restoration is "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SERI 2006). But under the changing conditions imposed by AGW, to what reference point should ecosystems be restored? Faced with extreme uncertainty about future conditions, restorationists have begun to ask whether they should be restoring historic species assemblages (the traditional focus of ER) or strive instead to establish ecosystems that combine desirable functional traits (Harris *et al.* 2006). If ecosystem function becomes the focus of ER, it is likely that AGW will force restorationists to consider the deployment of novel species assemblages in future restoration projects.

Taking AM "to the edge"

Assisted migration has the potential to buffer commercial forests, urban ecosystems and restoration efforts against some of the effects of AGW. Indeed, if the low-probability, extreme-consequence right-hand tail of the sensitivity spectrum is the one that plays out in the end, AM may become a necessity in all of these sectors. Where mixed-species stands are being planted, managers may find themselves establishing communities of species with no current analogues.

The design of no-analogue forest stands is clearly highly experimental, but there are reasons to suppose that the tree communities we see on today's landscapes are not as immutable as they appear. Paleoecological evidence demonstrates that rearrangement of community assemblages is not new to the landscape. The mixed woodlands of red oak (*Quercus rubra* L.), white spruce (*Picea glauca* [Moench] Voss) and black spruce, and tamarack that grew 14 350 years BP in Iowa (Jackson 2004) are one example of associations that have no analogue today.

(Lechowicz 1984) suggests that northern hemisphere hardwoods are imperfectly adapted to their current realized niches because their phenology is a legacy of ancient tertiary

environments in which they evolved. Current tree associations may therefore reflect accidents of dispersal as much as the outcome of environmentally or competitively mediated community development. If Lechowicz's (1984) perspective is correct, it may even be possible to design no-analogue mixtures of native species that are more productive than those we have at present.

Novel tree communities could be designed to combine compatible growth patterns and functional traits. Indeed, tree communities are already designed with these factors in mind. Stratified mixtures of local and non-endemic species have been established in Europe for over a century (e.g., Pommerening and Murphy 2004). Nitrogen-fixing trees are being combined with non-nitrogen fixing trees in some mixed stands (Parrotta 1999, Binkley *et al.* 2003, Maas-Hebner *et al.* 2005). These intimate mixtures potentially avoid down-regulation due to nitrogen limitations that can result from elevated CO₂ concentrations (Franklin 2007). An experimental silvicultural system in the UK combines a nurse tree (e.g., western red cedar [*Thuja plicata* Donn ex D. Don]) and the N-fixing shrub autumn olive (*Elaeagnus umbellata* Thunb.) to improve both the growth and form of common walnut (*Juglans regia* L.) (Clark *et al.* 2008). Tree communities could also be designed to minimize future fire risk by selecting species that produce less flammable litter (Kane *et al.* 2008, Schwilk and Caprio 2011), or those that resist the development of crown fires (Kafka *et al.* 2001).

AM presents us with opportunities to leverage climate change as well as the possibility of mitigating its effects. But which future climate should forest managers prepare for? Given the high levels of uncertainty about the full extent of AGW, the answer should perhaps be "all of them". This is the idea captured by the concept of "options forestry", which involves exploring multiple future scenarios or establishing a variety of silvicultural experiments, in the knowledge that uncertainty about the future is too great to "bet the farm" on supposedly optimal solutions (Bormann and Keister 2004). Clearly, many such experiments would fail. Others might be rescued through timely adaptive interventions as the trajectory of future climate becomes clearer. A lucky few might be well adapted to the actual climate scenario that eventually plays out.

What would these experiments look like, and how should they be distributed across the spectrum of future climates? For a start, they would probably be small-scale, but large enough to test hypotheses about interspecific interactions. Small-scale experiments are amenable to being more widely replicated than ambitious large-scale trials, and would allow a larger range of trials to be established with different purposes in mind. As for targeting future climate scenarios, perhaps experiments should be allocated in proportion to currently accepted probabilities for given increases in temperature. That is, the majority of experiments would be aimed at the mid-range of 2°C to 4.5°C; somewhat fewer would target warming of 6°C to 8°C, and fewer still would be aimed at the low-probability but high-consequence 10°C plus end of the range.

Alternatively, the larger long-term shifts in climate might be avoided by planting fast growing trees adapted to the anticipated climate over the next 15 to 30 years. Once harvested, climate trends would be re-evaluated, and a new cohort of

trees adapted to the next 15- to 30-year period would be planted. While this strategy might not be suitable for ecosystem restoration, it might find limited applications in urban forestry or agriculture, and would fit into the TRIAD zonation approach that is being tried in several jurisdictions (Messier *et al.* 2003, Messier *et al.* 2009b).

Forest Management and AM

If adopted, AM would likely necessitate local intensification of silvicultural practices. Forestry in Canada continues to be far more extensive than it is in most of the important forest jurisdictions around the world, with legal responsibilities for reforestation typically limited to achieving “free to grow” status. In the future, such extensive harvesting of the timber frontier will be less cost-effective as transport costs increase and pressures to protect large areas of the boreal forest intensify (Park and Wilson 2007). This view is reinforced by the International Energy Agency, which acknowledges that oil price rises are inevitable and that peak oil could be imminent (IEA 2010).

Our future capacity to implement AM or even to help existing forests acclimate to climate change is therefore likely to be limited by costs and geography. In fact, the majority of our forests may have to adapt in-situ with little management intervention (Spittlehouse 2005). AM experiments targeted at forest management will therefore have to be established close to existing infrastructure. Where commercial forestry is concerned, silvicultural intensification for the purpose of AM is likely to involve changes in landscape-level planning, investment decisions, and perhaps, provincial forest legislation. From the point of view of investment, data from many trials show that, in some cases, native Canadian species and hybrid poplars can achieve levels of production that rival tropical and warm temperate plantations (Park and Wilson 2007). Where AM is concerned, however, successful establishment, adaptability (to novel climates), enhanced pest resistance, and resilience in the face of natural disturbances and extreme weather may rival productivity as criteria for species selection.

Public Attitudes to AM

A potentially powerful obstacle to implementing AM in Canada arises from general attitudes to human interference with nature. Aubin *et al.* (2011) suggest that controversy around AM arises from the traditional divide between anthropocentric (utilitarian) and ecocentric views of nature. Some ecocentric authors state bluntly that AM is a techno-fix that distracts us from the need to take more direct action to mitigate AGW (Fazey and Fischer 2009). In Canada, opposition to AM may also be related to objections to planted forests in general. Plantations and intensively managed stands are accused of replacing “diverse native forests,” moving us away from an “ecological approach to forestry” (Conservation Council of new Brunswick 2001, Peaceful Parks Coalition 2002).

A related issue to public attitudes is the knowledge base from which such attitudes arise. Unfortunately, the available evidence shows that public knowledge of the biosphere and of pressing environmental issues is depressingly low. Summarizing its 2004 survey, The National Science Foundation concluded that both Americans and Europeans were ignorant of

basic science, and that their levels of knowledge had not advanced since 1990 (National Science Board 2004). Survey respondents from six nations frequently confused global warming with air pollution and ozone depletion (Dunlap 1998), and understanding has scarcely improved over time (Leiserowitz *et al.* 2010).

Similar surveys on public attitudes to forestry are in short supply, and none address the subject of AM. Answers to stewardship-related questions in existing surveys suggest that AM will not be well received by the public. When asked for their views on forest management, 58.5% of Fort Nelson residents felt that there was “too much focus on timber supply”, 71.1% agreed that “the balance of nature is delicate and easily upset”, and 72.3% thought that “when humans interfere with nature, it often produces disastrous consequences” (Harshaw *et al.* 2006)³. Even among forestry professionals, conflicting interpretations are attached to management concepts like “adaptive management” (Bormann and Keister 2004), emulation of natural disturbance (Klenk *et al.* 2008) and historic range of variability (Landres *et al.* 1999, Millar *et al.* 2007).

We are not arguing that public opinion should be excluded from the debate on AM. But we do suggest that widespread deferral to public opinion as an arbiter of AM projects without a concomitant investment in education will be a recipe for confusion and policy stalemates. In spite of the fact that much of the early literature on AM called for both stakeholder input and dissemination of information, little if any such outreach has been conducted (Hewitt *et al.* 2011).

Discussion and Conclusions

Thinking about AM in Canada is in its early stages, and it is far from certain when, if ever, it will be implemented. Quite apart from our lack of experience at moving genetic material for climate change adaptation purposes, there are significant knowledge barriers to be overcome and intractable uncertainties that will have to be accounted for if AM schemes are to be realized. As we have shown in this paper:

- Uncertainty about future climate sensitivity is greater than generally acknowledged. Temperatures could increase by as little as 2°C, requiring only minor adjustments to current management, or by as much as 10°C or more, necessitating major changes in the way forest lands are managed.
- There are major uncertainties around the responses of trees to AGW. Epigenetic phenomena and the acclimation of respiration in some species to warmer temperatures suggest that trees may be more robust to some level of AGW than previously thought. But we do not yet know what the limits of such acclimation might be.
- Invasiveness is a potential negative outcome of AM. Although the risk of invasion is not to be taken lightly, there is a low probability that native North American trees will become invasive, except under rather restricted circumstances.
- AM must be seen in the context of socio-economic changes that will inevitably affect the forest industry.

³These figures refer to residents who “strongly agreed” or “mildly agreed” with the statements on a five-point scale, with fewer than 7% answering “don’t know” to any question.

Transport costs will rise over time, undermining Canada's traditional strategy of harvesting extensive tracts of timber and extending the timber frontier to get fresh supplies. AM, if implemented, is likely to be a local phenomenon and may be suited to the implementation of TRIAD-style zonation of silvicultural activities.

- Public opinion will influence planning for AM, and may determine whether or not it is ever done. Without a concerted educational effort to acquaint the public at large with the facts and issues around AM, public consultation is unlikely to yield useful feedback.

Assisted migration, like the larger challenge of climate change, is a classically "wicked" problem (Rittel and Webber 1973). Its "wickedness" derives from the uncertainties that plague every level of knowledge generation, the challenge of achieving adequate levels of education among public and managers alike⁴, and the significant lags built into the climate system and any attempt to adapt forests to climate change. The lags that attend any attempt to do AM stem from the nature of trees as long-lived organisms that are slow to establish, as well as our inability to precisely predict the results of our interventions. Furthermore, trees planted today as seedlings must establish in the current climate while growing into and adapting successfully to the unknown climate of the future. Managers therefore face the dilemma of delaying action until knowledge improves—thereby risking climate induced loss of productivity and health in trees adapted to the current climate—or initiating AM experiments that run the risk of being maladapted to both the current and future climate. Either way, the manager risks failure. This double jeopardy potentially breeds paralysis, since even winning policies will be accompanied by inevitable losses.

The potentially serious problem of establishment failure raises the question of how to allocate efforts in silvicultural experiments. At a recent workshop on AM chaired by the authors, participants suggested that we should commence with analyses of data that we already have from common garden trials, many established decades ago for other purposes. This strategy has already been applied in British Columbia (Wang *et al.* 2006, LePage and McCulloch n.d.). These types of analyses suggest that some species and provenances may acclimate successfully to a 4°C to 5°C rise in temperature (Carter 1996, Rehfeldt *et al.* 1999, Wang *et al.* 2006). We do not know whether these temperatures represent hard limits, or whether acclimation can further stretch the limits of adaptation. We have also only just begun to explore the relationships between acclimation to temperature and other climatic parameters (Andalo *et al.* 2005, Thomson *et al.* 2008, Wang *et al.* 2009).

In our opinion, further progress in this area is likely to depend on the establishment of a wide variety of new field trials. To date, however, only BC's Assisted Migration Adaptation Trial (AMAT; O'Neill *et al.* 2011) has addressed the

needs of commercial forestry, while the Western Nursery Growers Group's TRUST trial addresses the need to produce new ornamental cultivars for urban forests and private gardens on the prairies (Krahn 2009). As described above, a potentially fruitful approach to new experiments would be to allocate trees and silvicultural treatments in proportion to the probability of different levels of AGW. With the possible exception of revised seed zones, the vast majority of Canada's forested lands would be likely to remain as controls on such experiments, providing benchmarks against which to assess the performance of translocated provenances and species.

References

- Agrell, S. 2011.** Hot enough for you? Preparing for Canada's 100-year heat wave. *The Globe and Mail*: Saturday, June 4th, 2011. A4.
- Andalo, C., J. Beaulieu and J. Bousquet. 2005.** The impact of climate change on growth of local white spruce populations in Québec, Canada. *Forest Ecology and Management* 205: 169–182.
- Andreae, M.O., C.D. Jones and P.M. Cox. 2005.** Strong present-day aerosol cooling implies a hot future. *Nature* 435: 1187–1190.
- Araújo, M.B. 2005.** Equilibrium of species' distributions with climate. *Ecography* 28: 693–695.
- Aubin, I. et al. 2011.** Why we disagree about assisted migration 1: Ethical implications of a key debate regarding the future of Canada's forests. *The Forestry Chronicle* 87: 755–765.
- Beardmore, T. and R. Winder. 2011.** Review of science-based assessments of species vulnerability: Contributions to decision-making for assisted migration. *The Forestry Chronicle* 87: 745–754.
- Binkley, D., R. Senock, S. Bird and T.G. Cole. 2003.** Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. *Canadian Journal of Forest Research* 182: 93–102.
- Bolstad, P.V., P. Reich and T. Lee. 2003.** Rapid temperature acclimation of leaf respiration rates in *Quercus alba* and *Quercus rubra*. *Tree Physiology* 23: 969–976.
- Bolte, A., C. Ammer, M. Löf, P. Madsen, G.-J. Nabuurs, P. Schall, P. Spathelf and J. Rock. 2006.** Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scandinavian Journal of Forest Research* 24: 473–482.
- Bormann, B.T. and A.R. Keister. 2004.** Options Forestry: acting on uncertainty. *Journal of Forestry* 102: 22–27.
- Carter, K.K. 1996.** Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. *Canadian Journal of Forest Research* 26: 1089–1095.
- Clark, J.R., G.E. Hemery and P.S. Savill. 2008.** Early growth and form of common walnut (*Juglans regia* L.) in mixture with tree and shrub nurse species in southern England. *Forestry* 81: 631–644.
- Conservation Council of New Brunswick. 2001.** Forests not tree farms [online]. Available from http://www.conservationcouncil.ca/forestry/forest_farms.html [Accessed on May 11th, 2005].
- 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.
- Dunlap, R.E. 1998.** Lay perception of global risk: Public views of global warming in a cross-national context. *International Sociology* 13: 473–498.
- Fazey, I. and J. Fischer. 2009.** Assisted colonization is a techno-fix. *Trends in Ecology & Evolution* 24: 475.
- Franklin, O. 2007.** Optimal nitrogen allocation controls tree responses to elevated CO₂. *New Phytologist* 174: 811–822.
- Garzón, M.B., R. Alía, T.M. Robson and M.A. Zavala. 2011.** Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography* 20: 766–778.

⁴As an example, in a recent workshop on assisted migration, the concept of AM came as a novelty to several members of the NGO community, and some managers were unfamiliar with the multi-dimensional nature of the AM challenge. For the majority of people, AM is simply not on the radar.

- Gray, L.K., T. Gylander, M.S. Mbogga, P.-Y. Chen and A. Hamann. 2011. Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecological Applications* 21: 1591–1603.
- Gunderson, C.A., R.J. Norby and S.D. Wullschlegler. 2000. Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree Physiology* 20: 87–96.
- Harris, J.A., R.J. Hobbs, E. Higgs and J. Aronson. 2006. Ecological Restoration and Global Climate Change. *Restoration Ecology* 14: 170–176.
- Harshaw, H.W., S.R.J. Sheppard, R.A. Kozak and T.C. Maness. 2006. Canfor Sustainable Forest Management Public Opinion Survey 2005/2006: Results for the community of Fort Nelson. Vancouver, BC. University of British Columbia Collaborative for Advanced Landscape Planning., Vancouver, BC.
- Hewitt, N. and M. Kellman. 1998. Factors influencing tree colonization in fragmented forests: an experimental study of introduced seeds and seedlings. *Forest Ecology and Management* 191: 39–59.
- Hewitt, N., N. Klenk, A.L. Smith, D.R. Bazely, N. Yan, S. Wood, J.I. MacLellan, C. Lipsig-Mummie and I. Henriques. 2011. Taking stock of the assisted migration debate. *Biological Conservation* 144: 2560–2572.
- Hunter, M.J. Jr. 2007. Climate change and moving species: Furthering the debate on assisted colonization. *Conservation Biology* 21: 1356–1358.
- IEA [International Energy Agency]. 2010. World energy outlook 2010: Executive summary. Paris. Available from www.worldenergy-outlook.org [Accessed on February 8th, 2012].
- IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate Change 2007: Synthesis report summary for policymakers. IPCC Plenary XXVII, Valencia, Spain, 12–17 November 2007.
- Iverson, L.R., M.W. Schwartz and A.M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13: 209–219.
- Jackson, S.T. 2004. Modern analogs in quaternary paleoecology: Here today, gone yesterday, gone tomorrow? *Annual Review of Earth and Planetary Science* 32: 495–537.
- Johnsen, Ø., O.G. Dæhlen, G. Østreng and T. Skrøppa. 2005a. Daylength and temperature during seed production interactively affect adaptive performance of *Picea abies* progenies. *New Phytologist* 168: 589–596.
- Johnsen, Ø., C.G. Fossdal, N. Nagy, J. Møllmann, O.G. Dæhlen and T. Skrøppa. 2005b. Climatic adaptation in *Picea abies* progenies is affected by the temperature during zygotic embryogenesis and seed maturation. *Plant, Cell and Environment* 28: 1090–1102.
- Jump, A. S. and J. Peñuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* 8: 1010–1020.
- Kafka, V., S. Gauthier and Y. Bergeron. 2001. Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. *International Journal of Wildland Fire* 10: 119–127.
- Kane, J., J.M. Varner and J. Hiers. 2008. The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impeters. *Forest Ecology and Management* 256: 2039–2045.
- Kienast, E.S.M.F., P.B. Pearman, J.-C. Svenning, W. Thuiller, M. B. Araújo, A. Guisan and N.E. Zimmermann. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33: 1038–1048.
- Klenk, N., G. Bull and D. Cohen. 2008. What is the “END” (emulation of natural disturbance) in forest ecosystem management? An open question. *Canadian Journal of Forest Research* 38: 2159–2168.
- Knutti, R. and G. C. Hegerl. 2008. The equilibrium sensitivity of the Earth's temperature to radiation changes. *Nature Geosciences* 1: 735–743.
- Krahn, A. 2009. Prairie T.R.U.S.T. Project. Western Nursery Growers Group (WNGG) [online]. Available from <http://www.prairie-trees.ca/prairie.htm> [Accessed on February 13th, 2012].
- Kvaalen, H. and Ø. Johnsen. 2008. Timing of bud set in *Picea abies* is regulated by a memory of temperature during zygotic and somatic embryogenesis. *New Phytologist* 177: 49–59.
- Landres, P.B., P. Morgan and F.J. Swanson. 1999. Overview of natural variability concepts in managing ecological systems. *Ecological Applications* 9: 1179–1188.
- Lechowicz, M.J. 1984. Why do temperate deciduous trees leaf out at different times? *Adaptation and ecology of forest communities. The American Naturalist* 124: 821–842.
- Leiserowitz, A., N. Smith and J.R. Marlon. 2010. Americans' Knowledge of Climate Change. Yale Project on Climate Change Communication., Yale University. New Haven, CT. Available from <http://environment.yale.edu/climate/files/ClimateChangeKnowledge2010.pdf> [Accessed on February 13th, 2012].
- LePage, P. and L. McCulloch. n.d. Assessment of off-site tree plantations in the northwest interior of British Columbia: Project summary. Forest Genetics Council of British Columbia; Genecology and Seed Transfer Program. Available from http://www.for.gov.bc.ca/ftp/HTI/external/publish/Jack_Woods/Off-Site_Species_Assessment-Final_Report-opt.pdf.
- Maas-Hebner, K.G., W.H. Emmingham, D.J. Larson and S.S. Chan. 2005. Establishment and growth of native hardwood and conifer seedlings underplanted in thinned Douglas-fir stands. *Forest Ecology and Management* 208: 331–345.
- Matthews, S.N., L.R. Iverson, A.M. Prasad, M.P. Peters and P.G. Rodewald. 2011. Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. *Forest Ecology and Management* 262: 1460–1472.
- McLachlan, J.S., J. Hellman and M.W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21: 297–302.
- Meinshausen, M., N. Meinshausen, W. Hare, S.C.B. Raper, K. Frieler, R. Knutti, D.J. Frame and M.R. Allen. 2009. Greenhouse-gas emission targets for limiting global warming to 2°C. *Nature* 459: 1158–1162.
- Messier, C., N. Bélanger, J. Brisson, M. J. Lechowicz and D. Gravel. 2009a. Comment on “Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter?”. *Canadian Journal of Forest Research* 41: 649–653.
- Messier, C., B. Bigué and L. Bernier. 2003. Using fast-growing plantations to promote forest ecosystem protection in Canada. *Unasylva* 54: 59–63.
- Messier, C., R. Tittler, D.D. Kneeshaw, N. Gelin, A. Paquette, K. Berninger, H. Rheault, P. Meek and N. Beaulieu. 2009b. TRIAD zoning in Quebec: Experiences and results after 5 years. *The Forestry Chronicle* 85: 885–896.
- Millar, C.I., N.L. Stephenson and S.L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17: 2145–2151.
- Minteer, B.A. and J.P. Collins. 2010. Move it or lose it? The ecological ethics of relocating species under climate change. *Ecological Applications* 20: 1801–1804.
- National Science Board. 2004. Science and Technology: Public attitudes and understanding. Chapter 7 *In Science and Engineering Indicators 2004* [online]. National Science Foundation, Division of Science Resources Statistics, Arlington, VA. Available from <http://www.nsf.gov/statistics/seind04/toc.htm> [Accessed on Feb. 25th, 2009].
- Nicotra, A.B. et al. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15: 684–692.
- Niemiera, A.X. 2009. Invasive plants: A horticultural perspective [online]. Virginia Polytechnic Institute: Virginia Cooperative Extension. Available from <http://pubs.ext.vt.edu/426/426-080/426-080.html> [Accessed on March 23rd, 2012].

- O'Neill, G., M. Carlson, V. Berger and N. Ukrainetz. 2011. Assisted Migration Adaptation Trial Workplan (Updated January 2011) [online]. Research Branch: BC Ministry of Forests, Mines, and Lands. Available from http://www.for.gov.bc.ca/hre/for/gen/interior/AMAT_workplan_21.pdf [Accessed on Feb 16th, 2011].
- O'Neill, G.A. et al. 2008. Assisted migration to address climate change in British Columbia: recommendations for interim seed transfer standards. Tech. Rep. 048, B.C. Ministry of Forest and Range, Research Branch, Victoria, B.C. Available from www.for.gov.bc.ca/hfd/pubs/Docs/Tr/Tr048.htm [Accessed on Nov 1st, 2010].
- Park, A. and E.R. Wilson. 2007. Beautiful Plantations: can intensive silviculture help Canada to fulfill ecological and timber production objectives? *The Forestry Chronicle* 83: 825–839.
- Parrotta, J.A. 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *Forest Ecology and Management* 124: 45–77.
- Peaceful Parks Coalition. 2002. Industrial tree plantations planned for Ontario [online]. Available from http://www.peacefulparks.org/ppc/campaigns_forest_tpl.htm [Accessed on May 27th, 2012].
- Pedlar, J.H., D.W. McKenney, J. Beaulieu, S.J. Colombo, J.S. McLachlan and G.A. O'Neill. 2011. The implementation of assisted migration in Canadian forests. *The Forestry Chronicle* 87: 766–777.
- Pommerening, A. and S.T. Murphy. 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77: 27–44.
- Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A. Hamilton Jr. 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs* 69: 375–407.
- Ricciardi, A. and D. Simberloff. 2009. Assisted colonization: good intentions and dubious risk assessment. *Trends in Ecology & Evolution* 24: 476–477.
- Rittel, H.W.J. and M.M. Webber. 1973. Dilemmas in a general theory of planning. *Policy Sciences* 4: 155–169.
- Roe, G.H. and M.B. Baker. 2005. Why is climate sensitivity so unpredictable? *Science* 318: 329–632.
- Schwilk, D.W. and A.C. Caprio. 2011. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology* 99: 970–980.
- SERI [Society for Ecological Restoration International Science & Policy Writing Group]. 2006. The SER International Primer on Ecological Restoration. Society for Ecological Restoration International, Tucson, AZ.
- Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. *The Forestry Chronicle* 81: 691–695.
- Ste-Marie, C., E.A. Nelson, A. Dabros and M.-E. Bonneau. 2011. Assisted migration: Introduction to a multifaceted concept. *The Forestry Chronicle* 87: 724–730.
- Svenning, J.-C. and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* 10: 453–460.
- Thompson, K. and M.A. Davis. 2011. Why research on traits of invasive plants tells us very little. *Trends in Ecology and Evolution* 26: 155–156.
- Thomson, A.M., C.L. Riddell and W.H. Parker. 2008. Boreal forest provenance tests used to predict optimal growth and response to climate change: 1. Jack pine Canadian Journal of Forest Research 38: 157–170.
- Tjoelker, M.G., J. Oleksyn and P.B. Reich. 1999a. Acclimation of respiration to temperature and CO₂ in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology* 49: 679–691.
- Tjoelker, M.G., J. Oleksyn, P.B. Reich and R. Ytkowiak. 2008. Coupling of respiration, nitrogen, and sugars underlies convergent temperature acclimation in *Pinus banksiana* across wide-ranging sites and populations. *Global Change Biology* 14: 782–797.
- Tjoelker, M.G., P.B. Reich and J. Oleksyn. 1999b. Changes in leaf nitrogen and carbohydrates underlie temperature and CO₂ acclimation of dark respiration in five boreal tree species. *Plant, Cell & Environment* 22: 767–778.
- Trenberth, K. 2010. More knowledge, less certainty. *Nature Reports: Climate Change* 4: 20–21.
- Trenberth, K.E. et al. 2007. Observations: Surface and atmospheric climate change. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller, (eds.). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge University Press, Cambridge, UK.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.
- Wang, T., A. Hamann, A. Yanchuk, G.A. O'Neill and S.N. Aitkin. 2006. Use of response functions in selecting lodgepole pine populations for future climates. *Global Change Biology* 12: 2404–2416.
- Wang, T., G.A. O'Neill and S.N. Aitkin. 2009. Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications* 20: 153–163.
- Webber, J., P. Ott, J. Owens and W. Binder. 2005. Elevated temperature during reproductive development affects cone traits and progeny performance in *Picea glauca* × *engelmannii* complex. *Tree Physiology* 25: 1219–1227.
- Winder, R., E.A. Nelson and T. Beardmore. 2011. Ecological implications for assisted migration in Canadian forests. *The Forestry Chronicle* 87: 731–744.