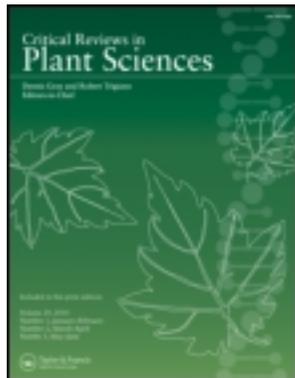


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Can Boreal and Temperate Forest Management be Adapted to the Uncertainties of 21st Century Climate Change?

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Can Boreal and Temperate Forest Management be Adapted to the Uncertainties of 21st Century Climate Change?

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Considerable uncertainties remain about magnitude and character, if not general direction of anthropogenic climate change. Global mean temperature could increase by 1.5–4.5°C or more over historic levels, and extreme weather events—drought, storms, and flooding—are likely to increase greatly in frequency. Although ecologists and foresters agree that the practice of forestry will be transformed under climate change, these uncertainties compound the challenge of achieving sustainable, adaptive forest management. In this article, we (i) present a multidisciplinary synthesis of current knowledge of responses of temperate and boreal tree species and forest communities to climate change, and (ii) outline silvicultural strategies for adapting temperate and boreal forests to confront climate change. Our knowledge synthesis proceeds through critical appraisals of efforts to model future tree distributions and responses to climate change, and reviews physiological, phenological, acclimation, and epigenetic responses to climate. As is the case of climate change itself, there are numerous uncertainties about tree species and provenance responses to climate change. For example, acclimation of respiration and epigenetic conditioning of seed embryos has the potential to buffer species against limited warming. Provenances within species also display idiosyncratic responses to altered climates, implying that soem varieties will be more resilient or resistant to climate change than others. Genetically determined limits to climatic tolerance, and the limits of tree community resistance and resilience (speed of recovery from dis-

turbance) in the face of climate-related disturbances are largely unknown. These unknowns require managers to adopt a portfolio of silvicultural strategies, which may range from minor modifications of current practices to design of novel multi-species stands that may have no historical analogue. Forest managers must be prepared to respond nimbly as they develop, incorporate new insights about climate change and species responses to warming into their practices. Marshalling all strategies and sources of knowledge should enable forest managers to mount (at least) a partially successful response to the challenges of climate change.

Keywords acclimation, adaptation, climate change, ecophysiology, epigenetics, forest management, forestry, phenology, predictive modelling, silviculture

I. INTRODUCTION

Future forests and many trees that are present right now are likely to grow into a rapidly changing climate with more variable weather and more pronounced climatic extremes. Managers of temperate and boreal forests must therefore develop silvicultural strategies that enable trees to survive as seedlings in today's climate while allowing them to mature successfully into an altered future climate. To successfully manage this transition, forest managers will have to negotiate multiple changes in

ecosystems, genetic adaptation, ecophysiology, and ecosystem resilience that are expected to accompany climate change.

Climatic trends capable of influencing ecological processes are already emerging from the background noise of random variation in the weather. Global average temperatures rose by $0.74 (\pm 0.18)^\circ\text{C}$ from 1906 to 2005 (IPCC, 2007), with greater warming recorded in mid- to high-latitudes than in the tropics. Temperatures in Canada's prairie provinces, for example, have risen by 1.6°C since 1895, (Sauchyn *et al.*, 2008), and those in Alaska increased by about 2.2°C since the early 1950s (Parson *et al.*, 2007). Seasonal and diurnal temperature ranges have decreased, as has temperature seasonality in the northern hemisphere, where winter and spring warming has exceeded summer temperature increases (Solomon *et al.*, 2007). Annual precipitation has increased in some temperate and boreal locations (Girardin *et al.*, 2004; Vincent and Mekis, 2006).

Forest ecosystems will continue to experience shifts in average climate conditions over the long term, but are also likely to suffer increased numbers and magnitudes of extreme weather events (Katz and Brown, 1992). These include wind storms, heat waves, spring freeze-thaw events, drought, and floods (Smith, 2011; Reyer *et al.*, 2013). Both shifting climatic means and extreme events have the potential to change age class and species distributions of whole forests, and impact the ability of species to regenerate (Hansen, 2001; Johnston *et al.*, 2009; Lindner *et al.*, 2010), as well as increasing the frequency and magnitudes of forest fires (Soja *et al.*, 2007) and insect infestations (Fleming, 1996). There is an emerging expectation that extreme weather events will have greater influences over the fate of forest ecosystems than long-run shifts in mean climate parameters (Adams *et al.*, 2009; Nabel *et al.*, 2013; Reyer *et al.*, 2013). The signature of such extreme weather events may now be emerging from stochastic interannual climatic variation, with the magnitude of recent heatwaves and storms falling three to five standard deviations beyond their long-run averages (Coumou and Rahmstorf 2012; Hansen *et al.*, 2012).

Wholesale geographic shifts in bioclimatic envelopes to which tree species and species provenances are adapted are likely to occur as climate change unfolds (Geber, 2008; Matthews *et al.*, 2011). Changes in seasonal temperature may alter the timing and character of critical phenological events (Chuine, 2000; Aitken *et al.*, 2008), which may increase bud and flower vulnerability to weather extremes (Jönsson *et al.*, 2004; Augspurger, 2009). Seasonal shifts in precipitation from summer to winter (C. Talbot, personal communication) or decreased rainfall frequency (Knapp *et al.*, 2008) might reduce growing season soil moisture. Extreme events may cause rapid mortality or even the shift from one biome type to another (Smith, 2011).

A. Uncertainty in Climate Change and Ecosystem Responses

Wide confidence intervals around future magnitude of change in temperatures compound the difficulty of managing forests under an altered climate. The latest multi-model average pro-

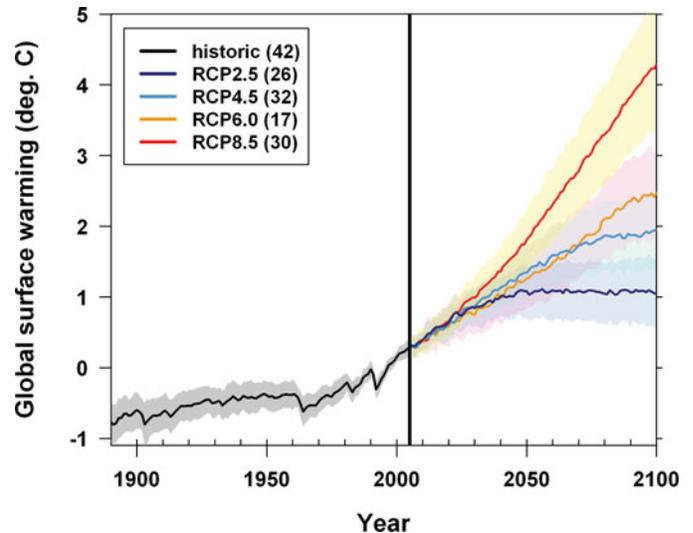


FIG. 1. Historic and projected future global temperature anomalies under Representative Concentration pathways (RCPs), relative to 1986–2005 temperature normals. Solid lines are averaged from representative runs of multiple GCMs (numbers in parentheses in legend), and shaded areas represent standard deviations of projected anomalies. This figure was redrawn from Knutti and Sedlacek (2013), Figure 1 using data kindly provided by Reto Knutti and his colleagues from the Institute of Atmospheric and Climatic Science, Swiss Federal Institute of Technology, Zurich.

jections of global warming suggest that temperatures will rise by $1.4\text{--}4.6^\circ\text{C}$ over 1990 levels (Van Vuuren *et al.*, 2008; Knutti and Sedlacek, 2013; see Figure 1). This range is contingent on uncertainties in future atmospheric CO_2 concentrations, which vary from 421 to 936 parts per million (ppm) by 2100 under the new Representative Concentration Pathways (RCPs) employed in IPCC projections (Meinshausen *et al.*, 2011).

Additional uncertainties are introduced by positive and negative feedbacks controlling climate sensitivity to rising atmospheric CO_2 . By the time global heat distribution equilibrates under these feedbacks, warming in excess of 8°C cannot be precluded (Andreae *et al.*, 2005; Meinshausen *et al.*, 2009). The enormous heat capacity of the oceans will delay the onset of such high equilibrium temperatures by centuries or even millennia (Friedlingstein and Solomon, 2005; Baker and Roe, 2009; Eby *et al.*, 2009). On the other hand, the boundaries of twenty-first century warming are no better constrained by new generation General Circulation Models (GCMs) than they were under previous versions (Knutti and Sedlacek, 2013). Forest managers will therefore have to manage their forests under high levels of uncertainty for the next few decades, but acknowledge that larger changes over the long term will commit forests to more profound, possibly unavoidable changes (Jones *et al.*, 2009).

If the magnitude of future climate change is uncertain, even greater contingencies attend the fate of forest ecosystems. Models designed to project future forest ecosystem conditions suffer from similar limitations to GCMs; indeed, they often

incorporate those limitations (McKenney *et al.*, 2011). Ecotones (Soja *et al.*, 2007) and species (Parmesan and Yohe, 2003; Beckage *et al.*, 2008) may already be undergoing geographical shifts in response to climate change. On the other hand, the possibility that natural selection could lead to rapid adaptation in some populations is being increasingly scrutinized (Rehfeldt *et al.*, 2001; Saxe *et al.*, 2001, Savolainen *et al.*, 2007; Lande 2009). Recent evidence also suggests that epigenetic acclimation to annual climatic variations may occur at the embryonic stage in certain conifers (Wagner *et al.*, 1996; Kvaalen and Johnsen, 2008; Dillaway and Kruger, 2010), but the significance of these findings for populations and individuals remains unexplored. This developing knowledge base raises important questions about adaptive limits of species and populations, and traditional views that seasonal phenology has a tight genetic relationships with local climate (Aitken *et al.*, 2008).

B. Risk, Opportunity, and Uncertainty in Forest Management

Our tenuous grasp of future climates and of the responses of tree populations to novel conditions creates an atmosphere of risk and uncertainty for forest managers and the forest industry. Increased frequency and variability of fires (Colombo and Buse (eds), 1998; Winnett, 1998; Soja *et al.*, 2007) and weather (Solomon *et al.*, 2001), northward migration of insect pests (Fleming 1996; Volney and Fleming, 2000), and the potential loss of local or regional climates for some forest types (Ohlson *et al.*, 2003) all demand a management response. Such risks are further compounded by the possibility that sudden climate regime shifts (tipping points) might occur in the future (Scheffer *et al.*, 2001; Ramanathan and Feng 2008), and that climates with no contemporary equivalents (no-analogue climates) might emerge, as they have in the past (Jackson, 2004).

Provided temperature increases remain relatively modest, climate change may also present opportunities for enhanced forest management. Longer growing seasons could increase forest productivity in the short to medium term (Johnston *et al.*, 2006), and warmer climates may allow foresters to expand the range of tree species that are planted. New commercial opportunities, such as using forests for carbon storage and establishing tree crops for short rotation biomass harvests may also occur (Hall and House, 1994; Saddler, 2002). Anticipation of increased growth rates and expanded ranges will, however, be tempered by species-specific responses to CO₂ enrichment (Loehle, 1995; Mohan *et al.*, 2007), altered competitive relationships (Caplat *et al.*, 2008; Clark *et al.*, 2011), and the constraints of nutrient limitation (Körner, 2006; Norby *et al.*, 2010; Penuelas *et al.*, 2011).

C. The Forester's Dilemma

Foresters have always been applied ecologists and geneticists, making decisions and acting on the basis of current ecological and biological understanding. They must now expand their ecological horizons to embrace recent findings of climate change science, global change biology, ecophysiology, and epi-

genetics. These changing perspectives must grow out of forest policy and management frameworks that historically treated climate as a constant factor (Cook, 1996). Thus forest growth models, stand-level silviculture, and landscape-level planning have traditionally been predicated on climates and disturbance regimes that varied within narrow, historically understood boundaries.

In recent decades, this normative view has been revised. Concepts like adaptive management, forest ecosystem management, and natural disturbance-based management (Grumbine, 1994; Everett *et al.*, 1996; Lertzman *et al.*, 1997; Gauthier and Grandpré, 2003; Fall *et al.*, 2004) have provided forester with a diverse collection of tools designed to build flexibility into, and cope with the inherent uncertainties that attend forest management. Foresters also have a large (but underutilized) toolbox of silvicultural techniques that can be used to modify successional trajectories of forest stands and growth patterns of individual trees (Smith *et al.*, 1997). In an unpredictable future climate, these tools should be deployed to favor species and species mixtures that can be managed within the limits of their climatic tolerances, edaphic environments, and competitive relationships. Practices that reduce the effects of transient extreme events, or foster rapid recovery from such events will also be favoured. Foresters are therefore required to understand and manage fundamental (or Grinnellian) niches of species, which are delimited by climate and physical environment (Figure 2), just as they currently manage the competition-limited realized (or Eltonian) niche (Silvertown, 2004; Jackson *et al.*, 2009; Soberón and Nakamura, 2009) using silvicultural practices. Seedlings and saplings typically tolerate a narrower range of conditions than adult trees (Figure 2, and see Jackson *et al.*, 2009), implying that special attention will have to be paid to silvicultural practices to nurture and establish regeneration. Effectively, foresters will be playing niche roulette, because they must establish species and provenances that will survive the hazards that attend seedlings, while rolling the dice on the ability of those seedlings to grow into the unknown future (Wang *et al.*, 2006; Garcia-Gonzalo *et al.*, 2007).

With these considerations in mind, foresters are now engaging in prospective analyses to explore forest management responses to climate change. Some treatments emphasize the inherent inertia of forests as ecosystems dominated by slow-growing, long-lived trees, and conclude that our ability to adapt is limited (Spittlehouse, 2005). Others advocate locating and focusing mitigation and adaptation efforts on forest regions that are particularly vulnerable to climate change (Johnston *et al.*, 2006), using a broader range of genetic material (Ray *et al.*, 2010), or establishing "neo-native" tree communities with no modern analogue (Bolte *et al.*, 2006). Nuanced evaluations of regional adaptations among provenances within species emphasize the importance of local adaptations and regional climate (Li *et al.*, 2010; Gray and Hamann, 2011; Richter *et al.*, 2012). To some degree, all strategies promote the adoption of flexible portfolios of strategies to confront escalating risks and uncertainties

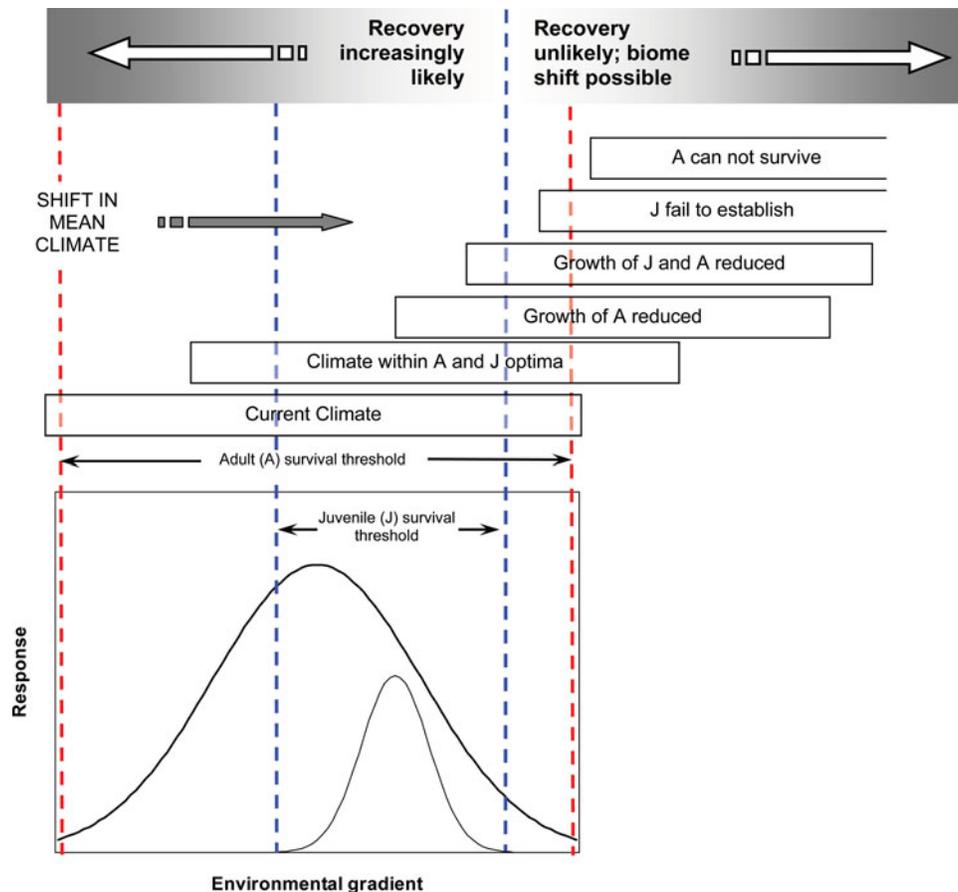


FIG. 2. Realized and fundamental niche spaces for regeneration and mature trees during climate change (after Jackson *et al.* 2009). Climate change can be conceptualized either as a gradual shift in climatic means, or in terms of weather extremes beyond historical bounds (Smith 2011). Conditions may therefore shift gradually or suddenly from the range where tree growth and juvenile establishment occur to conditions where juveniles fail to establish and relict adult populations survive for a while and finally to conditions that are fatal to adult trees.

(Spittlehouse and Stewart, 2003; Bormann and Kiester, 2004; Johnston *et al.*, 2006; Millar *et al.*, 2007; Crowe and Parker, 2008).

II. OBJECTIVES

Managed forests and the positive role that foresters might play in adapting them to climate change are often neglected in the ecological literature on forests and climate. We therefore have two major goals in this article: (i) to present a multidisciplinary synthesis of current knowledge about responses of temperate and boreal tree species and forest communities to climate change; and (ii) to use this synthesis as a springboard to explore management strategies that have the potential to adapt and modify temperate and boreal forests to confront climate change. Our primary focus is on temperate and boreal forests within North America, but we also draw on studies from Europe, which has a longer, richer history of managing forests for a multiple purposes.

We begin by briefly examining the insights and shortcomings of computer models designed to project responses of forests and tree species to climate change. We next evaluate empirical evidence from ecophysiological, ecological and genetic studies that probe the limits of tree adaptation and acclimation to climate. These lines of evidence are then synthesized with special reference to how they might be incorporated into silvicultural systems and practices designed to negotiate transitions into the future climate. Overall, we attempt to present management options that encompass the full range of potential climate futures, including low probability but high consequence climate scenarios and the challenges of extreme weather.

III. SYNTHESIS OF CURRENT KNOWLEDGE

A. Insights and Limitations of Models

Bioclimatic envelope models (BEMs), process-based models (PBMs), forest landscape simulation models (FLSMs), and empirical models derived from provenance trials are all relevant to studying climate effects on individual trees, forest stands, and

forest landscapes. Detailed critiques of these models have been published elsewhere (e.g., Loehle and LeBlanc, 1996; Schenk, 1996; Woodward and Beerling, 1997; Pearson and Dawson, 2003; Hampe, 2004; Heikkinen *et al.*, 2006), but because forest managers may turn to models as signposts to the future, we summarize the principal insights and critiques of models here. We also comment on technical developments that have made some model projections more robust and of potentially greater use to forest managers.

1. Bioclimatic Envelope Models (BEMs)

Because of their simple data requirements, BEMs are probably the most used predictive models of tree distribution. In BEMs, spatially explicit presence, presence/absence, or (exceptionally) abundance data for species together are correlated with an interpolated geographical grid of climate variables (Guisan and Thuiller, 2005; Morin and Thuiller, 2009). The climate envelope so produced is then coupled to climate projections from one or more GCMs to project potential spatial shifts in species-specific climate envelopes (Heikkinen *et al.*, 2006; Hijmans and Graham 2006; Botkin *et al.*, 2007).

Many BEMs predict large range shifts that lead to regional extirpation of tree species under different climate change scenarios. Shifts in climate envelopes as high as 800 km for red pine (Flannigan and Woodward, 1994) and 1000 km for sugar maple (McKenney *et al.*, 2007) are predicted by BEMs that use only climatic variables as predictors. Less dramatic range shifts (as low as 3 km) are reported when tree “movements” are further constrained by landscape, topographic, climatic and edaphic variables (Iverson *et al.*, 2008; Mbogga *et al.*, 2010). Inclusion of seed dispersal kernels to simulate dispersal limitations further restricts migration; dispersal-limited species are not projected to spread autonomously into new habitat by more than 20 km into over the next century (Iverson *et al.*, 2004). When large species assemblages that inhabit heterogeneous landscapes are considered, habitat gains as well as losses are projected for different species (Iverson *et al.*, 2008). BEMs have also been used to capture forest community structure using assembly rules based on species importance values, predicting, for example, losses of spruce-fir and aspen-birch forest types in the eastern USA, but habitat gains for oak-hickory and southern pine types (Iverson *et al.*, 2011).

BEMs have also been used to probe the degree to which tree species are currently occupying their potential ranges. In Europe between 34 and 72°N, 36 of 55 tree species filled less than 50 percent of their potential range, as predicted by a BEM, a finding attributed to severe dispersal constraints in Europe's complex geography (Svenning and Skov, 2004).

2. Process-Based Models (PBM)

Process-based models explicitly delineate relationships between physiology, growth, and environment. They therefore have the potential to portray more realistic responses to cli-

mate change than BEMs. Here we consider two large classes of PBMs: gap models and phenology-based PBMs.

Gap models. Gap models portray the responses of tree growth, mortality, and competition to environmental variables in small (~0.01 ha) forest plots (Bugmann, 2001; Robinson *et al.*, 2008). Physiological variables, such as stomatal conductance, feedbacks from differing light, temperature or CO₂ levels are included in some models. Scaling up to whole forest projections is done by aggregating results from many individual patches (Botkin *et al.*, 2007).

Hybrid models that combine individual tree growth and local interactions of gap models with forest inventories can provide insights that are potentially useful in forestry. Using this technique, Ehman *et al.* (2002) forecast the virtual complete loss of northern conifers and northern deciduous species from southern Great Lakes forests in response to temperature increases of 3.11 to 3.67°C along with a 2 to 14% rise in precipitation. Less dramatic species shifts from *Larix* and *Picea* to *Fraxinus*, *Quercus*, and *Tilia* spp were forecast in eastern Eurasian forests under moderate climate change (warming of 1.1–3.1°C and 0.2–5.6% more precipitation) (Zhang *et al.*, 2009).

When several gap models that use different algorithms constructed under slightly different assumptions are compared, their projections typically tend to diverge. For example, six gap models applied to five European sites under six climate change scenarios returned estimates of current tree biomass that were 44% to 559% of the actual biomass present. The same model/scenario combinations forecast changes to future biomass that varied from –41.1% to +40.3% of contemporary biomass (Badeck *et al.*, 2001).

Some models incorporate CO₂ fertilization into their projections. In contrast to BEMs, which forecast reduced ranges for Mediterranean pines and oaks by 2080, a gap model with CO₂ fertilization led tree productivity to increase by two to three times that of a non-fertilized control run (Keenan *et al.*, 2011). On the other hand, after allowing for a negative relationship between growth rates and longevity across a large suite of temperate trees at multiple sites, (Bugmann and Bigler, 2011) find that CO₂ fertilization effects may be offset by competition-induced growth reductions and increased mortality. Local interactions captured by gap models may therefore override processes that act globally (e.g. CO₂ fertilization), a result of great significance to foresters.

Attempts have been made to use gap models to explore forest management planning under climate change. Stem thinning operations combined with warming using the FINNFOR model increase growth in Scots pine (*P. sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst) and silver birch (*Betula pendula* Roth) (Briceño-Elizondo *et al.*, 2006). Using a model (GOTILWA) in which stomatal conductance and leaf area index (LAI) are modulated by temperature and CO₂, Sabaté *et al.* (2002) explored responses of Mediterranean trees to 4–7°C of warming. Under standard thinning treatments, growth rates increased for both coniferous (*Pinus* spp) and broad-leaved

(*Quercus ilex* L. and *Fagus sylvatica* L.) species in this study, but growth responses were mediated by different processes, depending on the species involved. *Fagus sylvatica* experienced increased life expectancy and growing season duration in response to higher temperatures, but growth rates of pines and *Q. ilex*, were reduced by increased foliage turnover. Finally, total wood production was maximized under 20-yr harvest intervals, which captured natural mortality better than 40 or 140 yr intervals. Temperature increases (up to 5°C) and doubled CO₂ combined with thinning also increased growth and timber yield of Scots pine, Norway spruce and silver birch in Finland (Briceño-Elizondo *et al.*, 2006). Notably, growth increases were up to 17% greater in the north of the country than in the south.

Increased growth under elevated CO₂ and temperature is, however, sensitive to changes in precipitation. In Finland, a simulated 20% decrease in precipitation reduced growth of southern populations of silver birch and Norway spruce. Similarly, reduced precipitation and drought-prone soils reduced growth of Radiata pine (*Pinus radiata* (D. Don)) plantations in southwestern Australia that were subjected to rising temperatures and CO₂ (Simioni *et al.*, 2008).

Phenology- and physiology-based PBMs. It is now axiomatic that phenology (seasonal timing of critical life events) will play an important role in the adaptation or maladaptation of trees to climate change (Badeck *et al.*, 2004; Nicotra *et al.*, 2010; Polgar and Primack, 2011). Phenology-based PBMs, such as PHENOFIT (Chuine and Beaubien, 2001), and models that link empirical growth data to tree physiology (e.g., 3-PG; Landsberg and Sands, 2011) accurately predict species presences in 74–96% of landscape cells (Morin *et al.*, 2007; Coops *et al.*, 2009). Successful predictor variables can then be used to gain insights into factors that limit current species ranges. In agreement with the thermal limitation hypothesis (Morin and Chuine, 2006), northern distribution limits of sugar maple, bur oak (*Quercus macrocarpa* Michx.) and several other hardwood species appear to be limited by the time needed for fruit maturation. By contrast, southern range limits were associated with inadequate chilling, resulting in failure to break dormancy, or premature flowering being punctuated by frost (Morin *et al.*, 2007). Coops *et al.* (2009) used the physiology-based PBM 3-PG to correlate four simple climate variables with year-round photosynthesis in widespread conifers from western North America. Subsequent regression tree analyses demonstrated that high temperatures and moisture deficits were limiting on Sitka spruce (*Picea sitchensis* (Bong.) Carr), but that western juniper and Ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) had low sensitivity to the same variables.

Phenology-based PBMs that simulate frost tolerance and chilling requirements (Leinonen, 1996; Sykes *et al.*, 1996) predict complex relationships between spring phenology and climate extremes. Leinonen's (1996) model, which subjected needles of Scots pine to winter temperatures 4.4–6.2°C warmer than at present, predicted that frost damage would be inversely proportional to minimum frost-hardy temperatures and the du-

ration of required chilling. Trees in the process of dehardening become vulnerable to “temperature backlashes”—periods of reversion to sub-zero temperatures following the breaking of dormancy and budburst. Under projected winter warming of 2–4.5°C, backlash frequency and subsequent frost damage were predicted to increase across the range of Norway spruce in Finland, especially in the south of the country (Jönsson *et al.*, 2004).

3. Forest Landscape Simulation Models (FLSMs)

FLSMs emphasize interactions between large forest stands (Xi *et al.*, 2009) and natural disturbances (He *et al.*, 1999; Perry and Neal, 2006) at scales of 1.0–10⁷ ha. By including natural disturbances, FLSMs incorporate indirect climatic influences that could affect forest species composition more profoundly than direct climate change effects. Fire risk and frequency, for example, are closely related to continental-scale, semi-predictable weather patterns. Wildfires in some forest types in the Pacific Northwest are associated with blocking high pressure systems, which divert storm tracks and cause dry easterly winds that increase fire hazard (Gedalof *et al.*, 2005). Drought and fire risks in Canadian boreal forest are modulated by decadal cycles in the North Atlantic and the North Pacific circulation, with drought coinciding with high pressure over the Gulf of Alaska and Baffin Bay (Girardin *et al.*, 2004).

By coupling landscape models to PBMs or forest inventory models, large scale changes to biomes can be projected. Loss of boreal species in Wisconsin after a century of gradual warming was forecast by coupling a gap model (LINKAGES), which simulates decomposition, mineralization and soil water status (Pastor and Post, 1986), with a landscape model (LANDIS) (He *et al.*, 1999). A similar coupled model was used by Xu *et al.* (2007) to explore interactions between rising CO₂, photosynthetically active radiation (PAR), soil moisture, and forest succession in the Boundary Waters Canoe Area (BWCA). As in Keenan *et al.* (2011), rising CO₂ increased tree growth by reducing photorespiration. But under 5°C of warming, the model predicted a widespread transformation of boreal mixedwoods to pines on dry soils. Forest composition in Karelia, Finland was also predicted to become dominated by pines by a coupled inventory-based FLSM and physiology-based PBM under a variety of rising CO₂ and warming scenarios (Nuutinen *et al.*, 2006).

4. Response and Transfer Functions

Response and transfer functions (RTFs) are statistical models that explore growth among provenances (regional varieties) grown in common gardens across a species range. Response functions relate different regional test climates to the growth of a single provenance planted at each regional site. The result is then used to predict the climate regime that will maximize a given provenance's growth. Transfer functions complement response functions by exploring relative performances of many provenances under a single regional or local climate, using

climate variables from their home sites as predictors (Thomson *et al.*, 2008a). The transfer function is therefore an attempt to locate optimally performing seed sources for particular sites.

A key result derived from RTFs is that optimally-performing provenances are not always local varieties that are assumed to be closely adapted to their sites. In trials established in the 1970s, northern provenances of lodgepole pine (Rehfeldt *et al.*, 2001) and black spruce (*Picea mariana* (Mill.) B. S. P.) (Thomson *et al.*, 2008b) increased height and diameter growth when transferred to warmer temperatures. Southern provenances of jack pine (*Pinus banksiana* Lamb.) benefit from being transferred to cooler sites while growth of northern provenances is reduced in warmer conditions (Savva *et al.*, 2007; Thomson *et al.*, 2008a). For a warming of 1–5°C, height growth of lodgepole pine provenances with the best performance at each site is projected to range from –100% to 147.1% of growth rates at their sites of origin (Wang *et al.*, 2006; see Figure 3a). By contrast, precipitation played a larger role than temperature in producing growth differences of about 20% in white spruce grown in common gardens in eastern Ontario (Andalo *et al.*, 2005). Smaller differences (–6.9 to 6.3%) in height growth were projected by RTFs for 60 provenances of white ash (*Fraxinus americana* L.), green ash (*Fraxinus pennsylvanica* Marsh), yellow birch (*Betula alleghaniensis* Britton), white pine (*Pinus strobus* L.), and nine other species exposed to 4°C of warming (Carter 1996; Figure 3b). In this study, most species experienced growth reductions when moved more than 1–2°C away from seed source locations, although these were not always pronounced. Exceptions were red maple (*Acer rubrum* L.) green ash, where the greatest height growth occurred in temperatures 4–5°C warmer than their points of origin (Figure 3b).

RTFs have the advantage of being empirically based, data rich, and relatively easy to calculate. Provided the geographical shift from a provenance's local climate to a test climate can be taken as an analogue for in-situ climate change in the future, RTFs may be directly linked to the management of seed zone boundaries and species selection.

5. Model Limitations

Extrinsic limitations on almost all models include scarcity and patchy distribution of data needed for their parameterization (McMahon *et al.*, 2011). Phenofit, for example, was parameterized using phenological data from just two locations (Morin *et al.*, 2007). Tree species respond idiosyncratically to shifting climatic means and elevated CO₂ (Loehle, 1995; Curtis and Wang, 1998), implying that forest species composition and competitive relationships will change as species adapt or migrate at different rates (Jackson, 2004; Williams and Jackson, 2007; Hartmann and Messier, 2011). Even models that successfully predict current forest species composition will need to be extrapolated beyond the limits of their supporting data and thus are likely to be less successful when prediction species composition under novel climate futures, which could occupy 4%–89% of the global land mass over the next century (Williams *et al.*, 2007). No-analogue paleoclimates featured species communities with

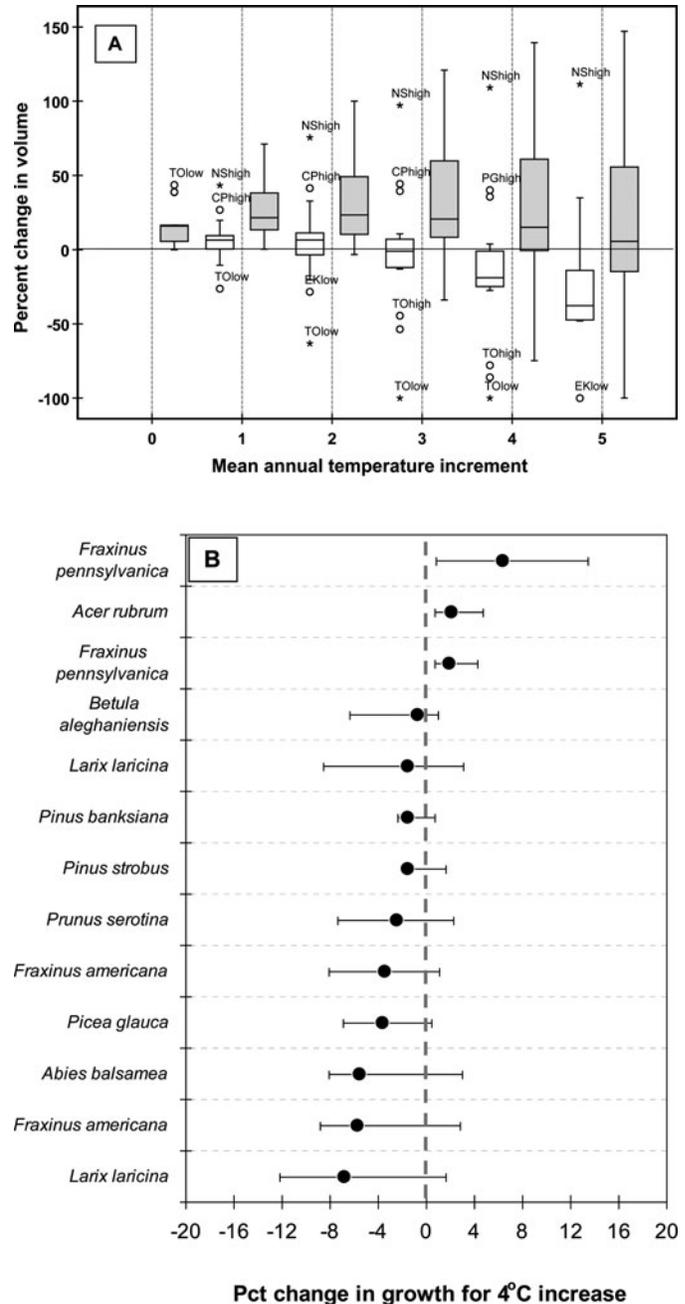


FIG. 3. (a) Projected percent changes in lodgepole pine stem volume ($\text{m}^3 \text{ha}^{-1}$) under warming of 0 to 5°C for 16 seed planning units (SPUs) in British Columbia (original data in Wang *et al.* 2006, Table 1). Clear bars are responses of SPUs grown at their site of origin. Grey bars are responses of optimally performing SPUs, which may have been shifted geographically from other areas. Note the consistently high performance of the NShigh SPU across the full range of temperatures. (b) Mean response and 95% confidence intervals for percentage change in height growth of northern hardwoods and conifers in response to being shifted through a 4°C increase in mean annual temperature (original results in Table 2, Carter, 2006).

no obvious modern equivalents (Williams *et al.*, 2001), such as mixed forests of red oak (*Quercus rubra* L.), white and black spruce, and tamarack (*Larix laricina* (Du Roi) K. Koch) that grew 14,350 years BP in southwestern Iowa (Jackson, 2004).

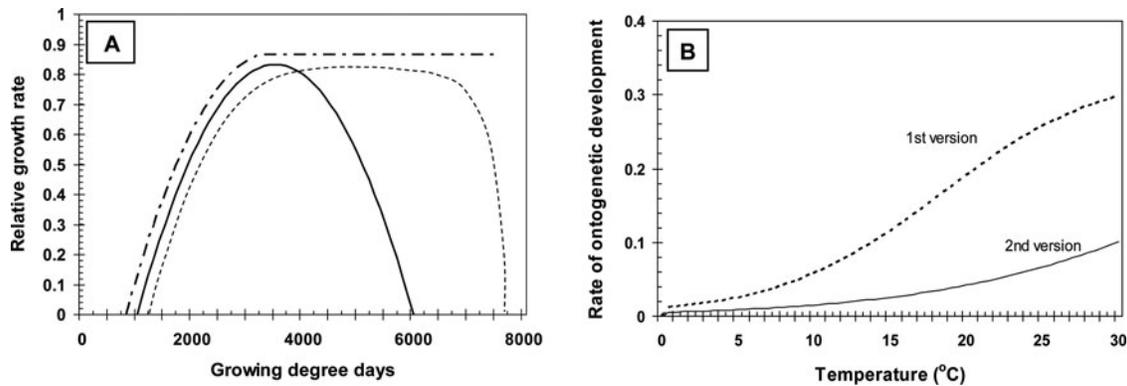


FIG. 4. (a) Parabolic relationship of growth with heat sum (solid line) contrasted with asymptotic growth equation used in Loehle (2000) (dash / dot line) and an extended parabola (Loehle and LeBlanc, 1996) that illustrates hypothesized growth beyond realized niche (dashed line). (b) Curves of ontogenetic development response to temperature forcing incorporated in two versions of a frost damage model for Scots Pine (Hänninen, 2006). The second version produced considerably less damage than the first one.

Although they have the virtue of simplicity, most BEMs exclude key biotic and abiotic variables that covary with climate (Roberts and Hamann, 2011). Excluded variables include symbiosis, trophic relationships, herbivory and competition (Pearson and Dawson, 2003), genetic variability (Hampe, 2004), habitat fragmentation (Heikkinen *et al.*, 2006), dispersal limitation (Botkin *et al.*, 2007), and natural disturbances. These variables help determine species' realized niches, and almost certainly mask the true climatic limits of tree species. The assumption that species are in equilibrium with current conditions (Araújo, 2005) is also undermined by evidence that some tree distributions are still shifting in response to past changes in climate (Payette, 1993; Svenning and Skov, 2005; Anderson *et al.*, 2006; Cheddadi *et al.*, 2006). For these reasons, simple correlations between climate and current species ranges are likely to underestimate the true extent of fundamental niches (Roberts and Hamann, 2011).

Heterogeneity among model designs and their driving equations produces widely divergent results between process-based models (Badeck *et al.*, 2001). Most mortality functions incorrectly assume that trees run a constant risk of death regardless of age (Bugmann *et al.*, 2001; Keane *et al.*, 2001), resulting in overly-conservative growth thresholds for mortality, especially in shade-tolerant species (Loehle, 1996). Mis-specified mortality functions combined with a parabolic growth response to temperature (see Figure 4a) underestimate many species' ability to survive at the edges of their geographic ranges (Loehle and LeBlanc, 1996; Schenk, 1996; Bugmann *et al.*, 2001). Actual growth rates increase towards the southern range limits of some boreal and temperate tree species (e.g. *Picea sitchensis*, *P. mariana*, and *Fraxinus americana* L. (Leblanc and Loehle, 1993; but see Carter, 2006). Asymptotic growth curves or extended parabolas (Figure 4a) are therefore proposed to provide more realistic fits of growth to yearly temperature sums (Loehle and Leblanc, 1996; Schenk, 1996).

Future no-analogue climates impose limits on the utility of RTFs for identifying climatically matched provenances. RTFs

are further limited when they are used in a quest for optimal (often read to mean *fast*) growth. Fast growing provenances are often recommended for widespread deployment (Wang *et al.*, 2006; see Figure 4a), but such recommendations ignore other imperatives, such as timber strength and quality, minimizing vulnerability to pest outbreaks, maintaining wildlife and other non-timber values, and the dynamics of mixed species communities. In the case of lodgepole pine, for example, past forest management inadvertently created age class distributions that were maximally susceptible to mountain pine beetle (*Dendroctonus ponderosae*) attack (Safranyik and Carroll, 2006). Secondary succession following beetle attack favors the development of mixed species stands (Burton, 2010) that may be less susceptible to catastrophic beetle outbreaks. Unless they explicitly incorporate pest damage and disturbance, transfer functions will have nothing to say about the resilience of such stands in the future.

6. Recent Model Improvements

Recent improvements in model design and data processing have offset some of the weaknesses discussed above (Table 1). After incorporating functional traits (as defined by Violle *et al.*, 2007), local environmental variables, and disturbance into model projections, Matthews *et al.* (2011) suggested that susceptibility to natural disturbances would be a key determinant of species' area occupancy as climate warms. Species such as black ash (*Fraxinus nigra* Marsh.) have traits that make them vulnerable to both changing climate and disturbance (e.g., emerald ash borer), while others (e.g., Manitoba maple - *Acer negundo* L. and red maple - *Acer rubrum* L.) appear to be widely adaptable. Taking a similar approach, Kienast *et al.* (2010) found that BEM projections of current distributions of broadleaved and coniferous species in the Swiss Alps were greatly improved by including a suite of biotic and abiotic variables in the model. Interannual climatic variation also has the potential to greatly modify dispersal and establishment (Nabel *et al.*, 2013). Model

TABLE 1
Selected recent model results with that have the potential to inform forest management under climate change

Model type	Results	Citation	
Bioclimatic envelope models	<ul style="list-style-type: none"> • Use of abundance data reduces range contraction under any given warming scenario. 	(Iverson <i>et al.</i> 2011)	
	<ul style="list-style-type: none"> • Species response to climate change highly individual, but species vulnerable to greatest range loss tend to be those most vulnerable to disturbance (e.g., <i>Fraxinus nigra</i>). 	(Matthews <i>et al.</i> 2011)	
	<ul style="list-style-type: none"> • Biotic (e.g., shade and stress tolerance, species community) and abiotic variables (topography, disturbance, climate) strongly and independently influence species climate envelopes. 	(Kienast <i>et al.</i> 2010)	
	<ul style="list-style-type: none"> • Use of seed dispersal kernels restrict migration into new habitat; dispersal of more than 20 km over a century considered unlikely. 	(Iverson <i>et al.</i> 2004)	
	<ul style="list-style-type: none"> • Choice of GCM introduces large differences in modeled tree distributions—uncertainty therefore still very high. 	(McKenney <i>et al.</i> 2011)	
	<ul style="list-style-type: none"> • Provenances within species show heterogeneous responses to warming. Some provenances may increase distribution under moderate climate change. 	(Garzón <i>et al.</i> 2011, Gray <i>et al.</i> 2011)	
	Process-based models	<ul style="list-style-type: none"> • Parabolic growth response to temperature projects greater dieback under warming than more realistic asymptotic functions. 	(Loehle 2000)
<ul style="list-style-type: none"> • Projected frost damage is also sensitive to shape of relationships between temperature and bud development, and of chilling with dormancy. 		(Linkosalo <i>et al.</i> 2006)	
<ul style="list-style-type: none"> • Models where freeze-thaw events “reset” forcing requirements, or critical heat sums induce irreversible development improve match of models to phenology, though mechanisms are hypothetical at this point. 		(Hänninen 2006)	
<ul style="list-style-type: none"> • Northern distribution limits of sugar maple and several other species may be limited by insufficient time for fruit maturation. Southern range limits may be delimited by inadequate chilling or (in early flowering species) frost damage. 		(Morin <i>et al.</i> 2007)	
<ul style="list-style-type: none"> • Interannual variability in growing degree days (GDD), minimum winter temperatures and a drought index produce a wide variety of dispersal and establishment in European hop hornbeam (<i>Ostrya carpinifolia</i> Scop.). 		(Nabel <i>et al.</i> 2013)	
Response and transfer models		<ul style="list-style-type: none"> • Model performance improved by using height residuals as an index of non-climatic variation in response functions for lodgepole pine conditioned on eight climate variables. 	(O’Neill 2007)
		<ul style="list-style-type: none"> • Inclusion of environmental variables other than precipitation improves performance of RTFs, and help explain why local provenances do not always grow best at their sites. 	(Andalo <i>et al.</i> 2005, Thomson <i>et al.</i> 2008a, Wang <i>et al.</i> 2009)
	<ul style="list-style-type: none"> • Northern provenances of several conifers improve growth under moderate warming, while southern provenances may benefit from cooler temperatures 	(Thomson <i>et al.</i> 2008b, a)	
	<ul style="list-style-type: none"> • Number of internodes set in previous year, not phenology explains growth differences among provenances of <i>Pinus contorta</i>, and <i>P. monticola</i>. Provenances from stressful environments produce fewer internodes, maybe due to reallocation of carbohydrates to stress resistance. 	(Chuine <i>et al.</i> 2006)	

runs of TreeMig (a landscape-scale gap model) that incorporated stochastic interannual climate variability produced a diversity of dispersal and establishment patterns compared to projections based on gradual shifts in mean climatic parameters.

BEMs are increasingly being parameterized using the traits of provenances (geographically distinct varieties) within species. The inclusion of provenance trial data in BEMs led to a plurality of responses to climate change among geographical varieties of maritime pine (*Pinus pinaster* Solan), Scots pine (Garzón *et al.*, 2011), and Canadian seed zones of trembling aspen (*Populus tremuloides* Michaux.) (Gray *et al.*, 2011). An analysis that compared reciprocal transplant and common garden experiments with BEM projections supported northward transfers of aspen varieties from warmer to (currently) cooler seed zones in Canada's prairie provinces (Gray *et al.*, 2011). However, combined risks of late frost and spring drought are associated with later bud burst in aspen from dry regions in western North America (Li *et al.*, 2010), suggesting that adaptation and survival will be purchased at the price of lower productivity for this species in this region.

Like BEMs, RTFs are refined and improved by augmenting temperature with additional climatic, environmental or physiological variables. March precipitation and January minimum temperature are the best correlates of jack pine growth in northern Ontario (Thomson *et al.*, 2008a), and including annual precipitation doubles the R^2 of transfer functions for white spruce in Quebec (Andalo *et al.*, 2005) (Table 1). Using residuals from a height growth/climate regression to estimate non-climatic inter-site variation significantly improves RTF predictions for lodgepole pine (O'Neill, 2007). Furthermore, sensitivity of radial growth to climate among lodgepole pine provenances is conditioned by their temperature of origin. Provenances from cool climates were most sensitive to temperature changes, while warm climate provenances were more sensitive to aridity than temperature when they were grown in the same warm microclimate (McLane *et al.*, 2011).

Recent comparative studies demonstrate the sensitivity of all models to differences in their core equations and underlying assumptions. Parabolic growth responses to temperature in the gap model SORTIE produce large diebacks of northern hardwoods in response to simulated warming, whereas asymptotic growth response functions predict no such diebacks (Loehle, 2000). Species-specific biomass during 1500 years of climate change also differs between asymptotic and parabolic versions of the FORCLIM model (Bugmann, 2001). In frost tolerance models, differences in the equation form specifying cessation of dormancy and post-dormancy ontogenetic development produce large differences in frost damage to Scots pine (Hänninen 2006; see Figure 4b). The greatest algorithmic sensitivity may lie in the GCMs that produce the climate projections on which many BEMs and PBMs depend. Different versions of the same GCM produce radically different projections of future climate, and consequently, great differences in predicted species distributions (McKenney *et al.*, 2011).

7. Summary of Insights from Models

Greater detail and ecological realism increase the range of possible outcomes in BEMs and PBMs, while RTFs are improved by addition of local environmental variables. The use of large GCMs/climate scenario ensembles in BEMs arguably produces more robust models, but adds new sources of variability to projections of species distribution. These sources of uncertainty are compounded the further into the future projections are made, adding another cause of uncertainty for forest managers (Gray and Hamann, 2012).

One response to this inescapable uncertainty is a "bet-hedging" strategy for provenance selection that borrows from Portfolio theory for spreading risk in the stock market (Crowe and Parker 2008). Another precautionary approach is to recommend that forest managers focus on short term strategies, such as the revision of seed transfer zone boundaries. This recommendation follows the realization that a profoundly altered climate of the late 21st Century might require long-distance transfers of species and provenance outside of their current ranges (Gray and Hamann, 2012; see Section D.3 below). Such transfers might be accompanied by ecophysiological responses whose outcomes are not readily predicted by models. Indeed, the potential physiological responses of trees to climate change is the subject of intense empirical research, and many new findings have not yet been incorporated into models. It is to these issues that we turn next.

B. Adaptation and Acclimation of Phenology, Respiration, and Photosynthesis

1. The Importance of Phenology

A core axiom of phenology is that tree populations are locally adapted to synchronize growth, dormancy, flowering and bud-burst within a narrow range of climatic conditions (Lieth, 1974). This axiom leads to the prediction that rapid climate change will lead to a mismatch between species and climatic drivers of phenology and growth (Jump and Peñuelas, 2005; Cleland *et al.*, 2008; Miller-Rushing *et al.*, 2010). Such fears are fuelled by widespread advances in the timing of flowering and spring budburst in temperate and boreal forests during the 20th Century (Beaubien and Freeland, 2000; Parmesan and Yohe, 2003; Menzel *et al.*, 2006; Morin *et al.*, 2009).

Failure to achieve chilling requirements for leaf development or bud-burst (Kriebel and Chi-Wu, 1962), inadequate frost hardening (Campbell and Sorensen, 1973), or the occurrence of unseasonal frosts after bud-burst or flowering (Jönsson *et al.*, 2004; Gu *et al.*, 2008) are potent risks to tree health in temperate and boreal forests. These risks have a well-established genetic basis. The relationships between bud set and declining day length in seedlings, and the dependence of breaking dormancy on the right combinations of winter chilling and spring heat sum are associated with specific gene loci (Howe *et al.*, 2003). Common garden experiments (reviewed by Howe *et al.*, 2003; Aitken *et al.*, 2008) and surveys of natural populations (Vitasse *et al.*, 2009) identify geographic clines of phenology

timing that are caused by local natural selection. For example, Sitka spruce (*Pinus sitchensis* (Bong.) Carr) experiences a 13-day delay in budset for each degree added to average annual temperature (Aitken *et al.*, 2008). A 9°C altitudinal temperature gradient was reflected in a 62–117 day difference in canopy duration among four common European hardwoods (Vitasse *et al.*, 2009). Heritable latitudinal persistence in phenology (reviewed in Kimmins, 2004) underpin the increases in height growth achieved by southern provenances transferred to northerly latitudes (Aitken *et al.*, 2008).

The genetic basis of phenology implies that trees may be caught in a tradeoff between maintaining competitive rates of height growth and avoiding cold injury (Loehle, 1998). Unseasonably warm days in early spring may initiate bud burst and growth, only to be followed by freezing temperatures (Jönsson *et al.*, 2004; Picard *et al.*, 2005; Gu *et al.*, 2008; Augspurger, 2009). In temperate hardwoods and some conifers, chilling temperatures, duration of chilling, and accumulation of spring heat sums interact to determine not just susceptibility to frost damage, but whether buds and leaves develop normally. Inadequate chilling in sugar maple leads to abnormal leaf development, and excessive periods of cold inhibit bud burst (Kriebel and Chi-Wu, 1962). Budburst in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) depends on the ability of provenances to experience the right combination of chilling and forcing (sensu Harrington *et al.*, 2010), with the required forcing increasing exponentially as chilling period decreases (Harrington *et al.*, 2010; see Figure 5).

2. Phenological Acclimation and Adaptation

A growing body of research suggests that phenotypic plasticity (as defined by Nicotra *et al.*, 2010)¹ and intraspecific phenological variation could influence the adaptation of populations and acclimation of individuals to climate change. The genetic coupling of phenology with local climate may therefore be weaker than previously thought (St Clair and Howe, 2007), and a broader range of species responses to climate and transient weather may be possible. Species in relatively diverse North American temperate hardwood stands leaf out over four to six weeks (Lechowicz, 1984, Lopez *et al.*, 2008). Lechowicz, (1984) suggests that interspecific phenological differences may be evolutionary relics of the ancient tertiary environments where temperate trees evolved rather than an adaptation to current conditions. Lopez *et al.* (2008) note, however, that early leafing mid-story and understory species in the great Smoky Mountains receive up to 80% of their annual photon flux density prior to leaf development in the overstory canopy, whereas later leafing species received 15% or less (Figure 6).

A phenological heritage from ancient climates may give rise to pools of cryptic genetic variation (so-called “hidden reaction norms,” or HRN) that are only expressed in novel environments

¹Nicotra *et al.* (2010) define phenotypic plasticity as an epigenetic response: a mechanism of gene regulation that leads to heritable, but potentially reversible changes in gene expression.

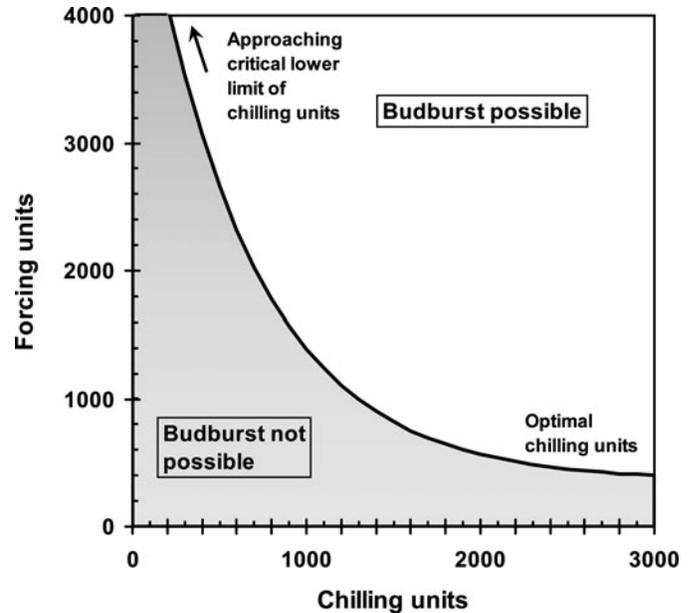


FIG. 5. Best fitting model of the interplay between adequate chilling and forcing units in Douglas fir provenances exposed to various combinations of winter chilling and spring forcing units, defined as hours spent at a given temperature multiplied by a chilling or forcing effectiveness index. The boundary line between budburst being possible and budburst not occurring is defined by forcing units (y) = $357 + 5123 * e^{(-0.0016 * \text{chilling units})}$ (adapted from Harrington *et al.*, 2010).

(Schlichting, 2008) (Figure 7). Reciprocal transplant experiments could reveal HRNs, and if they promote establishment and survival (Ghalambour *et al.*, 2007), HRNs could be of obvious use in forest management. Heterogeneity in phenological timing produced by localized differences in soil moisture (Lopez

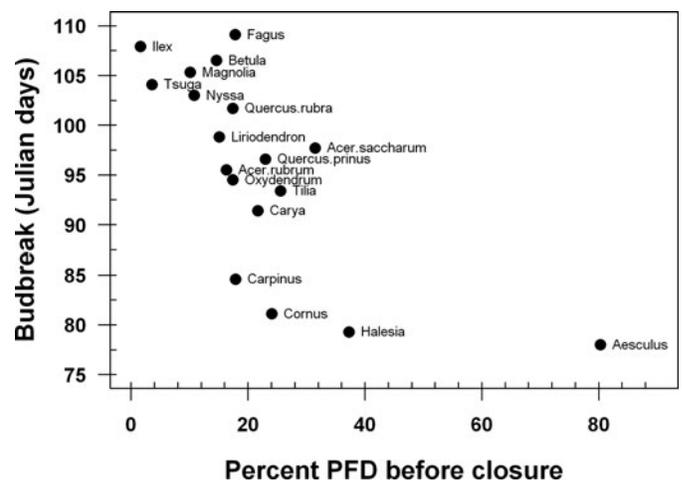


FIG. 6. Date of bud break (Julian days) as a function of the percentage of seasonal photon flux density (PFD) received by each species before canopy closure in diverse hardwood stands in Great Smoky Mountains National Park. There is a general tendency for understory and mid-story species to leaf out earlier than dominant canopy species, but early leafing came at the cost of 5.5% week⁻¹ increase in exposure to freezing temperatures (data from Lopez *et al.*, 2008, Table 2).

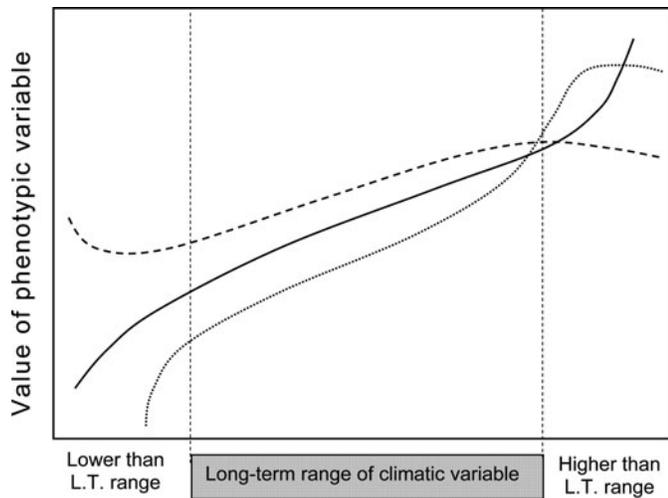


FIG. 7. Hidden reaction norms may cause phenological responses to change in unexpected ways as species are shifted away from the range of climates that represent their current realized niches. The diagram (after Ghalambour *et al.*, 2007) suggests that three genotypes (the lines on the graph) are adapted to an environmental gradient within their realized niche. But since they have not been historically exposed to conditions at the tails of the environmental gradient, their reaction norms will display cryptic genetic variation when those conditions arise. They may prove to be pre-adapted to, or fail unexpectedly in the novel conditions.

et al., 2008) and altitude (Vitasse *et al.*, 2009), as well as the experimental modulation of budburst by changes in photoperiod (Caffarra and Donnelly, 2011; Basler and Körner, 2012) hint that HRNs could be common. Phenotypically plastic genotypes may outcompete less plastic varieties of a species in stressful environments, but simulations also suggest that phenotypic plasticity and the evolution of local genotypes could produce similar responses to a given environment over time (de Jong, 2005).

Epigenetics. Observed phenotypic variation may also arise in response to differential gene expression in response to year to year climatic variation. Closely related individuals of silver birch (*Betula pendula* Roth) (Kelly *et al.*, 2003) and Norway spruce (Skroppa *et al.*, 2007) produce genetically distinct progeny during warmer or cooler years. Progenies of full and half-sib families of Norway spruce experience delayed budset and increased susceptibility to freezing injury in fall when the parent plants are exposed to warmer temperatures during embryogenesis (Johnsen *et al.*, 2005b). Day length and temperature also interacted to influence Norway spruce phenology. Seedlings from high temperature-short day or low temperatures-long day regimes had delayed bud break and shoot growth cessation, and were less frost hardy in the autumn than low temperature-short day and high temperature-long day regimes (Johnsen *et al.*, 2005a, Johnsen *et al.*, 2005b). Translating heat sum into geographical distance, bud set in Norway spruce varied by up to 6 degrees of latitude (or 2 hours of darkness) in phenotypes whose embryos developed under cold versus warm conditions (Kvaalen and Johnsen, 2008). White spruce x Engelmann spruce (*Picea engelmannii* (Parry)) seedlings raised from embryos ex-

posed to 22°C/8°C day/night temperatures also have significantly lower spring and fall frost hardiness than those from a 14°C/8°C regime (Webber *et al.*, 2005). Unlike Norway spruce, the timing of bud break in white spruce is similar, regardless of temperature treatment (Webber *et al.*, 2005).

The acclimation of seedling phenology to seasonal temperatures is evidently an epigenetic phenomenon—a change in gene expression with no change in DNA sequencing (Johnsen *et al.*, 2005b; Nicotra *et al.*, 2010). Heat sum during embryogenesis creates an “epigenetic memory” that influences phenology and growth of the progeny for an extended period (Yakovlev *et al.*, 2012). Epigenetic effects can be persistent. In Norway spruce seed orchards, differences in bud set, breaking of dormancy, and height growth were still discernable in seeds sourced from different locations 23 years after planting (Skroppa *et al.*, 2007). Clonal epigenetic effects have also been demonstrated in hybrid poplar genotypes. Poplar clones from common parental material planted in different environments display divergent patterns of stomatal conductance in a drought experiment. Remarkably, the strength of the epigenetic signatures declined with the elapsed time since the last propagation from the parent genetic material (Raj *et al.*, 2011).

Some researchers think that epigenetically induced phenotypic plasticity could buffer naturally regenerating tree populations against climate change (e.g., Yakovlev *et al.*, 2012). Such adaptation might play out over long periods in species that set seed and germinate annually, since warm and cold years would tend to produce offspring adapted to different sets of conditions. Superior height growth but risky late-season budset in “warm-year” seedlings could be offset by the less competitive but conservative early budset of “cold-year” phenotypes. The potential role of epigenetics in species that regenerate following periodic disturbance is more problematic. One possibility is that serotinous-coned species (e.g., jack pine) would store “meta-populations” of seed pre-adapted to a range of conditions determined by interannual climatic variation. Upon release following fire, natural selection might then weed out seedlings mal-adapted to post-disturbance weather of the year. Clonal species (e.g. trembling aspen) may be subject to environmentally induced “epigenome reprogramming,” which could buffer clonal individuals against lack of genetic diversity, and facilitate long-term acclimation to climate (Raj *et al.*, 2011).

The role of photoperiod. Although breaking dormancy is traditionally thought to depend on accumulated growing degree days (GDD), some conifers and late successional hardwoods require both photoperiodic and temperature cues to break dormancy successfully. Photoperiodic signals are powerful enough to inhibit bud break in e.g., *Celtis*, *Quercus*, and *Fagus* species when they are transferred to subtropical environments (Körner and Basler, 2010). By contrast, early successional pioneer genera, such as *Betula*, *Corylus* and *Populus* respond principally to chilling and heat sum (reviewed in Polgar and Primack, 2011). Short photoperiods significantly retard complete bud burst in a variety of European hardwoods (Caffarra and Donnelly, 2011;

Basler and Körner, 2012). Photoperiod may act as a failsafe mechanism to minimize consequences of temperature backlashes following unseasonably warm winter weather (Körner and Basler, 2010; Polgar and Primack, 2011).

Determinate and indeterminate growth. The balance between determinate and indeterminate growth may modulate the tree's responses to seasonal climate, thereby affecting the risk of cold damage. Young seedlings and early successional species often have indeterminate growth in which successive flushes of leaves can continue late into the growing season. Coniferous species with indeterminate growth may be at greater risk of late season frost injury relative to those with determinate growth, in which bud set and growth cessation often occur early in the growing season (Howe *et al.*, 2003). Thus, in Douglas fir seedlings, there is a clear inverse relationship between frost damage and the elapsed time from budset to killing October frosts (Campbell and Sorensen, 1973). Hardwoods may experience the risk of frost differently. In a pioneering study relating wood anatomy and growth patterns to phenology, Lechowicz (1984) suggested that eastern hardwoods with indeterminate growth only risk losing a few early-flushing leaves to spring frosts. The seasonal risk profile of conifers, in which growth of multi-year needles is concentrated in leaders on stems and branches, may therefore be quite different to that of hardwoods, where growth is distributed more evenly throughout the crown.

3. Acclimation of Respiration and Photosynthesis

A variety of temperate and boreal tree species experience a transitory increase in respiration in response to rising temperatures, followed by a partial re-adjustment back towards pre-warming rates. Seedlings of paper birch, tamarack, jack pine, and black spruce exposed to warming demonstrate acclimation by having lower Q_{10} values for respiration than those grown in cooler ambient temperatures (Figure 8), regardless of CO_2 concentration (Tjoelker *et al.*, 1999a, Tjoelker *et al.*, 1999b). Similarly, when adjusted to a reference temperature of 24°C, three-year-old red oak and white oak (*Quercus alba* L.) had 13–40 percent lower respiration rates after exposure to a 32/19.7°C day/night regime compared to those grown at 20/8.8°C (Bolstad *et al.*, 2003). Respiratory acclimation among jack pine provenances also increases with temperature differences across which genetic material is transferred (Tjoelker *et al.*, 2008), suggesting that this species can respond flexibly to a wide range of conditions. Respiratory acclimation to temperature in boreal species appeared to be strongly associated with reduced foliar N, especially in conifers. Counterbalancing the effects of N, doubling CO_2 concentration led to increasing concentrations of non-structural carbohydrates (NSCs), which in turn, increased respiration (Tjoelker *et al.*, 1999b).

Photosynthesis increases with rising temperatures in many species, but acclimates weakly or not at all (Way and Oren, 2010). When exposed to warming of 4°C (from 27 to 31°C) in growth chambers, latitudinally distinct provenances of sugar maple increased photosynthesis by 14% and reduced respira-

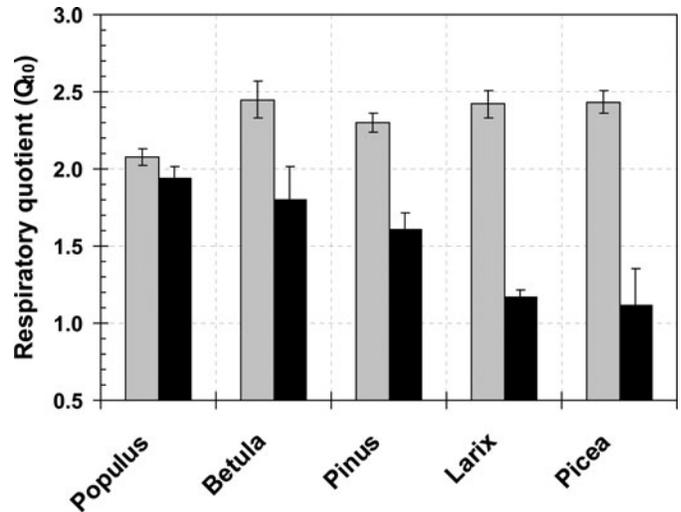


FIG. 8. Acclimation of respiration rates among 18–97 day-old seedlings of five boreal tree species. Short term Q_{10} (gray bars \pm standard error of the mean) is calculated increase in dark respiration rate between 12°C and 24°C of a plant raised in a 18/12°C day/night temperature regime. The long term Q_{10} (black bars) is the response of plants grown in a 30/24°C regime to warming from 12°C to 24°C. The lower the long-term Q_{10} , the more acclimated are the plants, and a Q_{10} of 1 would imply similar respiration at all temperatures (Tjoelker, 1999b, Mark Tjoelker, personal communication).

tion by 10% compared to unacclimated individuals. A parallel experiment in open-topped field chambers failed to increase photosynthesis over three growing seasons, although respiration acclimated as before (Gunderson *et al.*, 2000). Foliar respiration was reduced and photosynthesis increased during spring to summer transition in 8-year-old *Radiata* pine (*Pinus radiata* D. Don) and 20-year-old eastern cottonwood (*Populus deltoides nigra* var. *italica*) (Ow *et al.*, 2010). By contrast, temperate and boreal tree species in common gardens distributed across an annual temperature gradient of 12°C had similar photosynthetic temperature optima regardless of location of origin (Dillaway and Kruger, 2010).

A large majority of acclimation studies have been done on seedlings or saplings (Way and Oren, 2010), but a few studies have revealed acclimation among larger trees. Seasonal acclimation of respiration contributed to high photosynthetic efficiency (ratio of carbon gained to water lost) in adult Aleppo pine (*Pinus halapensis* Mill.) during hot, dry Mediterranean summers (Maseyk *et al.*, 2008). Respiration acclimated to a similar degree in 20 climatically distinct jack pine provenances distributed among common gardens spanning a 7°C range in mean annual temperatures (Tjoelker *et al.*, 2008).

4. Downregulation of NPP

CO_2 fertilization increases NPP in mature conifers and hardwoods (Norby *et al.*, 2005), but these initial growth advantages may be transient (Körner, 2006). In free air CO_2 enrichment (FACE) experiments, increases in NPP averaging 23% under

550 ppm CO₂ (Norby *et al.*, 2005) were reduced to $\leq 10\%$ by the tenth year of measurements (Körner, 2006, Norby *et al.*, 2010). Tree growth failed to respond to enhanced CO₂ in a Swiss hardwood forest despite 42–48% increases in net photosynthesis (Körner *et al.*, 2005; Bader *et al.*, 2010). One explanation for these observations lies in downregulation of NPP production by nutrient shortages, particularly of nitrogen (N) (Körner, 2006). The progressive nitrogen limitation (PNL) hypothesis (Luo, 2004) proposes carbon enrichment feeds back negatively to available soil N by sequestering it in increased biomass and dead organic matter. Countering this trend, plant-available N could be liberated if increased growth augmented by enhanced N-use efficiency increases C:N ratios (Luo, 2004; Norby *et al.*, 2010). The balance between these two opposing feedbacks may determine whether the CO₂ fertilization effect is downregulated or not.

Downregulation of NPP in juvenile sweetgum (*Liquidambar styraciflua* L.) under 550 ppm CO₂ was primarily caused by N-limitation (Norby *et al.*, 2010). Nitrogen fertilization of this stand caused an immediate revival of woody mass production. By contrast, a sustained rise in NPP under CO₂ enrichment was observed in a 20–25-year old stand of loblolly pine (*Pinus taeda* L.) (Drake *et al.*, 2011). In this case, canopy expansion and greater fine root production were accompanied by enhanced litter turnover and decomposition rates, which in turn were stimulated by C-mediated increase in microbial activity. Where growth is unresponsive to rising photosynthesis or acclimated respiration, the additional carbon can follow many alternative metabolic pathways, including root turnover, production of volatile compounds, exchange with mycorrhizae and microbes, or storage in NSCs (Körner, 2006; Sala *et al.*, 2012).

5. Drought

Amplification of the hydrological cycle is expected to increase the incidence and duration of heat waves and drought (Knapp *et al.*, 2008). Indeed, climate change induced droughts may already be causing episodic tree mortality in multiple taxa and ecosystems (Adams *et al.*, 2009; Allen *et al.*, 2010; Carnicera *et al.*, 2011; Michaelian *et al.*, 2011). Consequences of drought ripple through forest ecosystems, causing direct reduction of photosynthesis, loss of leaves, as well as increasing the severity of insect and fungal defoliators (Carnicera *et al.*, 2011). Plants grown in elevated CO₂ may be especially vulnerable to leaf loss. In the sweetgum FACE experiment severe drought and a 38°C heat wave accelerated leaf senescence compared to non-CO₂ enriched plants (Warren *et al.*, 2011), a phenomenon observed in other temperate hardwoods (Bassow *et al.*, 1994).

Combined high temperature and drought produce acclimatory responses that can be maladaptive under persistent water stress. Two major responses to drought have been identified. Anisohydric species allow leaf water potentials (ψ_l) to fall under drought, while maintaining photosynthesis, while isohydric trees maintain ψ_l within tight boundaries by closing their stom-

ata (reviewed in McDowell *et al.*, 2008; Wang *et al.*, 2012). Anisohydric species risk damage and mortality from cavitation and leaf desiccation under critically low soil water potentials. Isohydric species, on the other hand, risk death due to carbon starvation, since metabolic demand for carbon must be satisfied even when photosynthesis is minimal.

Evidence exists for drought-induced mass tree mortality under both of these mechanisms. Recent mass mortality of aspen (an anisohydric species) in the western USA and Canada is likely due to hydraulic stress. Aspen ramets under drought had xylem water potentials (ψ_x) of -1.6 to -2.2 MPa lose up to 70% of their xylem conductivity (Anderegg *et al.*, 2012). By contrast, anisohydric oneseed juniper (*Juniperus monosperma* Engelm.) experienced negligible mortality during a prolonged drought in New Mexico, while isohydric piñon pine (*P. edulis* Engelm.) suffered 97% mortality during the same period (McDowell *et al.*, 2008). The piñon pine may have suffered carbon starvation during the extended drought, even as they controlled water loss, but oneseed juniper resisted xylem cavitation down to a ψ_x of -8 MPa or lower (McDowell *et al.*, 2011). Carbon starvation and depletion of NSCs (Sala, 2012) appear to be likely causes of delayed mortality in Scots pine (Galiano *et al.*, 2011) and holm oak (*Quercus ilex* L.) (Galiano *et al.*, 2012) some years after severe drought. A similar dynamic may be in play when sugar maple weakened by defoliator outbreaks succumb to a second outbreak some years later (Hartmann and Messier, 2008).

6. Acclimation of Individuals or Rapid Adaptation?

Epigenetic acclimation of offspring to parental environments suggests that cross-generational adaptation may be modified by transient climatic events, which may enable some species to adapt in place to climate change (Saxe *et al.*, 2001; Johnston *et al.*, 2009, p.18). Such acclimation is only likely to be adaptive if climatic norms transition smoothly from one climate state to another. If sudden transitions and trend reversals occur, phenotypes acclimated to one set of conditions may be severely maladapted to new climatic states.

The climatic limits of epigenetic acclimation will ultimately depend on the plasticity of individual genotypes. When the magnitude of change exceeds these limits, only adaptation through natural selection will enable populations to persist. Some studies suggest that natural selection could act rapidly enough to track the pace of climate change. Using standard assumptions in a genetic heritability equation, (Rehfeldt *et al.*, 2001) estimated that some lodgepole pine populations in BC would require only 2–3 generations in northern latitudes to adapt to a climatic change, but might require 10–15 generations in more southern parts of the distribution. Saxe (2001) suggests that individual plasticity and a high degree of genetic variability are associated. Genetically diverse populations that support a variety of phenotypes with a high degree of plasticity may therefore enjoy a selective advantage during climate change.

7. Summary: Phenology, Physiology, and Climatic Futures

Phenological and physiological coupling between provenances and climate may be less brittle and more resilient than suggested by short term studies. If proven true, forest managers might be able to conserve current species and varietal mixes with relatively little change to favored genotypes. Respiratory acclimation, phenotypic plasticity and epigenetic effects suggest that acclimation in place and even long-distance transfers of tree varieties might be feasible. On the other hand, rising temperatures and CO₂ affect multiple axes of physiological and phenological variation in trees, making firm predictions of future responses to climate change difficult. The CO₂ fertilization effect, which some scientists expect to increase short- to medium-term forest growth (Kolström *et al.*, 2011), is likely to be transient (Körner, 2006). Extreme weather events and pathologies, either alone or in combination, are also likely to breach the limits of acclimation in some species, negating any growth advantages of higher temperatures. Non-structural carbohydrates (NSCs) may provide a critical buffer against drought and disease, but their role in tree survival is poorly known, and they have yet to be incorporated into process based models (Sala, 2012).

Nevertheless, some tentative predictions have been made. Early successional species with minimal chilling requirements and weak photoperiod response break dormancy opportunistically, giving them a potential competitive advantage over other species (Polgar and Primack, 2011). Diffuse porous hardwoods experience fewer winter xylem emboli than larger vessel diameter ring porous trees (Wang *et al.*, 1993). Depending on drought duration and severity, either anisohydric or isohydric species can increase mortality mediated by different mechanisms. Risks of drought-related mortality have increased (Bréda *et al.*, 2006; Jump *et al.*, 2006), and are likely to worsen. Synergistic stresses imposed by periodic droughts and other stressors, such as insect infestations appear to be responsible for increased tree mortality, e.g., tent caterpillar infestations on aspen in the Prairie provinces (Hogg *et al.*, 2002; Hogg and Bernier, 2005). Some scientists (e.g., Jump and Peñuelas, 2005) suggest that the increasing amplitude of extreme weather might require trees to possess “near perfect” phenotypic plasticity to adapt to new conditions. Others (e.g., Saxe, 2001) argue that genetically diverse populations with a high degree of plasticity may be resilient to change.

These last observations raise important questions for forest managers. The climatic limits to phenotypic plasticity, beyond which further phenological adaptation can be achieved only through natural selection, are unknown for most species, but may be within reach. Other important questions include which drought response mechanism will lend trees greater resilience to severe drought–isohydry or anisohydry? Should forest stands be diversified to lend the tree community greater resilience (Kolström *et al.*, 2011) and if so, what traits should be represented in future mixed species stands?

The answer to these question will be site, species, and time-scale dependant. In the face of these uncertainties, forest managers will have to address a broad range of potential future

conditions, and find ways to assimilate and use the modeling and experimental insights described above.

IV. ADAPTING TEMPERATE AND BOREAL FORESTS AND FORESTRY TO CLIMATE CHANGE

Forest managers will address climate change through silvicultural systems and the stand-level silvicultural practices that are part of those systems. Silvicultural systems are named for harvesting methods that are geared towards particular modes of regeneration (e.g., clearcut, shelterwood, group selection). Each system implies a planned program of treatments, such as planting, tending, and modifying stand structure that extend from one harvest cycle to the next.

We suggest that forest managers can adopt three broad strategies to adapt silvicultural systems and practices to the uncertain future. They can (i) increase *resistance* and/or *resilience* of forest stands to changing disturbance regimes or intensified environmental stresses (Millar *et al.*, 2007); (ii) *avoid* consequences from long-term climatic trends by planting tree species or varieties that grow rapidly into commercial maturity; or (iii) prepare ecosystems for an unknown future climate by enhancing adaptive capacity (Puettmann, in review). Resistance refers to the degree to which ecosystems remain unaltered in the face of disturbances, while resilience, at least in its original engineering sense (Holling and Gunderson, 2002), refers to their ability to recover from disturbance. Ecological resilience expands the engineering concept to consider transitions between alternative stable states, elasticity (speed of recovery), resistance to state transitions, and trajectory stability (tendency to continue along particular successional paths) (Grimm and Wissel, 1997; Park, 2011).

Avoidance would reduce temporal windows of climate variability for which managers must aim, thereby improving their chance of making sound short-term silvicultural decisions. In many cases, elements of avoidance, resistance and resilience will be combined in an adaptive management framework (Bormann and Kiester, 2004), leading to a series of short-term silvicultural objectives that would sequentially transform stand structures or species composition as the climate changes. Enhancing adaptive capacity could incorporate elements of resilience, resistance and avoidance, with the added realization that unforeseen changes in species composition and forest structure are inevitable.

To cope with climatic uncertainty, these broad strategies will be implemented using silvicultural interventions that range from low risk modifications of existing practices to complex experiments with uncertain outcomes (Figure 9). Management interventions across this gradient include (i) fine-tuning current systems and practices to adapt forest stands to specific local threats, trends, or predictions; (ii) introducing new species or provenances to existing stands, along with revised silvicultural systems; and (iii) speculative experiments, known as “designer forests” (Sarr and Puettmann, 2006) or “Options Forestry” (Bormann and Kiester, 2004), designed to cope with more extreme climate change conditions.

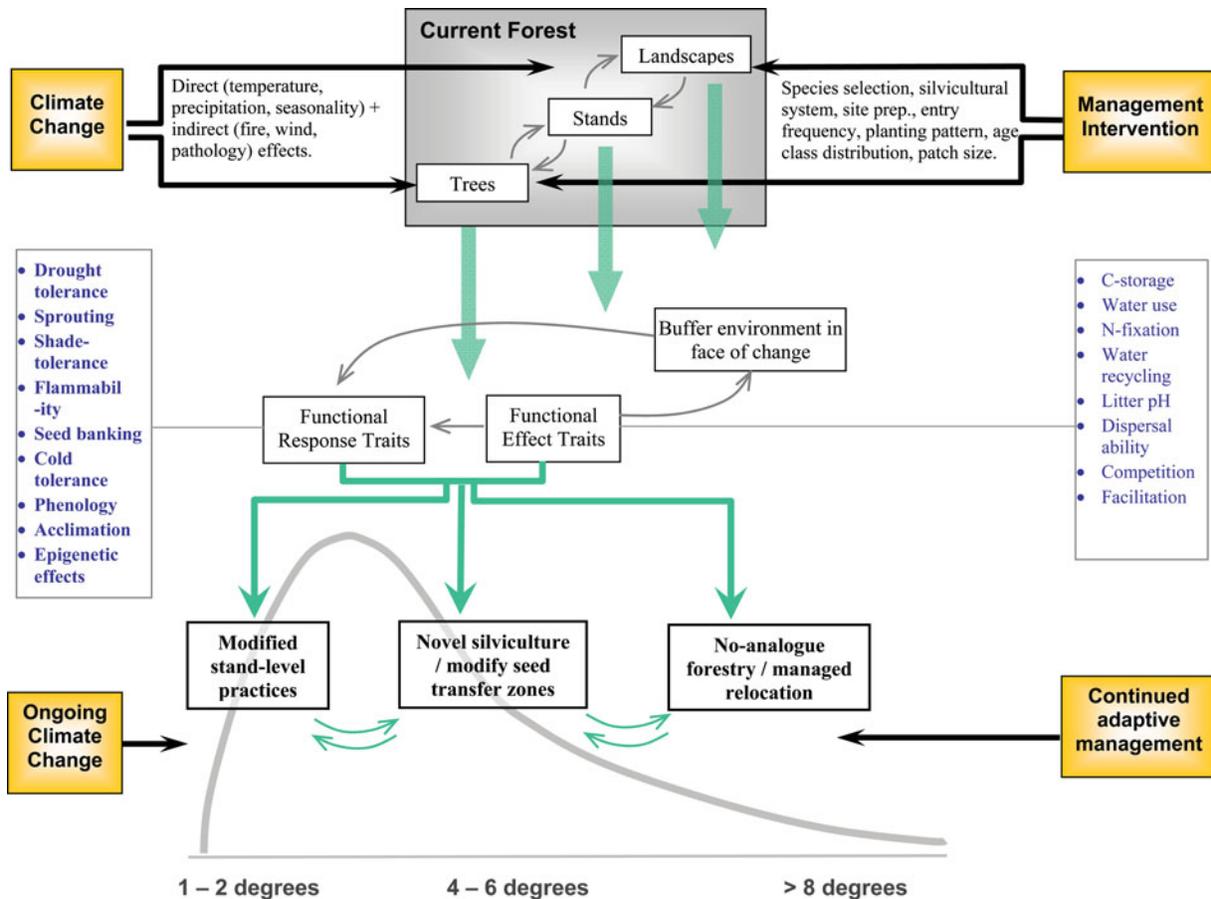


FIG. 9. Conceptual model relating climate change to management interventions designed to manipulate stand structure, species composition, the functional traits expressed by species, and qualities of the local stand environment. The level of departure from current practices depends on climate sensitivity, and will be subject to continuous adaptive management, as well as the vagaries of ongoing climatic change.

A. Modifying Silvicultural Practices

1. Modifying Post-Harvest Practices

Reproduction methods, the core activities of silvicultural systems target the regeneration of desired species. These desired species may or may not be those that existed at a site before harvesting. If the previous species composition is desired, silvicultural systems may be selected to be an analogue to native natural disturbance regimes (Seymour *et al.*, 2002). Thus, the clearcut system is more suitable in areas where stand-replacing fires foster monospecific stands of fire-dependent species. Group shelterwood encourages species to regenerate that tolerate moderate shade, as is the case for many oak species. Selection cutting may be used to regenerate the most shade-tolerant species (e.g., sugar maple) or to mold stand structures of stratified mixtures of tree species that can regenerate under heavy shade.

Increasing heat and drought stress is likely to cause the most damage in regenerating clearcuts. Managers may be able to moderate such stresses by using patch cuts or group shelterwood systems where the silvics of the regenerating species demand it. These micro-environmental modifications may be

most successful under moderate warming of 1–3°C. They may implement site preparation practices, such as use of prescribed fire to foster intense episodes of natural selection among naturally regenerated seedlings, which would presumably mostly be drawn from the local gene pool (Galatowitsch *et al.*, 2009). This strategy potentially taps into a reservoir of genetic variation not fully represented in seedlings that are obtained from selective environments of seed orchards and nurseries (Axelson, 2010). To facilitate such treatments, sizes of cutblocks may need to be reduced to permit seeds to disperse into stands from surrounding forests. Seed tree cuts, as opposed to complete clearcuts, are another desirable option, provided residual seed trees are wind firm, free of disease, and produce adequate seed crops.

2. New Roles for Density Management

The guiding rationale for stand thinning will change under climate change. Traditionally, thinning was implemented to relieve residual trees from competition (thereby improving diameter growth and increasing vigor). In a warming world, thinning is also more likely to be carried out to modify other

environmental impacts of climate change, such as soil water regulation, fuel density reduction (Stephens *et al.*, 2010), and improving wind-firmness in tree populations (Puettmann, 2011).

Reduction of overstory tree densities have the potential to dampen fluctuations in soil water, and buffer stands against water shortages. This effect has been demonstrated by reductions in water consumption of up to 75% in thinned red pine stands (Papadopol, 2001b). Ecophysiological effects of thinning in a 250-year-old ponderosa pine (*Pinus ponderosa* Laws.) stands included improved water availability, higher pre-dawn water potentials, greater stomatal conductance, and increased basal area increments (McDowell *et al.*, 2003). Although thinned Norway spruce suffered growth depression during a severe drought, heavily thinned stands demonstrated resilience by recovering to pre-drought growth rates more rapidly than lightly thinned or unthinned stands (Kohler *et al.*, 2010).

Likely limitations of future soil water availability should inspire greater consideration of the role of roots in seedling establishment and survival. The timing of the regeneration cut in shelterwood systems (in which partial overstory removal frees up growing space and increases light and moisture levels for regeneration), may be altered to maximize seedlings' chances of survival. In regenerating mixed-species oak stands on dry sites in the Ozark Mountains, for example, slow-growing seedlings and root sprouts develop extensive root systems that support rapid growth when canopies are eventually opened up (Larsen *et al.*, 1999). Arguably, delaying overstory removal, while trading off aboveground growth for root development, would increase resilience of oak populations to transient droughts.

Thinning regimes may be designed to protect stands and landscapes from climate-enhanced natural disturbance regimes. For example, the province of Alberta has learned from British Columbia's experience with Mountain Pine Beetle (MPB) by adopting aggressive programs of pre-emptive sanitation cutting in identified MPB infection centres. Resistance against MPB is improved by diversifying age distributions of stands and thus reduce the acreage in vulnerable age classes (Government of Alberta, 2009). In areas where wind damage is thought to be more likely due to climate change, thinning should be done earlier in stand development. Earlier thinning will shift dependence of stand stability from mutual shelter by trees in close proximity to each other to characteristics of individual stems, such as increased root mass, diameter, and stem tapering (Wilson and Oliver, 2000). The timing of thinning treatments will also influence trade-offs between different types of disturbance. For example, avoidance of drought through thinning may render a stand more susceptible to windthrow in the short term (Kolström *et al.*, 2011).

3. Regenerating Forest Stands

Genetic diversity and epigenetics. Much of the response of existing forests to climate change will be achieved as part of the regeneration process. Choice of functional traits and genetic diversity of planting stock will be crucial to future forest

health, even under mild climate change. Functional traits can be considered as physiological or morphological *responses* to the environment or from the point of view species' *effects* on ecosystem function (Puettmann, 2011; see Figure 9). They can be exploited to buffer existing forest communities against climate change, or to change stand composition altogether.

Increasing genetic diversity within species or promoting more species diverse stands can increase functional response and effect trait diversity. But which traits should be fostered? Studies of functional traits have tended to focus on easy to measure characteristics with global biogeographical significance (e.g., specific leaf area, seed mass, or dispersal mode; Weiher *et al.*, 1999; Harrison *et al.*, 2010). Foresters faced with climate change will need to consider traits with a direct impact on trees' ability to establish and thrive in a rapidly changing climate. Provenance performance evaluations should be extended to include tests of tolerance for high temperatures, drought, and resistance to a variety of diseases as selection criteria, thus emphasizing the trees' functional responses to new conditions.

Definitive results from orchard and field trials may take years or decades to obtain. Nor will recent discoveries of gene loci for phenological traits and stress resistance be commercialized any time soon (Kolström *et al.*, 2011). In the meantime, in the absence of complete knowledge, resistance and resilience to climate-related stressors and pathologies could be enhanced by planting a wide variety of genotypes, not just the limited selection that are locally adapted or which display superior growth rates. Such a hedging strategy may reduce average short-term growth rates, but achieve greater production over longer time periods through enhanced forest health and reduced mortality. In this context, the common practice of planting a single fast growing genotype (as recommended by Wang *et al.*, 2006) is equivalent to an unhedged investment in a single mutual fund. If, for example, pleiotropy (a cascade of altered gene expression flowing from changes in the action of a single gene) were to link fast growth to increased vulnerability to diseases, fast growing genotypes would likely not be the most productive in the long term, as diseases will eventually appear. Under these conditions, planting mixtures of genotypes and species stands may be a smart forest health strategy (Paquette and Messier, 2009).

Given sufficient knowledge, epigenetic effects (Section 3.2.2) and ontogenetic development could be manipulated in nurseries to acclimate provenances to warming. For example, of the long-term echo of epigenetic conditioning observed in Norway spruce (Skroppa *et al.*, 2007) could presumably be strengthened if we knew more about how environmental signals interact with genomes. Manipulation of seedling environment can already be used to precondition seedlings to certain stresses. Drought preconditioning of three *Cedrus* species enabled treated seedlings to maintain substantially higher photosystem II (PSII) activity than untreated seedlings at temperatures up to 45°C (Ladjal *et al.*, 2000). When transferred to identical climates, Greenwood and Hutchingson (1996)

found significant height differences in 5 of 12 full-sib *Larix* sp crosses that had been raised in contrasting environments. Even seeds may be preconditioned, as demonstrated by reduced freezing- and drought-induced damage in black spruce and jack pine whose seeds were exposed to a synthetic anti-oxidant (Greenwood and Hutchinson, 1996).

Planting strategies. Underplanting desired provenances or species beneath progressively opened up canopies of trees can be used to modify trait values or the mix of functional traits operating within stands. Many examples of successful stand transformation are known, usually involving changing even-aged conifer plantations to more complex species compositions and forest structures (Parker *et al.*, 2008; Kerr *et al.*, 2010; Noack, 2011). Such plantings can be highly successful. For example, eight year survival rates of 61–94% were recorded for big-leaf maple (*Acer macrophyllum*, Pursh.), red alder (*Alnus rubra*, Bong.), western red cedar, and western hemlock planted beneath 30-year-old Douglas-fir plantations, although vigor of some species was low (Maas-Hebner *et al.*, 2005). Similar (11 year) survival rates were recorded among red oak, white ash (*Fraxinus americana* L), and eastern white pine (*Pinus strobus* L.) underplanted beneath thinned red pine plantations on aeolian sands in southern Ontario (Parker *et al.*, 2008).

The rooting environment is obviously crucial for seedling establishment and is open to manipulation. Deep tap roots of naturally regenerated red oaks may initially give them greater drought tolerance than planted stock, which tend to develop fibrous root systems (Future Forest, undated). Where stand transformations to a new species composition is possible, shallow rooted jack pine or red pine could be replaced by more deep rooting red and white oaks, American beech, or European larch (*Larix decidua* Mill.), which can more easily access deep water tables (Papadopol, 2001a). While rooting depth can be regarded as a response trait, hydraulic lift, the passive recycling of deep water to superficial soil layers with low water potential, is a functional effect of species on site properties. Hydraulic lift has been demonstrated in poplars, sugar maple (Caldwell *et al.*, 1998), and ponderosa pine, among others. In ponderosa pine, redistribution of water from adult trees to their seedlings appears to occur via mycorrhizal networks (Warren *et al.*, 2008), strongly suggesting facilitation by adult trees. Ectomycorrhizal (EM) networks are also important in maintaining growth rates in Douglas fir seedlings on dry sites (Bingham and Simard, 2012), and there is evidence suggesting that site-specificity of ectomycorrhizae plays a role in growth differences observed in provenance trials (Kranabetter *et al.*, 2012).

B. More Extensive Changes to Silvicultural Systems

1. Regeneration Under Overstory Cover

The importance of EM networks, hydraulic lift and microenvironmental modification suggests that maintaining continuous tree cover could make important contributions to stand resilience. Underplanting places seedlings into an environment where temperature extremes and humidity are buffered com-

pared to conditions in clearcuts, which could improve seedling establishment and survival in warmer, more variable climates. If pest outbreaks become more frequent or severe under a warmer climate (Ayres and Lombardero, 2000), protection functions of mature overstories may partially or fully offset growth reductions caused by competition for light and moisture (Krueger and Puettmann, 2004). For example, side shade and a deciduous canopy (often trembling aspen) have been shown to reduce incidences of weevil damage to Sitka spruce, white spruce, and eastern white pine (reviewed in Comeau, 1996). Maintenance of hardwood-softwood mixtures likewise appears to reduce the susceptibility of balsam fir and white spruce to spruce budworm (MacLean, 1996).

Shelterwoods in which white spruce are underplanted beneath trembling aspen overstories, are hypothesized to produce greater wood volumes than single-species stands (Kabzems *et al.*, 2009). Relationships between aspen density, available light, and white spruce growth have been quantified, and tentative recommendations for underplanting densities established (DeLong, 1997; Comeau *et al.*, 2009). Yield projections using a mixedwood growth model indicate that aspen-spruce mixtures could grow up to 21% more wood volume than spruce planted in monoculture (Kabzems *et al.*, 2009). Actions to buffer climate change in aspen-spruce mixtures could include planting seedlings from a wide range of genotypes and re-establishing aspen overstories with genotypes from warmer climates following overstory removal.

Over time, underplanted stands may become intimate mixtures stratified by height. If more species are added, response and effect trait diversity is likely greater than in monocultures or two-species mixtures. In Europe during the late 19th and early 20th centuries, some even-aged plantations were replaced by communities of species with different inherent growth rates. Along the German North Sea coast, for example, stratified mixtures of Caucasian fir (*Abies nordmanniana* (Stev.) Spach), sessile oak (*Quercus petraea* (Matt.) Liebl.), Japanese larch (*Larix kaempferi* (Lamb.) Carr.), European beech, mountain pine (*Pinus mugo*) and Sitka spruce were established. (Pommerening and Murphy, 2004). Mixed-species stands of western white pine (*Pinus monticola*, Dougl. ex D. Don), interior Douglas-fir, western red cedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (*Pseudotsuga menziesii* var. *glauca*) form naturally stratified mixtures in the Interior Cedar-Hemlock (ICH) biogeoclimatic zone of British Columbia. In these stands, overstory Douglas-fir may reach 100 m in height, while more shade-tolerant species, such as western hemlock, occupy subordinate canopy positions (Cameron, 1996).

These stratified stands in the ICH are already being managed experimentally using a group selection system with artificial regeneration (Jull *et al.*, 1999). This type of continuous cover forestry (CCF) has potential ecological and economic advantages over even-aged systems, which leave land bare of mature trees for part of the silvicultural cycle, although few comparisons

have been done to test this proposition (Stokes and Kerr, 2009). CCF emphasizes continuity of forest structure, maintenance of vertical canopy heterogeneity, reduction in wind damage (Pommerening and Murphy, 2004), and (at least in the classic “check or control system”) (Knuchel, 1953), improvement of timber quality and dimensions.

Climate change adds new dimensions to traditional roles of overstories in buffering the micro-environment experienced by seedlings and saplings (Pommerening and Murphy, 2004). Warmer temperatures increase evaporative demand from bare soils, which could reduce seedling survival in clearcuts or large patch cuts. Intact canopies, by contrast, reduce direct evaporation by solar radiation but intercept and transpire large quantities of water. This is of special concern, since shade tolerant species that regenerate in understories are typically less drought tolerant than light demanding species (Niinemets and Valladares, 2006). Whether or not planted seedlings gain hydrological benefits from overstory cover will depend on the balance achieved between water conservation and consumption by mature canopies. Since seedlings and saplings draw water primarily from the surface soil, treatments to buffer this layer against extremes, or overstory species that display hydraulic lift, as described above, will have added relevance in a warming climate.

2. Speculative Experiments and Designer Forests

Refinements to conventional silvicultural practices may mitigate the effects of global warming in the low- to mid-range of IPCC projections (i.e., about 2°C to 4.5°C; Roe and Baker, 2007; Knutti and Sedlacek, 2013). They will almost certainly be ineffective in the face of low probability but high consequence global climate scenarios ($\geq 8^\circ\text{C}$). And even under median projections, extreme weather will expose tree populations to conditions they have never experienced. Options Forestry (Bormann and Kiester, 2004), assisted migration (Minteer and Collins, 2010; Pedlar *et al.*, 2011), or the creation of “designer ecosystems” (Sarr and Puettmann, 2006) are management responses that explicitly acknowledge “unknown unknowns” that attend such extreme scenarios. Unfortunately, most models and adaptation proposals are aimed squarely at the median range of temperature sensitivities, which may lead forest managers to underestimate uncertainty and potential extent of changes that will attend climate change.

One way to acknowledge the risks and opportunities of the more extreme climate change scenarios may be to engage in a wide diversity of small-scale experiments. Many of these might fail, but the few successes would point the way to better-adapted silvicultural systems for the future (Bormann and Kiester, 2004). Needless to say, this approach would require foresters to rethink traditional approaches that involve searching for single, supposedly optimal solutions to management challenges. Striving towards a single solution risks either total success or total failure, and given the uncertainties in play, failure appears to be a more likely outcome.

Existing plans to modify seed transfer zones represent one such prospective experiment. In British Columbia, elevation limits have been modified upwards by 100–200 meters for a range of species (O’Neill *et al.*, 2008). Also in BC, the Assisted Migration Adaptation Trial (AMAT) expands the seed transfer concept to include 15 commercial conifer species from 48 seedlots, including sources from as far away as Idaho, Montana, and Oregon (O’Neill *et al.*, 2011). Elsewhere, proposals to actively modify forest species composition or disturbance regimes are being entertained. In northern Minnesota, for example, private forest owners and The Nature Conservancy are attempting to convert boreal forest stands to temperate hardwoods and to modify disturbance regimes to favor desired species (Galatowitsch *et al.*, 2009; Axelson, 2010). In support of these efforts, landscape simulation and envelope models, as well as expert opinion, were used to group species according to the likelihood that they would decline or prosper under future conditions (Frelich and Reich, 2009; Ravenscroft *et al.*, 2010). Soil and air warming experiments are also being conducted in the field to differentiate the responses of boreal and temperate species seedlings to increased temperatures (see <http://forestecology.cfans.umn.edu/B4WARMED.html>).

3. Assisted Migration and Designer Ecosystems

Common garden experiments typically move provenances by 5°C or less, but the unexplored potential for acclimation outlined in section III suggests that upper temperature limits could be a moving target. “Options Forestry” implies that we should simultaneously explore acclimation to higher temperatures among trees already in place, and the possibility that assisted migration (AM) of species to areas where they are not endemic will be needed to adapt to extreme warming. The AMAT experiment is aimed at establishing whether such transfers are possible across a wide temperature range and latitudinal gradient. The southernmost provenances in this experiment will be shifted by as much as 9.1°C and over 2500 mm of precipitation relative to their native climates, and seed will be shifted up to 10 degrees of latitude from their origin (O’Neill *et al.*, 2011). Both climatic and phenological limits will therefore be probed in this experiment.

Assisted migration is controversial in North America (McLachlan *et al.*, 2007; Minteer and Collins, 2010; Aubin *et al.*, 2011), but in fact has been widely practiced in forestry for at least two centuries. In the UK, exotics such as Sitka spruce and Corsican pine (*Pinus contorta* var. *maritima*) comprise 66% of planted forests. These species are now essentially naturalized and are an important component of UK conservation strategies (Humphrey *et al.*, 2003). In Germany, trials dating from 1880 show that red oak, Douglas fir, western red cedar, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and black locust (*Robinia pseudoacacia* L.) perform well under local climates. Currently, other non-endemic species are being assessed for their suitability for use in experimental silviculture (Bolte *et al.*, 2006). In Canada, European and non-endemic native conifers, including lodgepole pine, red, Scots, and ponderosa pines, Siberian larch (*Larix*

sibirica Ledeb.) and blue spruce (*Picea pungens* Engelm.) have been planted in upland forest “islands” in Canadian prairies since the 1920s. Some of these have grown to considerable size; for example, a 75-year-old red pine plantation was measured at 40 cm average dbh and 26 m in height (Bendzsak, 2006).

Trees shifted latitudinally by 5°C or more may be vulnerable to both weather extremes and normal weather variations in their new environment, especially during the seedling stage. These extremes can be buffered by establishing new species in shade of existing canopies, which can also mitigate competition from non-target species (Cameron and Watson, 1999). Underplanted species generally require more light as they grow (Messier *et al.*, 1999), but tolerate a broader range of climate extremes as they mature (Jackson *et al.*, 2009). Eventually partial or complete removal of the original overstory could be required to allow underplanted species to mature successfully. The timing, volume, and spatial pattern of overstory release will vary according to the desired balance between buffering weather extremes, maintaining soil water supplies, understory light levels and other site characteristics.

No-analogue climates may demand development of no-analogue, designer (or “neonative”; Bolte *et al.*, 2006) plantations in which trees are selected for their potential to combine compatible functional effect and response traits (Scherer-Lorenzen *et al.*, 2007). For example, because down-regulation of photosynthesis in elevated CO₂ could be induced by nitrogen limitations (Franklin, 2007), intimate mixtures that include nitrogen-fixing trees and shrubs provide a potential means to leverage carbon fertilization effects. Nitrogen-fixing (e.g., alder species) and non-nitrogen fixing trees could and are already combined in mixed stands (e.g., Parrotta, 1999; Binkley *et al.*, 2003; Maas-Hebner *et al.*, 2005). For example, common (European) walnut (*Juglans regia* L.) has 22%–80% better height growth when planted in intimate mixtures with nurse trees (e.g. western red cedar) and a nitrogen-fixing shrub (autumn olive [*Elaeagnus umbellata* Thunb.]), relative to walnut planted alone or with only a nurse tree (Clark *et al.*, 2008; see Figure 10a).

Tree communities designed to combine traits that minimize disturbance effects are a logical response to projected increase in intensity and frequency of fire and insect outbreaks (O’Hara and Ramage, 2013). Leaf litter traits are potentially important predictors of fire severity. Leaf length is positively related to fire frequency in complex mixed forests of Colorado’s Sierra Nevada (Schwilk and Caprio, 2011) Flammability of litter also differs significantly among eight species of southern oaks. Litter of lobed leaved, highly deciduous oak species burned with greater intensity than leaves with entire margins that are retained on branches (Kane *et al.*, 2008). Ignition probability (Li, 2000) and the likelihood of crown fires (Kafka *et al.*, 2001) also differs markedly among pure conifer and mixed conifer-broadleaved stands. Lodgepole pine stands killed by mountain pine beetle are often replaced by mixed stands dominated by spruce, Douglas fir, and other species (Burton *et al.*, 2010) that

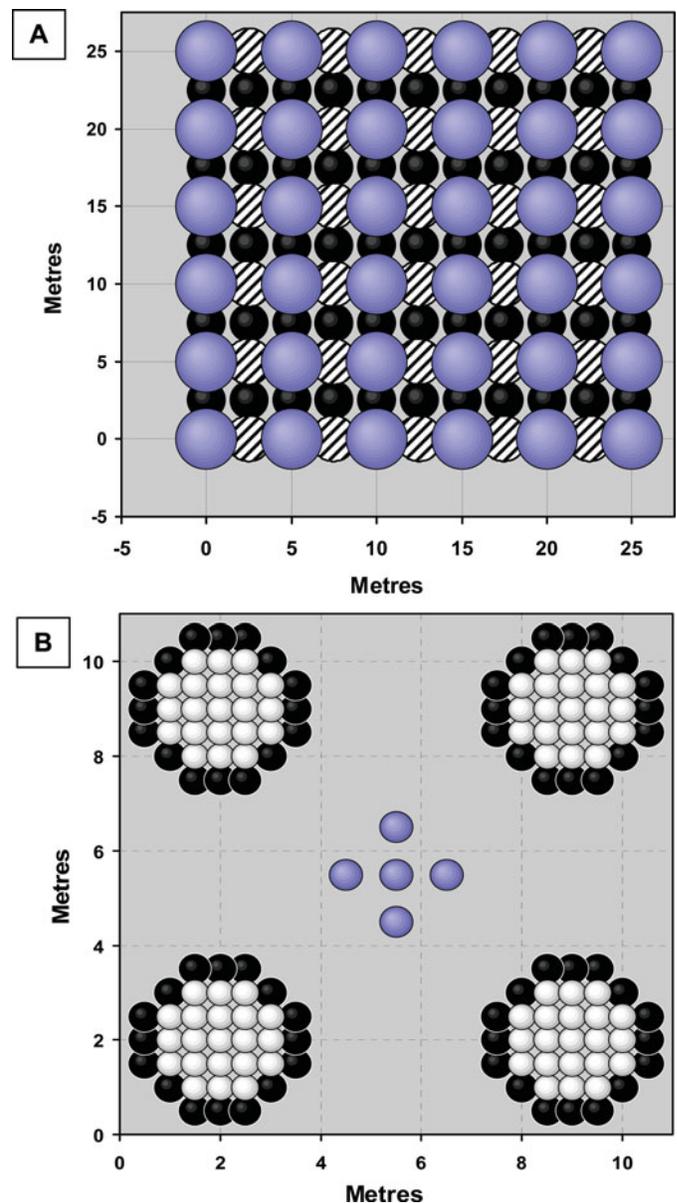


FIG. 10. Planting designs combining functional effect and response traits: (a) Approximate 20 year-old crown dimensions for an intimate mixture of common walnut (light blue), autumn olive (black) and a nurse tree—e.g. western redcedar (black hatching) (after Cameron *et al.*, 1999) (b) Oak nest planting with hornbeam as the nurse tree (black), an oak species as the major crop tree, and faster growing, short rotation trees (e.g. willow) filling the spaces between clusters (redrawn from Pommering, 2004).

may be more resistant to catastrophic beetle incursions. Similarly, $\geq 35\%$ hardwood cover reduced conifer mortality from spruce budworm by up to 40% in New Brunswick (MacLean, 1996), an effect that has been observed elsewhere (O’Hara and Ramage, 2013).

4. Species Selection and Survival in Designer Forests

Selection of compatible species mixtures is key to establishing complex no-analogue forests. Clearly, mixing species

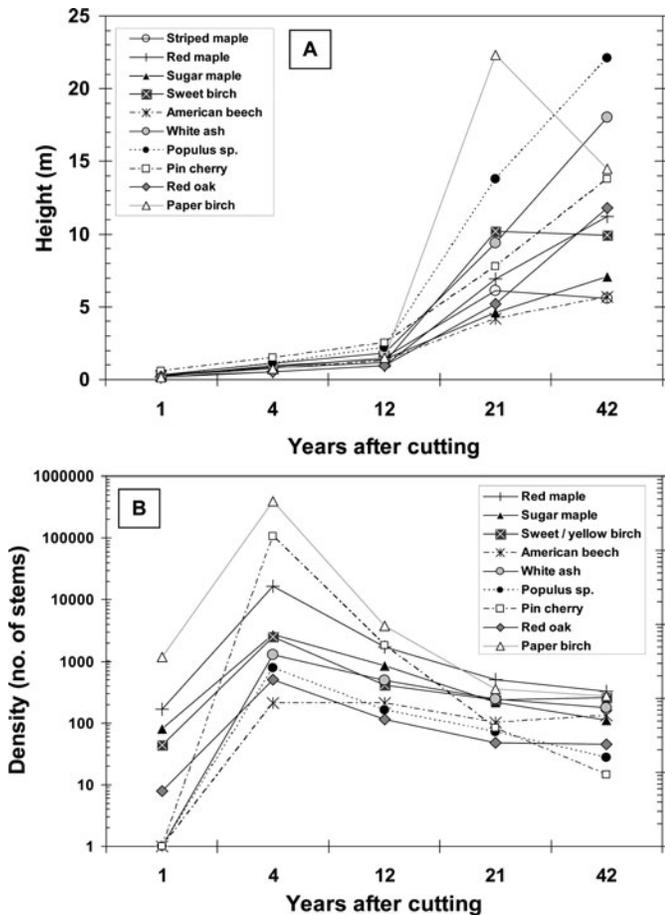


FIG. 11. Stratification of (a) height growth and (b) stem density (note the logarithmic scale) among naturally regenerated northern hardwoods in strip-clearcuts (data from Allison *et al.*, 2003).

that can grow together and complement each other with desirable traits (e.g., low flammability, reduced susceptibility to pests, resilient to drought) is desirable. Unfortunately, quantitative data on traits like flammability are lacking for the majority of species, and relationships between key traits like shade tolerance, drought and waterlogging resistance, are weak or negative (Niinemets and Valladares, 2006),

One response to these challenges is to mimic the species composition of forests from contemporary climates that resemble the projected climatic future in target planting areas. There is no shortage of natural successional patterns to serve as models for the successional trajectories of mixed species stands (Liptzin and Ashton, 1999; Allison *et al.*, 2003; Paluch, 2007). Figure 11 illustrates changes in relative dominance of species in diverse hardwood stands during a relative short post-harvest successional sere (Allison *et al.*, 2003). Natural replacement patterns could also be used to filter species selection and generate working hypotheses about stand development. Combinations of species differing in shade tolerance (e.g., Figure 6) could be used to create intimate mixtures, as in the Swiss Jura (Knuchel, 1953).

Such hypotheses must be regarded as tentative, however. Rising atmospheric CO₂ accompanied by changing temperature and precipitation may alter historically documented replacement patterns. Individual differences and micro-environmental effects may also swamp the influence of broader climatic trends, at least in the short term. In a study carried out in North Carolina, average interspecific differences in seedling responses to elevated CO₂ fertilization were exceeded by heterogeneous growth among individuals. These individual responses were conditioned by microenvironmental variables, especially the degree of shade (Mohan *et al.*, 2007). In a related study, species responded idiosyncratically to the combined effects of spring temperatures, summer moisture availability and light environment (Clark *et al.*, 2011).

Given these complex responses to the environment, the design of “no-analogue” tree communities will require marshalling of all available ecological and silvicultural information. Species selection may begin by locating trees that grow in closest climatic analogues to the expected future climate at the planting site. In the UK, a climate-matching index has been developed to guide species transfers (Broadmeadow *et al.*, 2009). Climate matching, combined with growth potential, ecological impacts and socioeconomic filters is also used in Europe to broaden the list of non-native species that might be planted (Schmiedinger *et al.*, 2009).

Isolated forest patches that are relicts of former climates may also provide models for no-analogue silviculture. One example of such a forest occurs in Kandiyohi County, Minnesota, where there American (*Ulmus Americana* L.), slippery (*U. rubra* Muhl.) and rock elm (*U. thomasi* Sarg.) form a mixed stand with basswood (*Tilia Americana* L.). This unusual forest appears to be a remnant species association dating back to the Holocene warm period (Axelson, 2010), and may therefore provide a starting point for no-analogue stand designs.

Unfortunately, few examples of reciprocal transplant or deliberately established no-analogue communities exist by which to judge possible outcomes for transplanted tree species. Those that exist have produced equivocal results. Seventeen hardwood species relocated between sites in the Carolina Piedmont and montane sites in the southern Appalachians grew at similar rates to resident species, regardless of environmental conditions (Ibáñez *et al.*, 2009). On the north shore of Lake Superior, first year survival of sugar maple seedlings transplanted to boreal forest sites was lower than for seedlings in native sugar maple forest, but once established, survival in boreal forest sites was greater (Kellman, 2004). Four year survival of native hardwoods transplanted into a southern Ontario woodlot was around one percent, indicating inertia imposed by existing stands against seedling establishment, even of native species (Hewitt and Kellman, 1998).

5. Hypotheses to Drive Designer Forest Experiments

Correlations between phenology and characteristic tree growth patterns provide one avenue towards working

silvicultural hypotheses. Lechowicz's (1984) speculation that species with indeterminate growth and multiple flushes of leaves might be buffered against spring frosts is an ecological hypothesis that could be tested silviculturally. Other hypotheses could be constructed around the contention of a hard trade-off between height growth potential and cold tolerance (Loehle, 1998). Loehle (1998) compared growth rates of a diverse collection of temperate and boreal trees across a broad climatic gradient representative of temperature changes that could take place in the future. Could competitive advantage in northern tree populations shift from adaptations to cold to the capacity for fast vertical growth? Acclimation of respiration to higher temperatures suggests that such a shift could occur. But seasonality of growth also matters. In northern climates subject to unpredictable spring and fall weather, trees that grow fast during short growing seasons may have a long term advantage over those that grow more slowly over a longer period. Seasonal growth patterns and critical phenological events will therefore interact over longer periods, implying that short term studies may fail to capture key events that shape tree species communities (Clark *et al.*, 2010; Clark *et al.*, 2011).

Finally, there is a great need to understand interactions between effects of climate, competition, and local microsites on tree growth and survival. For example, growth of 40 year-old European beech is highly sensitive to competitively induced water stress at high stem densities and high temperatures. At lower tree densities, however, growth was favored by high temperatures (Cescatti and Piutti, 1998). This agrees with general findings that crown and stem development are highly contingent on density and identity of conspecific trees (Cameron and Watson, 1999; Liptzin and Ashton, 1999; Webster and Lorimer 2003). By contrast, soil moisture had no clear influence on growth rates among southern temperate hardwoods planted at two extremes of a soil moisture gradient (Ibáñez *et al.*, 2009).

Silviculturists may be able to leverage these developmental idiosyncrasies by varying planting patterns, species densities, and microsites. Resistance to fire propagation may be greater where cluster reforestation and lower planting densities are deployed (Stephens *et al.*, 2010). "Oak nest planting" makes innovative use of planting patterns to protect trees from both the physical environment and herbivory (Figure 10b). The technique was inspired by observations of natural dispersal patterns in oak woodlands, and consists of central "nests" of oak seedlings buffered against competing vegetation, frost damage, and deer browsing by protective rings of hornbeam (*Carpinus betulus* L.) or smallleaved lime (*Tilia cordata* Mill.) (Pommerening and Murphy, 2004). Although these damaging agents are not directly connected to climate change, they do predispose trees to mortality resulting from direct climatic effects, such as drought (Wang *et al.*, 2012).

Other general rules of thumb can be derived from conventional silviculture. Vertically stratified mixtures of trees should combine shade tolerant with mid-tolerant or intolerant species. Where growth form and wood quality is important, the choice

of appropriate nurse trees to "train" height growth and crown form in target trees may be important (Cameron and Watson, 1999; Clark *et al.*, 2008). For example, Sitka spruce nursed by lodgepole pine had smaller branches, shallower crowns, and less juvenile wood than those planted with hybrid larch (*Larix x eurolepis* Henry) (Cameron and Watson, 1999). Cherrybark oak (*Quercus pagoda* Raf.) limits sweetgum (*Liquidambar styraciflua* L.) crown width by mechanically abrading its twigs, which are more brittle than those of cherrybark. Cherrybark's ability to outcompete sweetgum in height growth may stem from its spatio-temporal pattern of bud break, which occurs basipetally (from crown top to crown base), whereas budbreak in sweetgum occurs acropetally (from crown base upwards) (Lockhart *et al.*, 2006).

C. Avoidance of Consequences and Super-Intensive Silviculture

Even in temperate and boreal regions, harvestable stands of fast-growing species can be produced in 30 years or less. This strategy would minimize risk due to long-term consequences of climate change by planting trees that only need to be adapted to conditions projected for 10–30 years. First, short-term projections are arguably more reliable than those for the more distant future. In intensive plantations, willows, hybrid poplar, and hybrid larch can attain annual growth increments of $\geq 30 \text{ m}^3 \text{ ha}^{-1}$, and achieve stocking of over $300 \text{ m}^3 \text{ ha}^{-1}$ in less than 20 years (Sedjo and Botkin, 1997; Labrecque and Teodorescu, 2005; Paquette and Messier, 2010). Fast-growing trees also have potential to reduce costs and environmental impacts by concentrating production on a small portion of the land base, providing flexibility to implement less intensive forest management elsewhere.

Short rotation tree crops would allow managers to fine-tune their silvicultural strategies at intervals short enough to avoid the worst consequences of climate change. Clone or seed selection could be adjusted after each harvest to match emerging climatic trends. For example, the planting of hybrid poplar has been proposed as a strategy for restoration of degraded floodplains (Braatne, 1999), opening up possibilities that traditional riparian restoration strategies might be overhauled to embrace serial, short term adaptive management objectives. Hybrid poplar and willow are subjects of experimental biomass production systems that would see even shorter rotations on marginal or abandoned farmlands (Saddler, 2002; van Oosten, 2004). There are even ongoing attempts to integrate hybrid poplar with long-term silvicultural objectives by using clones as a nurse crop for temperate hardwoods (Ontario Stewardship Centre, undated).

Unfortunately, effects of climate change on viability of fast-growing hybrid trees have yet to be considered in detail. Climate change was judged to be beyond the scope of a recent risk assessment of hybrid poplar plantations in Canada (Volney, 2006). However, risks posed by drought can be addressed to some degree, since drought-resistant poplar clones have been developed for the prairie regions (Dickman, 2006). A recent study also

compared growth and hydraulic properties of native trembling aspen and hybrid poplar clones. In this study, aspen clones had more negative water potentials, higher water use efficiency, and greater resistance to cavitation than hybrid poplar (Schreiber *et al.*, 2011). Height growth of hybrid poplar and trembling aspen was greater in genotypes with narrower vessels, suggesting that xylem diameter is a potential trait that could be used to select climate-resilient trees.

D. Summary of Silviculture

Silvicultural treatments may be used to improve resistance, resilience to climate change and climate-related disturbances. Alternatively, the consequences of long-term, gradual shifts in average climatic conditions may be avoided by shortening silvicultural cycles, using fast-growing trees or harvesting slow-growing trees prior to maturity. Silvicultural interventions can be aligned along a climate change severity gradient from minor modifications to existing practices (e.g., enhanced thinning regimes, replacing clearcuts with seed-tree cuts) to major changes (novel species mixtures and assisted migration of species and provenances from warmer to cooler climates, Figure 9).

Our discussions of phenology and acclimation suggest that many existing provenances could possess greater flexibility in the face of global warming than previously thought. This perspective implies that some forests could be adapted to moderate (2–3°C) levels of temperature increase with comparatively minor modifications to silvicultural practices, without altering species composition or geographical transfers of genetic material. Practices that promote within-stand genetic diversity should be encouraged, since pleiotropy may exist between traits of interest; for example, between growth rates and vulnerability to pathogens.

Continued uncertainty around the precise details of even moderate climate change suggests that many genotypes should be encouraged to grow together as a bet-hedging policy. Likely consequences of such a strategy would be that short-term stand growth would be sacrificed for long-term benefit of improved forest health and, possibly, greater wood production over time. An emerging consensus suggests that mixed species stands will be better at buffering climate-related pressures than monocultures (O'Hara and Ramage, 2013). Mixing different potentially compatible combinations of response and effect traits, such as shade tolerance, foliage flammability, rooting depths, and nutrient demand, will increase the chances that such mixtures will be productive, resistant and resilient.

At the upper limit of climate projections ($\geq 8^\circ\text{C}$ of warming), forest managers may have to contemplate fundamental changes to both species composition of forests and existing practices. Low probability but high risk climate futures might necessitate high risk management interventions in the absence of complete knowledge. Some jurisdictions are already contemplating localized versions of such interventions by combining "silvicultural triage" (e.g. sanitation and salvage cutting to reduce fire

risk) with pre-emptive movement of species (Frelich and Reich, 2009). The great challenge to planting and tending such "neo-native forests" will be to select species with traits that will lend climate-resilience to the resulting stands.

V. DISCUSSION

As anthropogenic climate change proceeds, traditional silvicultural activities will be coerced into meeting novel objectives to cope with constantly changing circumstances. Traditional management paradigms that presupposed a constant climate are no longer valid, and managers have to plan, not just for one future climate, but for a range of climatic futures framed by great scientific uncertainty. There is increasing recognition that even moderate climate change will lead to increased severity and frequency of natural disturbances (Niinemets and Valladares, 2006; Rouault *et al.*, 2006; Galatowitsch *et al.*, 2009; Seidl *et al.*, 2011). Climate change is also likely to promote the spread of native and exotic pests and diseases, making commercial forestry species more vulnerable to their effects (Frelich and Reich, 2009). Stand level practices, such as thinning, fuel reduction varying planting density and establishing genetically diverse stands will increasingly be used to reduce conditions that predispose stands to physical and biotic disturbances (Galatowitsch *et al.*, 2009; O'Hara and Ramage, 2013). Foresters must also recognize that previous practices have increased forests' vulnerability to climate-induced disturbances. Warmer winters combined with silvicultural history established the conditions for catastrophic mountain pine beetle outbreaks in British Columbia (Burton, 2010; Sambaraju *et al.*, 2012). European analyses also demonstrate that both forestry practices and extreme weather events significantly affect the vulnerability of forest stands to disturbance (Jactel *et al.*, 2009; Seidl *et al.*, 2011).

A. Insights from Models

Although all models have methodological or data parameterization deficiencies, recent model innovations provide insights that can begin to guide species selection and management. BEMs combining climate envelopes with functional traits and vulnerabilities reinforce the important role of natural disturbances in molding future forest composition. But incorporating interannual climatic variability into BEMs increases the range of future outcomes through effects on dispersal and survival (Nabel *et al.*, 2013). The plurality of growth responses that appear when provenances in common gardens are modeled with BEMs (Li *et al.*, 2010; Garzón *et al.*, 2011; Gray and Hamann, 2011) indicate that provenance will have idiosyncratic responses to climate. RTFs confirm these idiosyncrasies (Wang *et al.*, 2006; Wang *et al.*, 2009), and confirm the importance of other aspects of local environments to provenance adaptation (O'Neill, 2007).

Models provide clues to limits of adaptation that must be further explored in empirical studies. Northern limits on the time needed for fruit maturation, and the consequences of inadequate chilling for breaking dormancy and tissue development (Morin *et al.*, 2007) accord with observations (e.g. of sugar maple),

but require more extensive investigation. Predictions that frost tolerance would be inversely proportional to frost-hardy temperatures and duration of chilling (Leinonen, 1996; Sykes *et al.*, 1996) also require more work. The roles of acclimation, epigenetics, non-structural carbohydrates, and species-specific responses to drought in adapting trees to climate change have also been neglected in process-based models, and a new modeling effort is needed to address these deficits.

B. Phenology, Physiology, and Species Choice

Although some species and provenances may grow successfully in an altered climate, they will be increasingly vulnerable to disturbances, pathogens, and climatic extremes. Damage to trees is sometimes a consequence of causal pathways that require considerable research to understand, as in the interactions between soil moisture, snow cover, rooting depth and nutrient acquisition that explain the decline of yellow cedar (*Callitropsis nootkatensis* [D. Don] D. P. Little) (Hennon *et al.*, 2012). Environmental pressures acting at multiple scales against different tree life stages are likely to drive transitions between biomes in sensitive ecotones, such as the prairie-forest boundary (Frellich and Reich, 2010). Transitions between forest types or from forest to grassland could be mediated by the balance between isohydric and anisohydric responses to drought and the duration of dry conditions (McDowell *et al.*, 2008; Wang *et al.*, 2012).

Epigenetic acclimation of seed embryos may reduce climatic vulnerabilities for some species, but we do not know how widespread this phenomenon may be. No studies have systematically probed thresholds beyond which acclimation fails to buffer individuals against rising temperatures, and population level consequences of phenotypic acclimation remain unexplored. Further important research questions include: will acclimation of bud set to the climate of embryogenesis lead to seedling populations that are more or less vulnerable to frost damage over time? Does phenotypic acclimation in young seedlings persist into adulthood, and how does it play out against observed phenological differences between juvenile and adult trees (e.g., Augspurger and Bartlett, 2003)? To what extent will hidden reaction norms (Schlichting, 2008) come to the fore as climate continues to change, confounding attempts to extrapolate from observed phenology / environment relationships?

Common garden and reciprocal transplant studies provide clues to temperature differences through which species might be transplanted. In many species, growth reductions occur when they are moved more than 1–2°C away from seed source locations, but a few display positive growth responses when shifted by up to 5°C (Figure 3) (Carter, 2006; Wang *et al.*, 2006). Changes in growing temperature are also confounded with shifts in latitude and changes in precipitation and the physical environment, all of which must be accounted for when considering changes to seed zone boundaries or assisted migration. Our uncertainty about locations of damage thresholds and vulnerability along the continuum of environmental change will continue to drive the need to experiment with different silvicultural treat-

ments, from minor interventions already practiced to the design of “no analogue” ecosystems (Palmer *et al.*, 2004; Sarr and Puettmann, 2006).

C. Selection for Traits

Functional response and effect traits potentially provide a framework for guiding species choice and silvicultural strategies (Figure 9). The role of functional traits as drivers of biodiversity / ecosystem production relationships is well documented for grasslands, and is a key consideration in new tree diversity experiments (Scherer-Lorenzen *et al.*, 2007). But open questions include which functional effect or response traits will be useful in designing future forests? How many such traits should be represented? Empirical work suggests that overyielding (greater productivity in polycultures relative to reference monocultures) occurs where species differing in shade tolerance are grown in stratified canopies (Boyden *et al.*, 2009; Zhang *et al.*, 2012; Vila *et al.*, 2013). Meta-analyses provide strong support for the contribution of shade tolerance and species evenness to overyielding (Zhang *et al.*, 2012), and record positive relationships between productivity and species richness up to a maximum of about six species (Vila *et al.*, 2013).

Different mixtures of traits will alter the strength of diversity-ecosystem function relationships (Scherer-Lorenzen *et al.*, 2007; Schleuter *et al.*, 2010). We suggest that selected traits should be those that are potentially maximally responsive to environmental drivers that will change with the climate. In addition to shade tolerance, successional status and compatibility with local edaphic conditions, silviculturists may need to consider inherent growth patterns, susceptibility to early or late frost, drought tolerance (and specific mechanisms by which drought is tolerated), budburst sequence within tree crowns, and rooting habits (Scherer-Lorenzen *et al.*, 2007; Hennon *et al.*, 2012). The interplay between winter chilling and spring forcing requirements is also an important consideration in choosing which species and provenances to plant. Our ability to move species geographically may be limited where temperature and photoperiodic signals determine the timing of budbreak (Polgar and Primark, 2011).

With sufficient knowledge, managers may establish trait combinations to guide the design of climate-resilient forest stands. Like productivity, trait diversity peaks for many real and simulated ecosystems at 4–8 species (Petchev and Gaston, 2007; Scherer-Lorenzen *et al.*, 2007). A silviculturist seeking to combine desirable traits may therefore be able to optimize functional diversity in a stand featuring three or four species (e.g. Figure 10a). Functional traits could also be combined in a temporal sequence of adaptive plantings targeted at different conditions along the climate continuum and forest succession.

D. Zonation of Silvicultural Activities

Given the vast areas covered by forests in Canada and the United States, it is hard to escape the conclusion that management-driven adaptation of forests to climate change will

only be possible across fairly small areas. The higher costs attached to more intensive silviculture imply that it may only be economical in locales that are well served by roads and proximity to markets (Park and Wilson, 2007). Intensive management zones and experimental silviculture will therefore have to be located within easy reach of management teams and mills (Park and Wilson, 2007).

Forest zonation, long discussed as a solution to timber supply and multi-resource management problems (Messier and Kneeshaw, 1999), provides one route to allocating silvicultural efforts. Companies are allying with academics to model and plan for zonation in large forest concessions using the TRIAD approach (e.g. Boyland *et al.*, 2004; Montigny and MacLean, 2006). TRIAD zonation divides forest holdings into strict conservation, extensively-managed and intensively managed zones, with some schemes allowing for an additional super-intensive zone of fast-growing tree species. Ecological processes in conservation and extensive management zones could be left to respond to climate change with minimal management intervention. Alternatively, stand-replacing disturbances could be manipulated to foster forest stands that have greater resistance to the propagation of future disturbances and climate change-induced weather extremes. Manipulation may take the form of changing stand structures, spatial patterns and densities, which will alter the character of some disturbances (Stephens *et al.*, 2010), or species composition could be reconfigured during the post-disturbance “reorganization” phase of the adaptive cycle (Holling and Gunderson, 2002). Less dramatic interventions in extensively managed zones would involve modifying silvicultural treatments to promote a range of conditions that would be adaptively managed. It is in the extensive forestry zone, for example, that under-planting of relocated southern provenances or non-endemic native trees has practical and economic potential to be implemented.

Zonation may allocate costs, but the risk of betting on the wrong management strategies remains. Climate-mediated, intensified natural disturbances, such as the mountain pine beetle epidemic in B.C., could engender greater risk aversion in an already risk-averse industry (Park and Wilson, 2007). The practice of discounting future benefits inevitably minimizes the amount of money that any company is prepared to invest in the productivity of long-lived trees. This is especially the case in Canada, where much of the boreal forest is dominated by small, slow growing trees with limited value. Ignorance of climate science and climate change scenarios on the part of both the public and managers (Bormann and Kiester, 2004; Ogden and Innes, 2007) adds additional unknowns to the risk profile of forest management. Risk assessments of different management strategies are sorely needed, but to date, few risk assessments of the effects of climate change on forest management strategies have been done.

E. Selected Research Recommendations

Our knowledge of fundamental niche limits, phenological plasticity, acclimation physiology, species traits, and proximate

causes of drought-induced mortality for tree species, but even more so for other species in forest ecosystems, is remarkably incomplete. Our knowledge of how these factors vary among provenances within species is even worse. There is a clear need to chip away at these knowledge deficits in order to develop more comprehensive data bases that can be used by managers in adapting forestry practices. In most cases, the inertia that is inevitable when working with long-lived organisms and time lags in development of new, adapted varieties mean that foresters will have to work with traits and adaptations of existing genetic material. Research is therefore needed to (i) improve understanding of plasticity and environmental limits of these traits and adaptations, and (ii) leverage theoretical advances and academic research to narrow down the range of operational experiments that are tried out in the field.

The lower ($\sim 1\text{--}2^\circ\text{C}$) and mid-range ($\sim 3\text{--}5^\circ\text{C}$) of warming scenarios (Figure 9) could be addressed using many existing field trials. For example, the phenology of latitudinally transplanted provenances and their offspring in seed orchards could be investigated for signs of epigenetic acclimation at relatively low cost. Phenology should also be closely monitored in common garden trials targeted specifically at climate change, such as the AMAT trial (O’Neill *et al.*, 2011), where both latitudinal (photoperiodic) and temperature effects could be investigated.

A variety of new field experiments is needed to investigate adaptive limits of trees with different trait combinations. Trials incorporating trees with different types and dimensions of vessel elements should shed light on relative susceptibility to cold and drought-induced embolism. The linkages of anatomy and ecological strategy (dispersal, successional status) to growth patterns (the gradient from determinate to indeterminate growth) and strategies for breaking dormancy (chilling, photoperiod plus chilling, no chilling) also need investigation. And given the growing importance of extreme drought (Breshears *et al.*, 2005), role of vascular system and other traits in drought tolerance needs to be investigated for a wide variety of species. The range of climates under which such trials are performed should encompass temperatures and latitudes that are likely to challenge the limits of adaptation, which the current review suggests are poorly known for most species. More of trials, such as AMAT and Carter’s (1996) work that investigates impacts of larger temperate changes, are needed, as are more analyses that investigate the joint effects of latitude, temperature, precipitation, and local edaphic variables.

At ecotones between forest types or between forest and grassland, experiments in easing the transition from one biome community to another are needed. Foresters have a long history of converting one forest type to another, including most recently in managing the transformation of exotic conifer plantations back to native hardwoods. These and natural patterns of succession that have been documented for different forest types, can act as preliminary models for management. Active management of forest transitions is being contemplated in parts of Europe and North America. At the prairie-forest ecotone in Minnesota, managers are designing strategies to improve forest resilience,

but acknowledge the possibility that combined disturbance and climate pressures could turn forest into savanna. (Frelich and Reich, 2009; Frelich and Reich 2010).

VI. CONCLUSIONS

1. Substantial global warming, with accompanying changes in precipitation patterns, seasonality, and frequency of extreme weather, is all but inevitable, but very large uncertainties remain about the magnitude, if not the general direction of these changes.
2. Our inability to predict the precise profile of climate change is compounded by uncertainties and methodological difficulties of using computer models to project tree and forest responses to global warming. Fundamental niches can not be modeled effectively, and physiological models are sensitive to functional forms of growth, mortality and phenological equations used in their formulation.
3. Recent model innovations have yielded important insights about the responses of provenances within species to being shifted across different climate zones. They illuminate the limitations that natural disturbance places on species' ability to migrate in response to climate change, and illustrate the additional uncertainties imposed by interannual climate variability on species establishment.
4. Common garden experiments provide insights into provenances that may thrive under some climate change scenarios. But even these experiments are limited by the range of environments available, the time it takes to get some reliable results, the limited numbers of species used, and the likely development of no-analog climates in the future.
5. Epigenetic effects and phenotypic plasticity could produce more flexible responses to climate change than have hitherto been anticipated. Acclimation of respiration also occurs in response to elevated CO₂ and warmer temperatures, separately and in combination. If these responses are widespread, they might ameliorate consequences of climate change for tree populations—up to a point.
6. Nevertheless, CO₂ fertilization of tree growth appears to be transitory in most FACE experiments. Nutrient limitations, alternative pathways for fixed carbohydrates, and drought all seem likely to limit any long term gains in NPP from CO₂ fertilization.
7. Forest management solutions that homogenize forest conditions and are targeted only at wood volume and productivity risk failure in a rapidly changing climate. To cope with uncertainty about future climates, forest managers should initiate diverse portfolios of silvicultural experiments. Many of these will fail, but some will succeed, and management interventions designed to increase forest resilience and resistance to changing conditions may indirectly improve forest productivity more than treatments aimed only at maximizing tree growth.
8. Such experiments may range from minor stand modifications aimed at buffering site-level effects of climate change to the design of no-analogue forests. Criteria for no-analogue species selection include their functional effects on ecosystem processes, complementarity and competition among species, their responses to local environments, and resilience to pests and intensified natural disturbance regimes (Millar *et al.*, 2007).
9. The integration of insights from ecophysiology and models into a program of silviculture represents a serious research challenge. Our fragmentary knowledge of traits and responses to climate of the majority of tree species used in forestry (Johnston *et al.*, 2009, p.90) needs to be overcome by research to minimize our knowledge deficits.
10. Silviculturists can benefit from managing forests as complex systems to increase adaptive capacity as climate change proceeds (Puettmann *et al.*, 2009; Messier *et al.*, 2013). Foresters must be prepared to respond nimbly to changes in physical environment, fresh knowledge about climate change, and ongoing insights into species and ecosystem responses to global warming. Researchers need to develop applied experimental results that would enable information about epigenetics and individual acclimation to be used in forest management. Marshalling these strategies and sources of knowledge should enable forest managers to mount (at least) a partially successful response to the challenges of climate change.

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