



NATIONAL COUNCIL FOR AIR AND STREAM IMPROVEMENT

**MODEL-BASED FORECASTS OF NORTH
AMERICAN FOREST GROWTH: A REVIEW**

**TECHNICAL BULLETIN NO. 1046
JANUARY 2018**

**by
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PRESIDENT'S NOTE

Because forest growth takes place over decades, changing environmental conditions could potentially impact forest growth and the resource base for the forest products industry. Forest certification standards ask their participants to consider the potential for climate factors to affect forests. For example, the 2015-19 Sustainable Forestry Initiative (SFI) Forest Management Standard and Fiber Sourcing Standard ask participants to broaden awareness of climate change impacts on forests, wildlife, and biological diversity. SFI participants who manage forests are also asked to consider the potential for climate factors to influence forest growth, estimates of forest inventory, and planned harvests. One approach to obtaining such forecasts is to use forest growth models.

Because a comprehensive review is lacking, this report summarizes and evaluates current state of the art of model forecasts of forest growth responses to rising CO₂ and hypothesized change in climate factors in North America, excluding Mexico, over coming decades. Climate models and forest growth models used in the reviewed publications are described, and projections of forest growth are summarized.

While it is difficult to make precise forest growth and yield predictions based on the publications examined, the reviewed results suggest increased forest growth in the regions where most commercial forestry takes place. This is so even when responses to the hotter global warming scenarios are simulated.

Given uncertainties in the actual trajectory that climate factors will take in any given location, however, forest managers should periodically check site index and yield table outputs to ensure that they match current growth responses. Planting trials also may warrant consideration as an ongoing precautionary measure. Based on the studies reviewed, the outlook for wood supplies seems positive in general, with projections for some regions such as the Southwest and western Canada being more uncertain.

A handwritten signature in black ink, appearing to read "Dirk Krouskop".

Dirk Krouskop

January 2018

NOTE DU PRÉSIDENT

Comme la croissance d'une forêt s'étend sur de nombreuses décennies, des conditions environnementales changeantes peuvent potentiellement avoir un impact sur sa croissance et sur le bassin de ressources de l'industrie des produits forestiers. Dans les normes de certification forestière, on demande aux participants de tenir compte de la possibilité que des facteurs climatiques puissent avoir un effet sur les forêts. Par exemple, dans la norme sur l'aménagement forestier et dans la norme sur l'approvisionnement en fibre de la *Sustainable Forestry Initiative* (SFI) 2015-19, on demande aux participants d'accroître la sensibilisation aux incidences du changement climatique sur les forêts, la faune et la biodiversité. On demande également aux participants SFI responsables de l'aménagement de forêts de tenir compte de la possibilité que les facteurs climatiques puissent influencer la croissance forestière, les estimations d'inventaire forestier et les récoltes planifiées. Un type d'approche pour faire de telles prévisions consiste à utiliser les modèles de croissance forestière.

Le présent rapport résume et évalue l'état actuel des connaissances sur les prévisions de croissance forestière obtenues par modélisation suite à une augmentation de CO₂ et à un changement hypothétique dans les facteurs climatiques en Amérique du Nord, à l'exception du Mexique, au cours des prochaines décennies. Le rapport décrit les modèles climatiques et les modèles de croissance forestière utilisés dans les publications examinées et résume les projections en matière de croissance forestière.

Bien qu'il soit difficile de prévoir la croissance forestière et le rendement de façon précise à partir des publications examinées, les résultats issus de ces études semblent indiquer une augmentation de la croissance forestière dans les régions où se déroulent la plupart des activités forestières commerciales. Il en est ainsi de même pour les réponses obtenues par simulation pour les scénarios les plus chauds de réchauffement planétaire.

Compte tenu des incertitudes sur l'évolution réelle des facteurs climatiques dans une région donnée, les responsables de l'aménagement forestier devraient vérifier de temps en temps les éléments de sortie liés aux indices de station et aux tables de rendement pour s'assurer qu'ils correspondent aux réponses de croissance actuelles. Des essais de plantation mériteraient aussi d'être pris en considération comme mesure de précaution de longue durée. Les perspectives concernant l'approvisionnement en bois semblent généralement positives d'après les études analysées, mais les projections pour certaines régions telles que le sud-ouest des États-Unis et l'ouest du Canada sont plus incertaines.



Dirk Krouskop

Janvier 2018

MODEL-BASED FORECASTS OF NORTH AMERICAN FOREST GROWTH: A REVIEW

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ABSTRACT

In the context of constantly changing environmental conditions, planning for forest management goals and projecting wood supplies becomes more complicated. Possible changes in precipitation, temperature, and CO₂ can affect tree growth substantially and potential effects differ by species and region. However, integration of potential forest growth responses to these factors can be achieved using models. Because of the need to understand the range of forest growth forecasts and the strengths and limitations of different modeling approaches, results from 18 studies of forecasted forest responses over coming decades were summarized. Some models used statistical relationships between tree rings and climate to forecast growth responses to potential future climate, some simulated net photosynthesis of a standard forest canopy, and many used tree or stand growth models at various levels of mechanistic detail. In general, models that included CO₂ responses predicted enhanced forest growth by 2100 across most of the commercial timberland areas of the US and Canada. For modest warming, most models showed growth enhancement in most regions. For hotter scenarios, many models and regions showed even more growth enhancement, but some regions such as the Southwest, mountain West, and southwestern Canada were predicted to experience drought stress, although projections in these regions were variable. Young stands, angiosperms, and early-successional species were predicted to exhibit the most positive responses. As a result, commercial harvest ages might be accelerated by several years, depending on species. Some simulations for the Midwest and Northeast US predicted a doubling or more of net primary productivity although other studies show a lesser response. Models that did not include mechanisms of CO₂ fertilization showed positive growth responses in only limited cases and generally showed growth declines. There also was some evidence indicating the potential spread of forest into woodland at shrub or prairie ecotones.

KEYWORDS

carbon dioxide fertilization, climate change, environmental factors, forest productivity, growth model, simulation

REVUE DES PROJECTIONS MODÉLISÉES DE LA CROISSANCE FORESTIÈRE EN AMÉRIQUE DU NORD

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RÉSUMÉ

Dans un contexte où les conditions environnementales changent constamment, planifier les objectifs d'aménagement forestier et faire des projections sur les approvisionnements en bois deviennent plus compliqués. Les changements potentiels dans les précipitations, la température et le CO₂ peuvent influencer considérablement la croissance des arbres et ces effets potentiels peuvent varier selon les régions et selon les essences. Cependant, il est possible d'intégrer les réponses de croissance potentielle à ces facteurs en faisant appel à des modèles. Pour comprendre l'étendue des projections de croissance forestière ainsi que les forces et les limites des différentes approches de modélisation, NCASI a résumé les résultats de 18 études portant sur les réponses prévues de croissance des forêts au cours des prochaines décennies. Certains modèles ont fait appel aux relations statistiques entre les anneaux de croissance des arbres et le climat pour prévoir la croissance en fonction d'un futur climat potentiel, d'autres ont effectué une simulation de la photosynthèse nette de la canopée standard d'une forêt et bon nombre ont utilisé des modèles de croissance des arbres ou des peuplements à différents niveaux de détail mécanistique. En général, les modèles qui présentaient des réponses en fonction du CO₂ prévoyaient une croissance forestière accélérée d'ici 2100 dans l'ensemble de la plupart des terres forestières exploitables commercialement aux États-Unis et au Canada. Dans un scénario de réchauffement modeste, la plupart des modèles prévoyaient une accélération de la croissance dans la plupart des régions. Dans les scénarios de réchauffement plus important, bon nombre de modèles prévoyaient une plus grande accélération dans un plus grand nombre de régions, mais certains modèles prévoyaient que des régions telles que le sud-ouest des États-Unis, les montagnes de l'ouest des États-Unis et le sud-ouest du Canada subiraient un stress relié à des sécheresses, bien que les projections dans ces régions étaient variables. Les modèles prévoyaient que les jeunes peuplements, les angiospermes et les espèces des premiers stades de succession végétale étaient ceux qui répondraient le plus positivement. Par conséquent, il est possible que l'âge de la récolte commerciale soit devancé de plusieurs années, selon les essences d'arbre. Pour les régions du Midwest et du nord-est des États-Unis, certaines simulations prévoyaient que la productivité primaire nette augmenterait par deux fois ou plus, bien que d'autres études prévoyaient une productivité moindre. Les modèles qui n'incluaient pas de mécanismes de fertilisation par le CO₂ prévoyaient une croissance positive dans quelques cas seulement et prévoyaient généralement une diminution de la croissance. Il y avait aussi un certain nombre d'indices indiquant l'étalement possible des forêts dans des écotones composés d'arbustes ou de végétation herbeuse (type prairie).

MOTS-CLÉS

changement climatique, facteurs environnementaux, fertilisation par dioxyde de carbone, modèle de croissance, productivité forestière, simulation

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MODEL-BASED FORECASTS OF NORTH AMERICAN FOREST GROWTH: A REVIEW

1.0 INTRODUCTION

Forest landowners and the forest products industry have a long planning horizon. Trees planted today may not be harvested for 30 to 70 years, depending on forest region and product desired. Manufacturing facilities that use wood represent a large investment that depends on reliable wood supplies. Some threats to local wood supplies such as fire and insect attack can be prevented to some degree or salvaged, while others such as hurricane damage largely cannot. Over recent decades, it has been argued that climate change also represents a potential threat to forests and wood supplies. Some forecasts project large forest growth declines (e.g., Coops and Waring 2011a, 2011b; Coops, Waring, and Law 2005; McKenney et al. 2011). While forecasted climate changes are not certain, these forecasts do form a basis for many government policy responses. For example, risks of species' extinctions are often assumed to be increased by projected climate change.

A summary of climate change science can be found in the Intergovernmental Panel on Climate Change reports (IPCC 2014). Scenarios of historical and hypothetical future driving factors (solar radiation, greenhouse gases, land use, etc.) are used to drive large, complex climate models to generate climate forecasts. The coarse-grid outputs of these models must then be downscaled to the regional level. For forest growth response forecasts, it is further necessary to use forest growth models to project long-term responses. In contrast to crop growth, which largely tracks annual climate, trees respond slowly to altered conditions and are slow to migrate. Thus, forest growth models must maintain realistic responses over many decades to lead to useful forecasts.

Climate factors most relevant to forest growth forecasts are temperature, precipitation, and CO₂ level. Secondary factors include changes in seasonality of temperature and precipitation, snowpack depth and duration, and drought episodes (as distinct from average rainfall). In general, it is argued that warming should cause shifts in species relative dominance, geographic range shifts (northward and upward in the northern hemisphere) (e.g., Hamann and Wang 2006) and possible dieback events from droughts (Luce et al. 2016). It is also posited that change could be too rapid for species to keep up, causing dieback at warm range margins and possible extinctions of species. Any of these changes would be detrimental to forests, forest landowners, and the forest products industry. On the other hand, vegetation models that incorporate CO₂ effects tend to project increases in growth. For example, Piao et al. (2013) compared 10 terrestrial carbon cycle models to flux tower and other data. They found an increase globally of 7% in net primary productivity (NPP) on average across models over the past three decades, due to rising CO₂, with more benefit in drier regions.

Because a comprehensive review is lacking, this report summarizes and evaluates current state of the art of model forecasts of forest growth responses to rising CO₂ and hypothesized changes in climate factors in North America, excluding Mexico, over coming decades. Climate models and forest growth models used in the reviewed publications are described, and then projections of forest growth response to potential changes in climate factors are summarized.

2.0 METHODS

Recent (post approximately 2008) studies of forest growth forecasts were identified based on a complete search of the contents of *Ecological Modeling* (2014-2017), *Canadian Journal of Forest Research* (2012-2017), *Global Change Biology* (2013-2017), and *Forest Science* (2015-2017), plus references obtained by key word searches ("climate change and forests") in Google Scholar. The initial search was limited to these journals as an entry point to the literature. Working back from the

latest issues in these journals, searches were stopped when no new articles were found. The literature cited sections in more recent papers were also searched for relevant publications. Thus, this review of post-2008 publications can be considered comprehensive. Only publications appearing post 2008 were included because older forest growth models often do not incorporate CO₂ effects, which have only recently been understood, and they also often use outdated climate models for input. Furthermore, forest growth models are constantly being improved and 2008 was chosen as the earliest that model results were likely to be still valid. Static species distribution models (discussed below) were considered not mechanistic enough and were also not reviewed. Studies that failed to meet these criteria but were still recent are discussed in the appendix. Consistent with reviewed publications, in this review, climate change is considered to include hypothesized effects of temperature, CO₂, and precipitation.

3.0 CLIMATE MODELS

The atmosphere is a turbulent dynamic system. Simulations of the Earth system using general circulation models (GCMs) incorporate this turbulence and therefore produce highly variable output (IPCC 2014). Any individual run of a single model will differ from other runs of the same model (IPCC 2014). Between-model variability is also high due to this same turbulence as well as due to different model formulations. The result of this variability is that a single model/model run cannot be assumed to be representative of future climate conditions (IPCC 2014). Simulations of forest growth can be affected by this variability, which increases forecast uncertainty (Loehle 2011).

A second consideration is that confidence in climate model output is greatest for global- and continental-scale results (IPCC 2014). The models are, at this time, unable to closely replicate climate histories at local to regional scales (IPCC 2014; Loehle 2011). This means that model outputs for any particular region used as input for a forest growth model may be not representative of actual future conditions.

Finally, different scenarios are run with climate models. The driver for the models is called the Representative Concentration Pathway, which defines the CO₂ and other greenhouse gas concentrations into the future. The RCP4.5 (moderately hot) and RCP8.5 (very hot) scenarios are often used. The lowest-end warming scenarios are not often tested for impacts on vegetation and, when they are used, forest growth forecasts may appear very similar to control runs. For the IPCC third assessment report (AR3) runs used prior to about 2012, the nomenclature is slightly different. Here, the hotter scenarios are designated with “A” prefixes (e.g., A1f1 or A2) and the cooler with “B” prefixes. The most extreme warming scenario/model combinations forecast rates of warming of up to 8°C per century (e.g., RCP8.5 for some GCMs). However, over the past two decades, there has been a pause in warming (Thorne et al. 2015). Thus, a radical change in the rate of warming, which is not evident to date, would be necessary for upper-end warming scenarios to be observed.

A growth model to be used under constant climate (e.g., for short-term studies) can be evaluated in the traditional way in terms of various measures of fit with calibration and test data. But for forecasting purposes, normal testing of growth models does not encompass the possibility that the climate drivers for the forecast could differ from actual values (or be wrong in other ways). For example, McKenney et al. (2011) showed that the three then-current climate models they tested produced variability in North American regional temperatures at the 2071-2100 time-period of up to 4°C and up to a 60% difference in precipitation. Such high variability is on the same order of magnitude as (or greater than) scenario changes. This means that caution is necessary when evaluating forest growth model results, especially if only a single model or a high warming scenario is used.

Climate models also are constantly changing. Early models often did not include precipitation as an output (Loehle 2011), an obvious limitation when forecasting forest growth. By the IPCC third assessment report (AR3) in 2007, models were much improved. However, the fourth assessment report (AR4) and corresponding climate models used in these studies (the Climate Model Intercomparison Project Five or CMIP5) are generally much better. Thus, studies cited here that use the earlier CMIP3 (CMIP Version 3) results as inputs are considered less reliable than those using more recent climate models.

4.0 FOREST GROWTH MODELS

There are multiple types and scales of forest models (Littell et al. 2011; Medlyn, Duursma, and Zeppel 2011). Very broad-scale models might only seek to emulate net primary productivity (NPP) without considering the details of forest dynamics, and may include cellular mechanisms of photosynthesis that incorporate CO₂ response. Similarly, broad models may seek to replicate the spatial pattern of vegetation types. More mechanistic models try to emulate basic processes of tree growth, competition, dispersal, and mortality. Various processes (e.g., dispersal, stand dynamics, CO₂ response) are included or excluded in the various models of this type. Such models have been calibrated and tested against multiple types of data and generally perform well (Sitch et al. 2003). Models of this type may enable predictions about changes in productivity, biodiversity, and species distributions. Statistical models based on historic growth as recorded in tree rings may enable the effects of forecasted changes in temperature and precipitation to be modeled, though CO₂ effects cannot be incorporated in such models. Finally, species distribution models (SDMs) use a statistical approach based strictly on the conditions where a species is currently found to project future occurrences. See Table 4.1 herein for a classification of models relevant to this study.

Table 4.1 Classes of Models Reviewed Ranked from Most to Least Realistic

Name	Description	CO ₂	Forest Dynamics	Metrics
Forest simulator	Models details of forest growth at various levels of resolution	yes/no ^a	yes/no ^a	NPP, biomass increment
Canopy level	Models photosynthesis of idealized canopy	yes/no ^a	no	NPP
Statistical tree growth model	Based on historical tree ring or plot data, climate correlates of growth	no	no	Ring width, biomass increment
Species distribution model	Uses correlates of geographic range to forecast future range	no	no	Geographic range

^a Yes/no = depends on particular model formulation.

Some basic facts of tree growth can be used to put model forecasts in context. Lin, Xia, and Wan (2010) performed a meta-analysis on results from 127 studies of plant responses to altered growing

conditions that did not include CO₂ effects. They found that woody plants responded to warming more than herbaceous species. Mean growth enhancements (biomass) for woody plants to 5°C and 6°C warming were 35% and 55%, respectively, and response to increased precipitation was linear. Such studies suggest that trees may respond positively to warming, at least where moisture is adequate.

There also is a vast literature, including field studies, showing that elevated CO₂ increases tree growth (see review in Loehle, Idso, and Wigley 2016). Plants adaptively reduce the number of stomates as CO₂ rises, which reduces water loss (Keeling et al. 2017). This is particularly advantageous in drier climates. In a historical model-data integration study, Huang et al. (2015) found that including CO₂ in their model increased projected water use efficiency globally under climate change. Elevated CO₂ also, in theory, raises the temperature optimum for photosynthesis, but this effect has been difficult to confirm (Baig et al. 2015). Swann et al. (2016) showed that projections of plant drought stress are cut in half when CO₂ is considered. Rising CO₂ generally enhances growth the most for broadleaf and early successional species (e.g., pines) (Loehle, Idso, and Wigley 2016). Thus, projections of forest growth need to consider both enhanced growth and reduced drought stress due to rising CO₂ (see Cheaib et al. 2012).

While the simple concept that vegetation will move north/uphill with warming in the northern hemisphere seems logical, the likely biological response is more complicated. Loehle (1998, 2014) argued that, while the cold/upper elevation range limit for trees is governed by cold, the warm edge range limit is governed by competition or moisture. Maximum growth rates for boreal or high-elevation species, for example, are much slower than for more southern species, even when grown in the same environments, as shown by Darychuk, Hawkins, and Stoehr (2012) who explicitly demonstrated a trade-off between growth rate and cold hardiness in maritime *Pseudotsuga menziesii* ((Mirb.) France) in British Columbia. Therefore, at the southern range margin of a northern species, a warming event will give more southern species a competitive advantage. However, this will result in a slow competitive displacement process (see Kruse et al. 2016; Loehle 2003) of decades to centuries. The southern margin of a tree species' range is thus unlikely to suffer dieback, as intuition might imply. This runs contrary to assumptions that failure to migrate fast enough will cause range loss (e.g., Loehle 2014).

Recent studies support this analysis. Ettinger, Ford, and HilleRisLambers (2011) studied climate effects on conifer growth in the Pacific Northwest using tree ring analysis. They showed that, at the upper limit of high-elevation species ranges, growth was tightly coupled to temperature/snowpack (which are correlated), with cold and deep snow inhibiting growth. At the low end of the elevation range of these same species, effects of climate became weak. Conversely, at the upper end of low-elevation species ranges, climate had a weak effect. However, at the lower elevation end of the range of these same species, moisture became a limiting factor. At the elevational ecotone of transition between the two groups, neither group was affected much by fluctuations in either temperature or precipitation. Instead, as Loehle (1998) hypothesized, competition was likely dominant. Ford et al. (2016) showed that in forests of Mount Rainier National Park, Washington, climate was related to growth of individual trees in open stands but not where stands were denser, because competition dominated growth responses in that case.

These relationships are supported by other studies (e.g., Peterson and Peterson 2001; Peterson, Peterson, and Ettl 2002) which have found that ecotones and elevational limits are, in many cases, correlated with temperature but not responsive to temperature. These results suggest that, at the warm end of their ranges, species may not be stressed by climate (except when the warm end is also dry), and thus may not respond to warming by exhibiting increased mortality and rapid range retreat as often assumed. The assumption that geographic ranges can be explained by correlations with abiotic factors and mapped accordingly for future climates is thus not well-supported (see also Loehle 2014).

These results account for the species distribution model (SDM) paradox. While growth models and experiments both suggest that trees should respond positively to warming in many cases (as noted above), SDMs predict drastic range shifts (see appendix). Because more southern species have a higher inherent growth rate, they will become relatively advantaged by warming even though northern species also are growing better, but must slowly migrate into a new zone and displace existing species to cause a change (Loehle 2003). Correlations of geographic range with climate, used to develop SDMs, are fundamentally uninformative about how rapidly or even whether range shifts will occur. Tree longevity (Morris et al. 2008; Loehle 2014) and environmental tolerance (Booth 2017; Woodward and Beerling 1997) should result in long periods of environmental disequilibrium and slow dieback or replacement (Svenning and Sandel 2013; Loehle 2014), perhaps over centuries. SDMs rarely capture refugia (Franklin et al. 2013), do not consider CO₂ effects, and produce highly variable output (e.g., Chambers et al. 2013; Pearson et al. 2006). While these models are widely used and their limitations sometimes mentioned, quantitative approaches for adjusting SDM predictions in light of these issues do not yet exist. In some ways, SDM forecasts can be considered possible remote future conditions rather than actual measures of risk. Thus, forecasts based on future geographic ranges with SDM models might take centuries to play out (Loehle 2003, 2014; Currie 2001; Svenning and Sandel 2013) and are thus less relevant to the present analysis. For these reasons, such studies are summarized in the appendix.

One issue sometimes considered in forecasts of forest growth is fire incidence (e.g., Mitchell et al. 2014; Littell et al. 2016; Halofsky et al. 2013). If an area experiences a drying trend or increased precipitation variability, droughts are more likely and wildfire risk may increase. However, historical data do not indicate a trend in wildfires to date. For example, Yang et al. (2014) compiled global fire data over the period 1901-2007. They found a declining trend in the tropics and extratropics and no trend at higher latitudes. While this may be partially due to climate, human land development may also play a role. For example, roads and farms act as barriers to fire spread (Loehle 2004). In addition, the US has a well-established and relatively effective network for controlling forest fires. Given these considerations, possible changes in fire incidence under future climates are not evaluated in this report.

5.0 PROJECTED RESPONSES OF FOREST GROWTH TO CLIMATE CHANGE

Eighteen modeling studies of forest growth forecasts were found for the US and Canada that met study criteria, i.e., post-2008 papers that included CO₂ effects. Some of the 18 studies compared multiple growth models and/or climate projections. The Pacific Northwest simulations explicitly evaluated southwestern Canada (Shafer et al. 2015) or are relevant to it (Sheehan, Bachelet, and Ferschweiler 2015). Seventeen modeling studies that did not include CO₂ effects and 10 SDM studies are described in the appendix because they did not meet the study criteria.

Simulations of climate impacts can be global or local/regional. In the following sections, results from global to regional studies are summarized first, considering the portions of their results that apply to the study region. Then, to facilitate comparisons, the remaining studies are summarized by region.

5.1 Large Extent Simulations

Alo and Wang (2008) used eight climate models to compare idealized preindustrial (275 ppm CO₂) and post-2100 (720 ppm CO₂, the A1B case) scenarios. Vegetation was simulated with a dynamic global vegetation model that included effects of CO₂ on NPP. Vegetation was allowed to immediately adjust to climate. All eight models predicted increased precipitation across North America except for a decrease in the Southwest and in three cases across the Southeast as well. North American mean annual temperature was projected to rise 3-9°C, depending on location. The eight models predicted strong increases in NPP globally. North America forests showed strong to very strong increases in

NPP of 0.05 to 1 Kg C m⁻² (versus typical values of 0.6 for the eastern US) except in Alaska (neutral in one case) and the Southwest (declines in two cases and neutral responses in three cases). There was a general northward shift of forest in North America into the tundra. These increases range from a 10% rise to a doubling of NPP, depending on the base level. The older AR4 climate model runs include very high warming which may bias these results.

Based on concern about black spruce (*Picea mariana*) response to climate in Canada, because it seems intolerant of high temperatures, Girardin et al. (2016) evaluated response to climate change using a physiological stand model combined with tree ring analyses. However, the NPP vs. tree ring index correlations were $r > 0.30$ at only 41.2% of locations and $r > 0.49$ at only 10.4% of locations. This suggests a great deal of uncertainty in results. Observed climate data across Canada were taken from Environment Canada sources for the period 1971-2004. Climate projections were based on a bias-corrected version of downscaled runs using the AR4 RCP 8.5 (hottest) scenario for 2011-2100. In the run without CO₂, most of the southern three-fourths of the boreal showed modest to severe growth reductions. With CO₂ included, this same region showed mixed reductions and enhancements resulting from the effect of topography on soil water availability. In both cases, a large region around Hudson Bay (approximately 0.25 and 0.4 of the total, respectively) showed mostly enhanced growth. Given the large uncertainty in the growth correlations and the high warming scenario, these results add up to a spatially mixed response (positive on moist sites, negative on dry sites) in the southern boreal and a positive response in the northern boreal over coming decades under likely warming.

Sitch et al. (2008) conducted a global analysis of projected vegetation response to changes in climate and CO₂ over the period 1860 to 2099 using the AR3 A1f1 (hot) and B1 (warm) scenarios. They compared five vegetation models that included CO₂ response, though being an older study, perhaps not as realistically as more recent studies. At the global scale, three vegetation models projected large increases in vegetation carbon for 2000 to 2100, one a slight increase, and one a slight decrease for the A1f1 scenario, and slightly less so for the B1 scenario in each case (their Figure 6). The only case they mapped (their Figure 7) was for the hotter A1f1 scenario. Two of the five models projected almost entirely positive growth responses for North America, two models projected positive growth except for the American West, which was neutral in response, and one model forecast positive growth except for the area from the US Mid-Atlantic coast toward the northwest between the Great Lakes and Hudson's Bay, which showed a strong negative trend. Overall, projected growth responses were positive, with some inter-model variability.

Charney et al. (2016) used 1457 sites from the International Tree Ring Data Bank to develop climate response functions from tree ring data. Sites chosen were single species, and the available data met quality criteria. Sites across North America (including Mexico) were grouped into ecoregions based on similar growth responses to climate. CO₂ was accounted for based on the theory that rising CO₂ increases water use efficiency (WUE). This was incorporated into the response functions by increasing the input precipitation from the climate simulations (2051-2099 frame) in proportion to the WUE increase. WUE increases of +0% (no CO₂ effect), +50%, and +137% (WUE directly proportional to CO₂ increase) were used for the very low (RCP 2.6) and very high (RCP 8.5) warming scenarios. Greenhouse gas (mainly CO₂) rise was roughly related to scenario warming magnitude. With no change in WUE, continent-wide growth declined 6.3% for RCP 2.6 and 19.4% for RCP 8.5. With the WUE proportional to CO₂ case, growth increased 2.4% (RCP 2.6) and 17% (RCP 8.5). The spatial pattern of response is also of interest. With no WUE change and RCP 8.5, only the Gulf Coast (including Florida), northeast Canada, West Coast states, and mountain areas of Yukon and British Columbia showed increased growth. Most of the interior showed growth declines of ~30% to ~75% (based on graphics). For the high WUE response and RCP 8.5, the picture was radically different. The entire US Southeast and West Coast show growth increased up to 75%. New England, eastern and western Canada, and parts of Alaska had mixed neutral to strong growth enhancements. The rest of

Canada and Alaska had a neutral response. The inland US West (except greening in Idaho) showed modest to strong (~30%) growth declines.

Jiang et al. (2012) used a dynamic vegetation model for the northern high latitudes (roughly all of Canada, Scandinavia, northern Europe, and Siberia) to evaluate responses of plant functional types to changes in climate and CO₂. There was no dispersal limitation in the model. The AR3 scenarios A1F1, A2, B1, and B2 were used as well as six scenarios from the Massachusetts Institute of Technology. The hottest scenario (A1F1) had an average temperature rise of 13.6°C/century and the coolest scenario (B2) 6.9°C/century. Results for Eurasia and North America were not separately tallied. For all 10 scenarios, temperate tree types increased in area and moved north, replacing boreal evergreen conifers. The rate of increase and replacement, respectively, were both greatest for the hottest scenarios. For the cooler scenarios, the loss of boreal conifers was negligible. NPP was not calculated. It is unclear if the boreal evergreens would have died back in the absence of rapid dispersal of better competitors.

Lenihan et al. (2008) projected vegetation response to climate change across the conterminous United States. They used the average of three climate models driven by the AR3 A2 and B2 scenarios (high and low warming). The MC1 model was used, which includes the response of plants to CO₂. They used high and low (23% and 8%) growth response to CO₂ doubling cases to account for uncertainty in this factor. Fire was simulated as either not suppressed or suppressed at historical levels. The simulated climates differed from those used in other studies. For example, under the A2 (warmer) scenario, by the 2070-2099 period (2085 central date) vs 1971-2000, much of the central third of the country was predicted to warm by 6 to 7°C (Tmax value) or a little less for minima (Tmin values). There was also an extensive simulated drought in the central third of the country, which was not projected by other models. A trend toward wetting in the Southwest was also the opposite of projections by other models, which forecast drought. The extreme and anomalous climate results could be due to a combination of using older climate models and by chance picking model runs with extreme regional forecasts, or due to other reasons.

Assuming current fire suppression levels, Lenihan et al. (2008) projected a strong effect of assumed CO₂ responses (high vs low) and warming scenario (their Figure 7). For all four cases, the entire west coast experienced reduced growth but interior western regions mostly experienced 10% to 40% increased biomass due to wetting and warming. Conifer forest tripled in area in the western interior under fire suppression. Overall, under fire suppression, western forests had between 3% and 20% productivity gains (20% for the A2 plus high CO₂ response case). Eastern forests showed declines of 5% to 15%, with only the high CO₂ response plus A2 scenario showing an increase (about 2%). All of these results seem dominated by precipitation changes which are known to have been unreliable in the early climate model runs (\approx 2006) used here, and thus should be viewed cautiously. Given advances in understanding responses to CO₂ since this study, it is likely that the high CO₂ response scenario is more realistic. It is not clear if their model included increased water use efficiency at elevated CO₂ levels because they simply forced a CO₂ growth response in the model (i.e., it was not mechanistic).

Peng and Dan (2015) conducted a global-scale simulation of the effect of CO₂ and climate change on vegetation using six earth-system climate models with a vegetation component. CO₂ rising at 1%/yr, which corresponds to relatively high warming, was used as the scenario and driver for the climate models. The climate change case without rising CO₂ caused stable to small decreases in plant productivity and leaf area. The scenarios with only rising CO₂ or with climate change and rising CO₂ both led to large increases in plant productivity (120 to 600 gC/m²/yr) and leaf area at the global scale. Projected responses for regions of North America were generally positive. For the climate change alone case, only the southern Great Plains showed a decrease in NPP for two models, with northern Canada and Alaska showing a modest increase in NPP for five of six models. For the CO₂ plus climate change case, three of the six models produced large increases in NPP across all or almost

all of North America. Two of the models projected neutral NPP responses (small change plus or minus) across about 40% of the continent and substantial positive responses in the rest, particularly in the eastern part (covering the region of hardwood forest in the central US, the Southeast, the Northeast, and eastern Canada). The final model projected a neutral response in most of the region except the US Southeast into the Northeast which showed a strong positive growth response. There was thus more agreement across the six models in terms of general trends than at regional scales. This model comparison also shows that including CO₂ responses of vegetation has a strong effect on outcomes.

Lucht et al. (2006) projected global carbon dynamics in response to climate change. They used the B1 scenario with the ECHAM5 climate model, with a 2.9°C average warming by 2100, and the A2 scenario with HadCM3, with a 5.3°C average warming. Regional warming differed from these numbers. The vegetation component was the LPJ-DGVM model, which included CO₂ effects. The cooler scenario yielded small positive and negative changes in aboveground vegetation carbon across the conterminous US and southern Canada, with strong increases in boreal Canada and Alaska. The warmer scenario produced increased growth in the US East, Southeast, Southwest, and Pacific Northwest; a decrease in the Great Plains; a strong decrease across southern Canada; and a strong increase across arctic Canada and Alaska. Note that the two scenarios were run with different GCMs, which may have led to some inconsistencies.

5.2 Southwest Simulations

Tague, Heyn, and Christensen (2009) evaluated conifer responses to climate change in mountain areas of Yosemite National Park in the California Sierra Nevada Mountains where snowpack duration determines when plants can grow. They used the RHESSys model, which simulates tree growth (including CO₂ response) and hydrology in mountain systems, including snow accumulation and melt. Two levels of spatial complexity were used. Climate change was emulated by adding 2, 4, 6, or 8°C to a 50-year historical record as a step function, at either 400 ppm CO₂ (baseline) or 600 ppm CO₂. As warming increased, snowpack amount and duration shrank. This shifted streamflow seasonality, with more in the winter and less in August (only 17% of baseline), but streamflow amount was unchanged. As expected, under warming there was a decrease in NPP at lower elevations and an increase at higher elevations, but total NPP was not affected by even the 8°C boost. NPP seasonality was shifted into cooler months. The increase in CO₂ from 400 ppm to 600 ppm caused a 25% increase in NPP across all temperature scenarios.

5.3 Pacific Northwest Simulations

Shafer et al. (2015) simulated vegetation response to climate change for the Pacific Northwest region (including southwestern Canada). They used the LPJ mechanistic model of vegetation growth, which simulates vegetation type (not species) growth in response to both climate and soils and includes mechanistic relationships for plant response to CO₂. Five climate model simulations from the CMIP3 data set were downscaled to the region. A high end (A2, similar to RCP8.5) warming scenario was used, with an endpoint in the 2070-2099 period. Precipitation change simulated by the models was both higher and lower compared to the baseline, depending on region. Compared to the remotely sensed vegetation data, the model exhibited a 93% agreement for forest pixel locations. Shrub and grass categories were less well predicted, which the authors attributed to greater effects from soils and fire that they could not account for. In spite of the large warming in the climate forecasts, the LPJ model forecast increases in forest extent, rising from 69.4% of the area to 75.5% to 89.7%, depending on climate model. Forest area expanded upslope, downslope, northward, and southward. The up to 30% increase in forest area by 2100 was likely via the creation of woodland in former shrubland areas or thickening of woodland, as has been seen in several regions (e.g., Brown et al. 2015; Conway and Danby 2014). The projected increase in extent was likely due to inclusion of CO₂ in the vegetation model. These forecasts are constrained by the lack of explicit simulation of plant dispersal and lags

that result from the requirements for plant maturity before further seed set and dispersal at leading edges. However, expansion of forest into shrubland or densification of woodland has been documented in the West to potentially occur at a rapid pace (Brown et al. 2015).

Halofsky et al. (2013) simulated vegetation response to climate change in central Oregon. This region is relatively dry, with the main forest type being Ponderosa pine (*Pinus ponderosa*). They used the MC1 forest growth model which simulates life-form mixtures based on physiology, including CO₂ level. The model includes a state transition module which accounts for the effects of stand aging, succession, and various types of disturbance, including fire. The model also explicitly simulates fire. Climate forecasts were derived from three models in the CMIP3 ensemble based on the high end (A2, similar to RCP8.5) warming scenario. Simulations showed a loss of higher elevation cool forest types and an expansion or stable areas of temperate needleleaf types (e.g., Ponderosa pine), depending on model. However, these transitions were delayed considerably by stand dynamics and species-specific fire tolerance and were precipitated mainly by fire events. It is not clear how realistic the increased fire incidence is, given that a very hot and dry scenario was used in the simulations.

5.4 Midwest Simulations

Handler et al. (2014) projected forest responses to climate change in the Lake States using three different approaches. Using a species distribution model, they forecast decreased areal abundance of typical northern species (*Abies*, *Picea*) and increased areal abundance of many typically central states species (*Acer*, *Quercus*), including expanded ranges. A spatially explicit simulation using LANDIS-II showed five typical boreal tree species to decline in population abundance under warming scenarios. Six species were projected to increase in abundance under the modest warming scenario but decrease under the high scenario. Nine species increased in abundance under both scenarios. The LANDIS-II simulations, which did not include CO₂ fertilization effects, projected a 3% decline in forest productivity by 2100 under the modest warming scenario, but a 40% decline for the high warming scenario. They also used the PnET-CN model, which is a physiological model for forest types that does include the effects of CO₂. Northeastern Minnesota was simulated (from Peters et al. 2013) with the spatial locations of each forest type fixed. For the cooler B1 scenario, broadleaf forest types all experienced a nearly 100% (doubling) growth increase and conifer forests a 40% growth increase. For the warmer scenario, broadleaf forest showed a 200% increase (a tripling) in productivity by 2100, pine forest a 150% increase, and spruce/fir forest a 100% increase.

This comparison clearly shows the importance of including CO₂ physiology in projections of forest growth. In this direct comparison, the niche model approach produced the most negative projections. The LANDIS-II analysis was neutral for the low warming but very negative for the high warming, due to CO₂ not being modeled. The PnET-CN simulation forecast large productivity gains, and the warmer scenario was the most positive. Allowing shifts in ranges (vegetation types were fixed in space) with PnET-CN might have increased productivity even further. These simulations can be assumed to be relevant to the regions of south-central Canada adjoining the Lake States, such as southern Ontario.

Also using PnET-II and LANDIS-II were Xu, Gertner, and Scheller (2012), who studied the Boundary Waters area of Minnesota. Seedling dispersal and establishment were specifically simulated, along with competition (mediated via aNPP levels), windthrow, and three levels of fire. Seven climate scenarios were simulated with multiple GCMs (25 total cases), with a range of warming by 2100 of 2°C to 10°C. For seedlings, scenarios with low levels of warming increased the probability of establishment for all species groups but those with higher levels of warming reduced it for all groups except *Acer-Fraxinus*, which was radically higher at the high scenario. In contrast, aNPP was higher under all warming scenarios. At the highest warming level, pine (*Pinus* spp.) aNPP rose 58%, aspen-birch (*Populus tremuloides* – *Betula* spp.) 83%, maple-ash (*Acer* spp. – *Fraxinus* spp.) 300%, cedar (*Thuja occidentalis*.) 50%, and spruce (*Picea* spp.) was unchanged. It is difficult to

reconcile the large decreases in seedling establishment with increased adult tree growth at the highest level of warming. Changes in forest composition were strongly driven by the seedling effects.

5.5 Northeast Simulations

Ollinger et al. (2007) conducted a simulation study of forest response to climate change in the Northeast. They chose five sites for simulation rather than conducting a spatial analysis and used the PnET-CN model for simulation of NPP. This model was parameterized for the forests being evaluated and included CO₂ effects. Two older climate models were used: the PCM (Parallel Climate Model) and the HadCM3 (Hadley Centre Coupled Model, version 3), each downscaled to a 10 km spatial resolution. Two scenarios, B1 and A1f1, were used. The B1 scenario simulated about a 1.5°C warming by 2100 with PCM, but a 3°C warming with the Hadley model. The warmer A1f1 scenario gave temperatures about 3.3°C warmer with PCM and 6.3°C warmer with Hadley. Without CO₂ fertilization, the low and high warming scenarios for both GCMs yielded neutral to slightly positive growth responses except for the A1 (hotter) Hadley case in Maine, where the mostly conifer forest declined strongly. With CO₂ fertilization in the model, results were quite different. The warmer A1f1 scenario showed nearly a doubling of NPP by 2100 for both models and all sites except Maine. The cooler B1 scenario showed about a 50% NPP increase for both GCMs and all sites except Maine. The Maine site was somewhat anomalous, showing modest increases with both models and both scenarios except the A1 Hadley model case which showed a large decrease (about 50%). These results for Maine were not explained by the authors but could have been due to the very high warming (6+°C) scenario combined with this forest type being at the southern edge of its range, peculiarities of the spatial simulation of climate, lack of responsiveness of northern conifers to warming (as postulated by Loehle 1998), and other factors.

Tang, Beckage and Smith (2012) modeled changes in New England (Connecticut N and E) using three AR3 climate models with three climate change scenarios. The region was generally simulated to become warmer and wetter. They applied the dynamic ecosystem model LPJ-GUESS which includes vegetation response to CO₂. Forest was modeled with eight plant functional types (e.g., oaks [*Quercus* spp.], aspen-birch). Trees could grow anywhere that the climate/soils were adequate (no dispersal limitation). If a tree experienced a negative carbon balance, it died. In the model, the type with the highest LAI in a grid cell was identified as dominant for classifying cells. This, combined with instant migration, tends to exaggerate both gains and losses because if a species is no longer the largest in its neighborhood, it is assumed to be lost. Conifers generally retreated to higher elevations, which made their distribution move south (where there are more mountains). Oaks increased from 21% to 60% of the area by 2099. There were multiple complex shifts in local dominance among the forest types. They found rates of change to be consistent with, but not as large as, an equilibrium analysis by Tang and Beckage (2010), discussed below. The migration rates were extremely high (1500 m/y for northern deciduous forest and 1390 m/y for oaks), likely due to the lack of dispersal limitation and the abrupt dieback model. Temperature alone had a negative effect on all species, and precipitation and CO₂ had a positive effect. The net effect of the warmer (A1B) vs. cooler (B1) scenario was positive for all types, with red-jack pine (*Pinus resinosa* - *Pinus banksiana*) showing the greatest LAI enhancement (0.2 m²m⁻² by 2099). The authors did not specifically quantify dieback or NPP, but the LAI increases point to rising productivity, consistent with the other forecasts for this region.

In a related study using the same climate models and underlying data, Tang and Beckage (2010) performed an equilibrium analysis using the BIOME4 biogeographic model, also including CO₂ effects. The models/scenarios predicted a 3° to 4°C rise in temperature by 2099. Without considering a rise in CO₂ (i.e., CO₂ fixed at 333 ppm), most of the boreal conifer forest was lost by 2085 but with CO₂ at 487 ppm these losses were cut in half. Net primary productivity, LAI, and forest dynamics were not modeled.

D'Orangeville et al. (2016) evaluated black spruce responsiveness to climate using tree ring analyses. They found that in northeastern Canada, this species is not moisture-limited and has responded positively to warming except at the southernmost points of their transect. They forecast generally positive growing conditions for both low and high IPCC warming scenarios for 2041-2070. This result is likely robust to the exclusion of CO₂ effects because CO₂ would further enhance positive growth responses (Swann et al. 2016).

5.6 Southeast Simulations

Miller et al. (2016) simulated forest responses to elevated CO₂ alone using the Ecosystem Demography (ED) model, which includes physiology and individual tree growth and competition. The model was calibrated using data from the Duke Free Air CO₂ Exchange (FACE) site and run using local historical weather data. CO₂ for the control run was 360 ppm and for the enrichment run 560 ppm (a 56% increase), to match the Duke field data. The ED model allows individual tree sizes to be simulated. Using this capability, the authors found that NPP was 26% to 33% higher under elevated CO₂ (closely matching experimental data) and individual trees reached size benchmarks earlier, indicating a potential for commercial rotation lengths to be shortened. The greatest acceleration in loblolly pine growth was for younger stands. They also found accelerations in hardwood growth that would lead to more rapid succession in unmanaged stands and a greater need for hardwood control in managed stands. This acceleration in early growth causing an altered growth trajectory was explicated by Loehle (1995).

6.0 SUMMARY

The studies reviewed here include 40 vegetation models or model versions (e.g., with or without CO₂ effects) and 114 climate model/scenario combinations. It is difficult to compare the many studies cited because they used different climate models and scenarios as well as different growth models that function at different levels of taxonomic and spatial resolution. Because of the high variability in spatial forecasts produced by GCMs, pixel-by-pixel forecasts may not be reliable; thus, we here look for broad conclusions.

There is general agreement across the studies cited that CO₂ has a strong impact on forest responses. Without this mechanism, many studies project neutral to strongly negative growth responses to warming (e.g., Charney et al. 2016; Hander et al. 2014; see also this report's appendix). With CO₂ included, modeled growth enhancements reached 50% to 100% or even 200%, especially for the Southeast, Pacific Northwest, and for angiosperms in the eastern and upper midwestern US. Accelerated growth due to elevated CO₂ could shorten commercial rotation lengths in some locations. Regionally, eastern Canada and British Columbia plus midwestern, northeastern, southern, and Pacific Northwest US forests showed consistent growth increases under even the warmest scenarios, except for Lenihan et al (2008), which showed neutral to reduced growth responses in these regions. Northern Great Plains, Rocky Mountains, southwestern US, and southern Canada regions showed inconsistent results among studies, largely due to the difficulties in forecasting precipitation. Jiang et al. (2012), assuming no dispersal limitations, showed little change with cooler scenarios, but very rapid replacement of boreal conifers under the hottest scenarios in Canada and Alaska that implies rapid dieback. Arctic Canada across to northern Alaska generally showed strong positive trends, but these areas are not forested.

A complication in interpreting these results is that regional climates can have natural multi-decadal fluctuations, particularly for precipitation. For example, precipitation in California (Kirby et al. 2014) and the West generally (McCabe and Dettinger 2002) up into western Canada (Cayan et al. 1998; Steinman et al. 2014) are linked to Pacific Ocean cycles. However, climate models are unable to forecast such cycles (IPCC 2014). Any particular future decade that is of interest might or might not

be simulated as being wetter or drier than average in this region, which might or might not correspond to what will actually happen. For the Southwest and the Mountain West, dry spells can be severe and would override other considerations such as subtle long-term trends in temperature, precipitation, and CO₂. The Southeast is also historically subject to long droughts (Pederson et al. 2012), though to a lesser extent. The Midwest and Central Canada are next in drought risks, with the Northeast and Pacific Northwest having little risk. Historical patterns of drought are likely to continue, superimposed on other trends. This needs to be kept in mind for planning purposes.

What are the implications of these studies for forest management planning? Many of the studies cited report NPP, which is difficult to convert into wood yield. These results would need translating via stand growth models using the forecast NPP values to obtain timber yield projections. However, the large increases forecast by some of these models (doubling or more of NPP) could lead to shorter rotations and higher yields. On the other hand, the relatively greater responsiveness of angiosperm trees to CO₂ enrichment might make conifer establishment more difficult and understory encroachment more problematic. Model results imply that site index classifications and yield tables, especially older ones, may need updating because benchmark heights could be achieved at earlier ages. That is, accelerated growth due to changes in climate factors could equate to an increase in site index.

Should forest managers base their planning on a large increase in future forest growth, such as a future doubling of NPP? Given uncertainties in the actual trajectory that climate will take in any given location, it would seem wise not to become so optimistic. Instead, these results should be considered when interpreting projections of future forest conditions. In addition, periodic checking of site index and yield table outputs would be in order, to ensure that they match current growth responses. Likewise, it may be premature to shift planting zones pre-emptively to match anticipated climates because change in climate factors to date might not require such shifts and too-early shifts in seed source could lead to adverse growth response and possible frost damage. For example, in a large planting trial of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var *latifolia* Englm.) in the Pacific Northwest, Montwé et al. (2016) found that after 32 years of growth, the trees planted far north of their sites of origin seem to have suffered from cold damage and thus did not perform as well as expected. Thus, planting trials may warrant consideration as an ongoing precautionary measure. Based on the studies reviewed, the outlook for wood supplies seems positive in general, with projections for some regions such as the Southwest and western Canada being more uncertain.

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APPENDIX

A number of studies that address the question of forest response to climate change did not meet the criteria set forth in this study for assessing likely future conditions. For forest growth models, enough is now known to include CO₂ fertilization effects. Species Distribution Models forecast equilibrium vegetation which may take many centuries to be achieved. Thus, studies that used SDMs and those that omitted CO₂ fertilization effects are briefly summarized below to illustrate their forecasts in the context of these known limitations.

GROWTH MODELS

Latta et al. (2010) based their analysis on statistical growth models developed from permanent plot data in Oregon and Washington. These models did not include CO₂ effects. They used the AR4 A1B, A2, B1, and COMMIT scenarios, which ranged from no warming (COMMIT) to about four degrees C warming (A2) by 2100. There was no precipitation trend. For forests on the west side of the Cascades, potential mean annual increment (PMAI) rose 7%, 8%, 5%, and 2% under the four scenarios, respectively. On the east side, PMAI increases were 20%, 23%, 15%, and 5%, respectively. East side forests do suffer from colder winters and this may account for the difference.

Liang, Hurteau, and Westerling (2017) studied response of Sierra Nevada mountain range forests to the AR4 A2 (hot) scenario simulated by three climate models. Forest response was simulated using the LANDIS-II model, with a module for fire. Due to the combined effects of altered climate and increased fires, the authors found reduced tree species diversity and growth rates as drought- and fire-tolerant species became more dominant. However, as noted in the main body of this report, there is no historical trend in fire over the 20th Century, and drought effects would have been less if CO₂ were included. In addition, they ran a very hot scenario.

Ford et al. (2017) evaluated tree and stand growth responses to PET and AET (potential and actual evapotranspiration) based on plot data from Mount Rainier National Park, Washington. They considered both tree size and competition for several species. For ensemble AR3 projections of climate for the A1B, A2, and B1 scenarios, they estimated that tree growth would increase, especially in uncrowded stands.

Fraser fir (*Abies fraseri*) is a semi-rare species found in the Appalachians. It has previously suffered mortality episodes and there is concern about climate change adversely affecting it. Kaylor, Hughes, and Franklin (2017) evaluated the current status and likely prospects for this species using a stage-structured matrix population model based on several decades of inventory data. They found that higher elevation populations are highly likely to recover but some lower elevation populations are not. Results from this analysis are, strictly speaking, applicable only over the next few decades because the study did not account for either future climate change or rising CO₂.

Loudermilk et al. (2013) simulated the response of forests in the Lake Tahoe Basin using the LANDIS-II forest simulator without CO₂. Climate was forecast from down-scaled results for the AR4 B1 and A2 scenarios (2°C and 5°C mean annual temperature rise by 2100, respectively, for the study area). Due to stand dynamics, they forecast a continued increase in biomass over the next 100 years, with little effect from the B1 warming scenario on either total carbon or ANPP. The A2 scenario produced a modest reduction in C and ANPP, mainly in the last few decades of the simulation.

Thompson et al. (2011) simulated the effects of forest succession, land use change, and climate on forests in Massachusetts to the year 2050. Their model allowed for timber harvest but did not include CO₂ effects. They used the AR3 B1 scenario of warming. In their model, later successional species built up larger pools of biomass. Stand aging and succession led to a 70% increase in above ground

biomass over 50 years. Land use change reduced this gain by 18% and timber harvest by 4%. Climate change increased gains by 18%. Inclusion of CO₂ would likely increase these gains further. Note that these numbers are for biomass, not NPP, and are thus confounded with stand aging.

Goldblum and Rigg (2005) evaluated growth responses of sugar maple (*Acer saccharum*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) at the deciduous-boreal ecotone in Ontario. Tree response was a statistical function of past tree ring indices of climate sensitivities. They used the AR2 A2a high warming scenario. CO₂ was not modeled. They found that climate sensitivity alone led to predictions of greatly enhanced maple growth, slightly enhanced spruce growth, and decreased fir growth. However, if CO₂ had been included, these results may have differed. The AR2 climate models are also out of date.

Lapointe-Garant et al. (2010) used tree ring data for trembling aspen across a North-South gradient in western Quebec to calibrate the individual tree growth model NE-TWIGS. For three climate models and the A2 and B1 scenarios from the IPCC third assessment, they found up to a 10% growth reduction at the southern end and a 5% increase at the northern end of their transect for the A2 and very little change for the B1 (cooler) scenario. Their statistical model did not include CO₂ effects.

Duveneck et al. (2014a) conducted a simulation of the forests of northeastern Minnesota and northern lower Michigan. The forecasts used included summer temperatures 3-11°C warmer by 2100, with the upper scenario being high (1.13°C/decade warming rate). The LANDIS-II model used did not include CO₂ effects. With the cooler B1 scenario, no difference in aboveground biomass was seen, but the hotter scenario led to large reductions in biomass for both regions. In a related paper using the same modeling approach, Duveneck et al. (2014b) tested the efficacy of reserves and silviculture for ameliorating climate impacts. They found that expanded reserves produced only a small benefit but silviculture increased total standing biomass for current climate and both future scenarios.

Ravenscroft et al. (2010) also evaluated this same area with PnET-II (without CO₂) and LANDIS-II for the AR3 A2 (6.9°C rise) and B2 (3.7°C rise) scenarios. They found large shifts in species dominance, with a tendency toward increased unforested areas under the warmer scenario. Forest management was found to have the potential to exacerbate or moderate these trends.

Crookston et al. (2010) conducted a simulation in which they linked mortality and regeneration to climate and altered growth rates by linking site index to climate. These relations were based on the climate niche as defined from geographic presence data rather than from actual growth responses. CO₂ was not included. This approach basically converts the climate niche into a dynamic model but still ignores the possibility that presence is governed by competition and long-term responses. While the model thus has more dynamics than a simple SDM, it enforces rapid compliance with spatial shifts in ideal habitat with climate change.

A series of papers using the same base models (Coops and Waring 2011a, 2011b; Coops, Waring, and Law 2005; Mathys, Coops, and Waring 2017) project future forest growth but omit CO₂ effects, do not consider tree longevity and other lag effects, and use the hottest scenarios. They generally show negative effects of warming on western forests.

Bachelet et al. (2008) compared results of using the MC1 model driven by either VEMAP or VINCERA climate, vegetation maps, and soils. The two cases had very different outcomes. However, the authors included only a primitive CO₂ analysis and the climate model was developed in 2008.

Sheehan, Bachelet, and Ferschweiler (2015) simulated Pacific Northwest vegetation using the dynamic global vegetation model MC2 (a C++ version of MC1) forced by 20 different climate models with low (RCP 4.5) and high (RCP 8.5) warming scenarios. The RCP8.5 scenario is quite hot. The model simulates fire with and without suppression, however, we only evaluate the “with suppression” case here. The MC2 model does not include CO₂ effects and it simulates vegetation

types, rather than individual species. Ensemble mean minimum temperature changes for the RCP 4.5 scenario were 2.18°C by mid-century (roughly 33 years away), for the coastal region. For the RCP 8.5 scenario, the rise was 5.87°C by 2100 for interior mountains, with other times and regions between these extremes. The main results of the study concern fire interval changes, which are not the main concern of this review.

Girardin et al. (2008) simulated the response of three tree species in boreal central Canada to warming under a doubled CO₂ scenario. They found that warmer summers resulted in a drying effect that reduced tree growth. The model did not include CO₂ responses (which affect drought tolerance).

The models mentioned here do not include CO₂ effects and some include extreme warming scenarios. In spite of this, multiple studies reported positive growth responses without considering climate (Kaylor, Hughes, and Franklin 2017), or in response to warming scenarios (Ford et al. 2017; Latta et al. 2010; Loudermilk et al. 2013; Thompson et al. 2011). Some showed mixed results by species, region, or scenario (e.g., Goldblum and Rigg 2005; Lapointe-Garant et al. 2010). Other studies focused on processes such as fire, or predicted very negative growth responses in the absence of realistic CO₂ physiology in the models.

SPECIES DISTRIBUTION (CORRELATIVE) MODELS

Several studies evaluated climate change impacts on forests using species distribution models. For example, McKenney et al. (2007) evaluated impacts for 130 tree species in North America. Using the AR3 A2 scenario and the mean of three general circulation models and assuming no migrations, they found some increases in geographic range but a mean decrease in range size of 58% and a northward shift of 330 km. The most species-rich zone shifted from the eastern US to the northeastern US and eastern Canada. The prime commercial timber zone of the Southeast became species-poor, though they do not show pine ranges per se. In an update to this work using the next generation of climate models, McKenney et al. (2011) found that their new niche projections were on average 10% larger than in the earlier study. However, from half to all of the eastern US still lost 60 to over 100 tree species and all of Canada still gained 11 to 84 species by the 2071-2100 period. Given that there has been little detectable range shift to date (Loehle submitted), such dramatic changes seem unlikely.

Hamann and Wang (2006) showed large range shifts in British Columbia. They used an older first-generation climate model with the IS92a emission scenario plus the AR2 A2 and B2 scenarios with two third-generation climate models. They used orthogonal discriminant functions to characterize the climate space for each species. Tree species with their northern range limit in British Columbia gained habitat at a rate of at least 100 km per decade, common hardwoods were largely unaffected, and common conifers lost a large portion of their range. For example, the Engelmann spruce-subalpine fir [*Picea engelmannii*-*Abies lasiocarpa*] type was displaced from the entire two-thirds of the province by 2085.

Schwartz et al. (2006) examined the relationship between current and projected ranges of 142 tree species in the eastern US. They used 1995 climate simulations, which are out of date, and did not specify the scenario. They found very large potential range shifts, with more potential overlap of old vs. projected habitats for species with larger ranges.

Clark and colleagues (Clark et al. 2014a, 2014b) developed an approach that takes into account both climate and biotic interactions, and which is able to predict both spatial presence/absence and population abundance. In response to the A2 scenario, Clark et al. (2014a) found a tendency toward savannification in the southeastern US. In contrast, the same approach applied to the entire eastern US (Clark et al. 2014b) led to a prediction of increasing basal area across the Southeast except for losses in southern Florida and Louisiana. There was some risk found in the Northeast and Lake States,

where species turnover is also highest. The contradictions in these two results were not addressed in either study.

Iverson et al. (2008) evaluated potential range shifts for 134 eastern US tree species with three climate models and moderate vs. hot scenarios. They found that for the hot scenario, approximately 66 species would gain and 54 species would lose at least 10% of their suitable habitat (they did not just draw range boundaries). The mean center of gravity of habitat moved northeast. They noted that lags would slow shifts and did not indicate that dieback would result. They forecast a significant increase in oaks and commercially important southern pines.

Currie (2001) used correlations of climate with species richness to assess climate impacts in the conterminous US. He predicted that woody plant richness would be fairly stable in the central and southeastern US, with large increases in the Pacific Northwest and northern Rockies. Large decreases were predicted for the Southwest. The author noted that these forecasts are at the millennial scale. Given the vintage of models used and the dependence of results on precipitation, which the older GCMs had difficulty with, a note of caution is in order.

Prasad et al. (2006) used four statistical techniques based on many variables such as soils as well as climate to evaluate importance values (not just presence) for four tree species in the eastern US. For the three tools that performed well compared to present distributions, loblolly pine was predicted to have a greatly expanded range, white oak (*Quercus alba*) a slightly reduced area (patchy losses), and American beech (*Fagus grandifolia*) and sugar maple major retreats toward the north and northeast (ranges in Canada not evaluated). These results correspond to drought tolerance. In a related study, Prasad et al. (2013) showed that under a warming scenario, four oaks were still filling most of their historic ranges. They forecast modest range expansion, mostly to the north (all four) and west (for two species).

Fernández, Hamilton, and Kueppers (2015) used historical weather data that reflect observed patterns of upwelling to evaluate impacts on coast redwood (*Sequoia sempervirens*). They found that observed anomalies that corresponded to GCM projections for 2020-2030 would lead to significant retraction at the southern range margin for this species. Given that this is only a few years away, such a sudden change seems unlikely.

Rogers, Jantz, and Goetz (2017) modeled vulnerability (a combination of suitable habitat and threats) for 40 tree species in the eastern US. They used an ensemble mean of 33 CMIP5 GCM runs. SDMs were calculated based on 100,000 forest inventory plots using climatic, soils, topographic, and other variables. Some southern states, the Gulf Coast, and West Virginia in particular showed a favorable outcome due to increased precipitation. The Midwest, upper Midwest, and New England showed high vulnerability. High species turnover followed the Appalachian Mountain chain.

Morin, Viner, and Chuine (2008) used a process-based SDM to evaluate 16 tree species in eastern North America under the AR3 A2 (+3.2°C) and B2 (+1.0°C) scenarios. Loss of habitat at the southern end of the ranges averaged 22% and 19%, respectively, by 2100. Note that with close to a 1° warming since 1850, no such radical range retreat is yet visible, so the B2 scenario seems implausible.

A possible direction for SDM improvement is provided by the study of Liénard, Harrison, and Strigul (2016). They categorized species in the conterminous US in terms of tolerance of extremes, particularly drought. They then projected where future climate could exceed drought tolerance limits. While this is an improvement over simple climate correlation models, it omits the effect of CO₂ on increased drought tolerance and is still a static (equilibrium) approach that ignores lags. Other approaches that incorporate dispersal limitation still assume that at the warm edge of the range, a species will die back. Fundamentally, trees have much broader climatic tolerances than are indicated by simple correlative models (Loehle 2014). This reflects the SDM paradox: even if a tree would

grow better under a future climate, an SDM reflects competitive effects of species that would grow even better and outcompete that species. However, these competitive interactions are likely to take centuries, not decades, to play out. Thus, such models are not predictive in the near term (~100 yr).

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