UNDERSTANDING THE ROLES OF CLIMATE, DISTURBANCE, AND FUNCTIONAL DIVERSITY IN THE TERRESTRIAL CARBON CYCLE: LINKING MECHANISMS FROM REGIONAL TO GLOBAL SCALES

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Abstract

Terrestrial ecosystems currently sequester ~25% of human carbon emissions annually, yet changes in climate and disturbance have the potential to impact the integrity of the terrestrial carbon sink. Despite its fundamental role in mitigating anthropogenic CO\(_2\) emissions, the terrestrial biosphere remains one of the largest sources of uncertainty in current predictions from global climate models because key physiological processes are often poorly understood and/or poorly represented in terrestrial biosphere models. In this thesis, I use observations and terrestrial biosphere models to gain a better insight into (a) the mechanisms driving the terrestrial biosphere response to changes in temperature, water availability, nutrients, atmospheric CO\(_2\), and disturbance and (b) the uncertainty associated with projections for how climate change will impact the terrestrial carbon sink.

Chapter 2 demonstrates that the representation of water-limited photosynthesis in terrestrial biosphere models comprises a large and uncertain component of the terrestrial carbon cycle, comparable to 3-286% of current global productivity. Chapters 3-4 focus on the boreal biome, which contains >30% of terrestrial carbon and has the potential to experience shifts in composition and decreased soil carbon storage over the next century due to rapid warming, intensifying disturbance, and drought. In Chapter 3, I find a significantly negative growth response stemming from atmospheric drought across Alaska. Then in Chapter 4, I parameterize a terrestrial biosphere model for the North American boreal forest and use it to show that a temperature perturbation of 4°C can decrease total ecosystem carbon by ~40% after 300 years due to aboveground-soil carbon feedbacks. In Chapter 5, I use the same vegetation model to
demonstrate that the high fire survival rate of thick-barked, large trees is key in the resistance of ecosystem carbon to increasing fire frequency.

Throughout this thesis, I highlight the importance of interactions between climate, disturbance, and functional diversity when understanding the trajectory of the land carbon sink. I further underscore important avenues for improvement and observational benchmarking of model processes. Projections of climate change impacts are not straightforward. However, incorporating process-oriented drought and disturbance mechanisms into models has the potential to significantly reduce uncertainty in carbon sink projections.
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1 Introduction

Forests are an important component of the global carbon cycle and hold significant potential for mitigating anthropogenic climate change (Pan et al., 2011). However, climate change impacts on terrestrial ecosystem vitality, and the ability of forests to continue to sequester anthropogenic carbon emissions, could be large, but are currently uncertain (Huntingford et al., 2013). Terrestrial biosphere models are our primary tools used for projecting changes in forest vitality with global climate change. Yet, key mechanistic processes that govern how ecosystems respond to environmental drivers, such as water and nutrient limitation, are poorly represented or absent in models, leading to major uncertainties in predictions of the future carbon cycle (Sitch et al., 2008) and the impacts of continuing anthropogenic emissions. Our current ability to project the effects of climate change is further limited by an insufficient process-based understanding of how multiple environmental drivers, such as temperature, increased atmospheric CO₂, water availability, nutrients, and disturbance, will interact to affect forest productivity and carbon drawdown. The aim of this thesis is to better understand (a) the mechanisms driving the terrestrial biosphere response to global change and (b) the uncertainty associated with projections for how global change will impact the terrestrial carbon sink. To accomplish this, I used a combined approach integrating numerical models with observations to unravel the interacting effects of climate, disturbance, and diversity in plant functional strategy.
1.1 Water Limitation and the Terrestrial Carbon Cycle

Several regional observational studies have attributed recent declines in forest growth and increases in mortality over a wide range of latitudes to climate change-induced drought (Barber et al., 2000; van Mantgem et al., 2009; Allen et al., 2010; Peng et al., 2011; Brienen et al., 2015; Walker et al., 2015; Restaino et al., 2016). Yet it is challenging to scale these results up to the globe: top-down estimates of the land carbon sink observe an overall strengthening during the past few decades (Ballantyne et al., 2012; Campbell et al., 2017) and current terrestrial biosphere model estimates project an increase in the land carbon sink over the next century due mainly to CO₂ fertilization (Huntingford et al., 2013; Friend et al., 2014; Sitch et al., 2015). In Chapter 2 of my dissertation, I began to address possible causes of this discrepancy of scales by understanding the uncertainty associated with drought-limited productivity and the terrestrial carbon cycle in terrestrial biosphere models. I then used this global uncertainty analysis to motivate investigation of productivity trends and drivers in two key contrasting regions of critical importance to the terrestrial carbon cycle (Pan et al., 2011): the boreal forest (with a focus on the North American boreal forest) and the tropics (with a focus on the Cerrado region of South America).

1.2 Climate Change and the Boreal Forest

Boreal forests are being subject to some of the most rapidly changing environmental drivers on Earth stemming from anthropogenic climate change. Atmospheric carbon dioxide concentrations have increased by 100 ppm since 1900 and could increase to 1000 ppm by 2100 in high-
emissions scenarios (IPCC, 2013). Air temperature has risen by 2°C at high latitudes since 1901, and is projected to rise by an additional 2°-11°C by 2100 (IPCC, 2013). This rapid warming lengthens the growing season, but also influences water availability and increases fire and insect disturbance (Kasischke & Turetsky, 2006; Hinzman et al., 2013; Zhu & McGuire, 2016).

Such rapid climate change has strong potential to disrupt the functioning, structure, and composition of these boreal forests. In Chapter 3 of my dissertation, I used statistical models and forest inventory measurements in interior Alaska to determine the relative importance of temperature, drought, competition, and insect disturbance for tree growth and mortality. I found that the differing climate responses between species have the potential to shift forest composition and substantially alter interactions with changing climate, disturbance, and boreal carbon drawdown. In Chapter 4 of my dissertation, I applied this observational knowledge to develop a terrestrial biosphere model of the North American boreal forest that mechanistically resolved the boreal plant functional response to key global change processes including fire disturbance, water limitation, and nutrient cycling. I then used this model, constrained with observations, to understand how perturbations in temperature, fire regime, atmospheric CO₂, and nutrient availability affected the composition and carbon storage of sites across the North American boreal forest.

1.3 Climate Change and Tropical Savannas and Forests

While the boreal forest and the tropics are dissimilar in many aspects, some key global change drivers, such as fire disturbance and water limitation, span biomes. Tropical savannas and forests
are projected to see increases in drought frequency and changes in fire regime (Malhi et al., 2008; Brando et al., 2014). In Chapter 5 of my dissertation, I parameterize a terrestrial biosphere model to represent trees with different tropical fire survival strategies and use this model to understand how tree fire survival strategy interacts with changes in fire and rainfall regime to affect tropical carbon stability under changing climate and disturbance regimes.

1.4 Publications and Coauthorship

The projects presented in this thesis are a result of the work done by me under the supervision of my thesis adviser, David Medvigy, and in collaboration with numerous coauthors. The research presented in Chapter 2 was performed in collaboration with David Medvigy, Justin Mankin of the Lamont-Doherty Earth Observatory of Columbia, and William Anderegg of the University of Utah and is currently under review (Trugman et al., in review-b). The research presented in Chapter 3 was performed in collaboration with David Medvigy, William Anderegg, and Steve Pacala of Princeton University, was presented on at the Ecological Society of America annual meeting in 2016 in Fort Lauderdale, and is currently under review (Trugman et al., in review-c). The majority of the research presented in Chapter 4 was performed in collaboration with David Medvigy, Nicole Fenton and Yves Bergeron of the University of Quebec in Abitibi-Temiscamingue, Lisa Welp-Smith of Purdue University, and Xiangtao Xu of Princeton University, was presented on at the American Geophysical Union Fall meeting in San Francisco in 2014 and 2015 and at the Ecological Society of America annual meeting in 2015, and has been published in the Journal for Advances in Modeling Earth Systems (Trugman et al., 2016). The
section on the regional analyses within Chapter 4 was presented on at the American Geophysical Union Fall meeting in San Francisco in 2016, is currently in preparation, and the Alberta forest inventory data were made available by John Caspersen of University of Toronto. The research presented in Chapter 5 was performed in collaboration with David Medvigy, Adam Pellegrini of Stanford University, and William Hoffman of North Carolina State University and is currently under review (Trugman et al., in review-a). In each case, I performed the research tasks and wrote up the result. Coauthors contributed data, inputs in conceptual project design, and improving the manuscripts.
2 Soil moisture drought as a major driver of carbon cycle uncertainty

2.1 Abstract

Terrestrial ecosystems are an important component in the global carbon cycle and hold significant potential for mitigating anthropogenic climate change (Pan et al., 2011). However, their status as carbon sinks could be compromised by more frequent and severe drought conditions (Allen et al., 2010). Current vegetation models typically regulate the plant photosynthetic response to soil moisture-driven drought through a rarely-tested empirical soil moisture function, rather than a mechanistic response of leaf and stem water potential (Powell et al., 2013; Xu et al., 2016). This representation of water stress could introduce significant uncertainty into projections of the global carbon cycle. Here we examined the use of the soil moisture limitation function in historical and RCP 8.5 future emissions scenarios in nine Earth system models. We found that drought-limited productivity across all models represented a large and uncertain component of the terrestrial carbon cycle, comparable to 3-286% of current global productivity and 41-3600% of current annual global fossil fuel emissions. Approximately 40-80% of the intermodel variability was due to the functional form of the limitation equation alone.
Our results highlight the importance of implementing mechanistic water limitation schemes in vegetation models and illuminate several promising avenues for improving the representation of water limitation on photosynthesis in models to improve projections of the land carbon sink.

2.2 Introduction

Terrestrial ecosystems currently sequester ~2.4 Pg C annually (Pan et al., 2011), but their ability to maintain these sequestration rates is uncertain and depends on potentially compensating impacts of both CO₂ fertilization and increased hydrologic stress (Roderick et al., 2015; Milly & Dunne, 2016; Swann et al., 2016). A number of regional observational studies have attributed recent declines in forest growth and increases in mortality over a wide range of latitudes to climate change-induced drought (van Mantgem et al., 2009; Allen et al., 2010; Brienen et al., 2015). Yet it is challenging to scale these results up to the globe: top-down estimates of the land carbon sink observe an overall strengthening during the past few decades (Ballantyne et al., 2012). Process-based global vegetation models (VMs), either run offline or incorporated into Earth system models (ESMs), are a practical tool for bridging this scaling gap and understanding the response of terrestrial ecosystems to increasing atmospheric CO₂ and changing drought conditions, but such VMs must include trait-based physiological mechanisms for them to be useful.

Current estimates project an increase in the land carbon sink over the next century due mainly to CO₂ fertilization (Huntingford et al., 2013; Friend et al., 2014; Sitch et al., 2015). However, predictions vary widely depending on both VM (Friend et al., 2014; Sitch et al., 2015)
and climate model (Huntingford et al., 2013), and VMs often underestimate gross primary productivity (GPP) in water limited regions (Ciais et al., 2013). The large inter-model variability and the apparent disagreement between model projections and observational trends highlight the need for a better understanding of the drought response mechanisms given that hydrologic stress is projected to increase and soil moisture is projected to decrease in many regions under all emissions scenarios (Dai et al., 2004a; Sheffield & Wood, 2007).

Most global VMs have simplistic representations of the effects of water stress on vegetation growth over long time scales (i.e. soil moisture-driven stress) (Powell et al., 2013; Xu et al., 2016). In many cases, either photosynthesis or stomatal conductance is down-regulated using an empirical function ($\beta$) that ranges between 0-1, with $\beta=0$ analogous to full stomatal closure due to soil moisture limitation. $\beta$ is generally dependent on available soil moisture and root distribution, and the functional form of $\beta$ varies between models (Supplementary Note). Several significant shortcomings result from this representation of plant hydraulic stress: First, $\beta$ does not capture widely-documented differences in vulnerability to soil moisture stress across plant species, heights, or functional types (Xu et al., 2016). Second, $\beta$ is unlikely to capture the complex and non-linear interactions between soil water potential and vapor pressure deficit that influence stomatal conductance through their influence on leaf water potential (Sperry et al., 2016). Third, the effects of different $\beta$ functions are not evaluated or compared across models, and their influence on simulated terrestrial carbon dynamics is largely unknown. Finally, lacking a mechanistic grounding, $\beta$ may not accurately capture ecosystem response to water stress (Powell et al., 2013; Xu et al., 2016), and thus increasing soil moisture constrained GPP with water stress could introduce significant uncertainty into future projections of the terrestrial carbon cycle.
We quantified the use of $\beta$ use in historical and the RCP 8.5 future emissions scenarios in nine ESMs in the Coupled Model Intercomparison Project, Phase 5 (CMIP5). Collectively, the models used seven different $\beta$ functions, seven unique soil grids, and four different spatial resolutions (Table A-1). $\beta$ was not archived as standard CMIP5 output, so we calculated its value using average monthly soil moisture, the known $\beta$ functional form (Table A-1), established curves for rooting depth, and soil texture from the Global Soil Wetness Project 2 (GSWP2) (Dirmeyer et al., 2002). (See Appendix A Methods for a validation of this inversion approach against direct model output of $\beta$ and sensitivity analyses on inputs to the inversion approach.) In each model, we further calculated the maximum amount that $\beta$ could reduce potential GPP (referred to as ‘$GPP_c$’) according to the following relation:

$$GPP_c = GPP_m \times \left( \frac{1}{\max(\beta, 0.1)} - 1 \right).$$

**Equation 2-1**

In Equation 2-1, $GPP_m$ is the model output GPP. $GPP_c$ is designed to quantify first-order uncertainty in estimates of productivity constrained by $\beta$ where $GPP_m + GPP_c \sim$ potential GPP. Note, however, that $GPP_c$ should not be interpreted as the GPP that “could have been supported” without $\beta$ because it does not include land-atmosphere feedbacks (Friedlingstein et al., 2006).

We asked: (i) What are the global patterns of $\beta$ and in what regions does $\beta$ constrain potential GPP? (ii) Is the average $\beta$ lower in RCP 8.5 (i.e. more water stress) compared to historical simulations? (iii) Is intermodel variation due mainly to variation in the functional form of $\beta$ or variation in other model infrastructure and/or climate? (iv) How large is the uncertainty in $GPP_m$ due to $GPP_c$ and what are the drought implications for terrestrial carbon cycle uncertainty?
2.3 Methods

2.3.1 Soil moisture limitation in CMIP5 simulations

We obtained total column soil moisture at the monthly level from historical runs and RCP 8.5 from the CMIP5 multi-model ensemble archive available at the Centre for Environmental Data Archival (https://services.ceda.ac.uk/) for one realization for each of nine models – BCC-CSM1-1, BNU-ESM, CanESM2, CCSM4, CESM1-BGC, GISS-E2-R-CC, HadGEM2-ES, MIROC-ESM, and NorESM1-ME. Only one realization was used in this analysis because the soil moisture equation used to limit photosynthesis ($\beta$) is a product of model structure and therefore fairly insensitive to initial conditions and present in all realizations. However, this method neglects possible multidecadal variability in soil moisture between different model realizations. To avoid confounding short-term variability in soil moisture and GPP, we computed the average soil moisture for each model for each month over the period from 1981-2000 and from 2080-2099 for the historical and RCP 8.5 simulations, respectively. For ease of comparison, model output was re-gridded to a 1° grid (Wieder et al., 2015) and the soil column was re-gridded to the CCSM4 grid that extends through 4.7 m. Our re-gridding calculations were performed in MATLAB using a nearest neighbor method from the "interp" function to preserve the spatial distribution of soil moisture as best as possible for each individual model.

We downloaded global maps at 1° resolution of volumetric soil water content at saturation, wilting point, and field capacity as well as soil water potential at saturation, and rooting depth encompassing 50% of root biomass from the GWSP2 database (Dirmeyer et al.,
2002). We further calculated soil water potential at field capacity and wilting point using the Clapp-Hornberger equation and downloaded soil parameters from the GWSP2. We also calculated the root biomass fraction in each soil layer by fitting an established rooting depth curve (Jackson et al., 1996) to the 50% root biomass fraction from the GWSP2 database. Finally, we masked out all locations covered in ice year round circa year 2000. After this post-processing, we averaged monthly-level values of \( \beta \) over the year for both the historical and RCP 8.5 simulations to obtain two global maps of \( \beta \) for comparison, one representing average conditions circa 2000 and one circa 2100.

2.3.2 Estimated of impacts of soil moisture limitation on simulated GPP

We downloaded average daily minimum temperature and GPP, averaged to the monthly level, from historical runs and RCP 8.5. For NorESM1-ME only, we used average monthly temperature rather than average daily minimum temperature because daily minimum temperature was not available. We processed and re-gridded these model outputs in the same manner as soil moisture. Because we were interested in examining the water limitation impact of \( \beta \) on GPP, we masked out GPP during months when average minimum temperature decreased below 273.15 K.

We then calculated the simulated global GPP (GPP\(_m\)) that was reduced by \( \beta \) (GPP\(_c\)) in each model according Equation 2-1. Though both soil moisture and atmospheric water demand independently regulate GPP\(_m\) at monthly time scales, soil moisture and atmospheric water demand are weakly correlated (average R\(^2\)=0.2) (Novick et al., 2016), making it unlikely that a significant portion of the estimated GPP\(_c\) is erroneously attributed as a soil moisture limitation.
response rather than atmospheric vapor pressure deficit. For numerical purposes, in our calculation of GPP_c, we limited the minimum value of β to 0.1. Though in some models β is used to regulate the maximum rate of photosynthesis and in others it is used to regulate canopy conductance (Appendix A Supplementary Note), GPP_m scales roughly linearly with β in either case and we treated both identically in our first-order estimates of GPP_c. After obtaining estimates of monthly-level GPP_c, we summed monthly-level values during the growing season over the year for both the historical and RCP 8.5 simulations to obtain global maps of GPP_c (using β functions associated with their own respective CMIP5 model) for average conditions circa 2000 and circa 2100. In an additional analysis, we applied all seven different β equations (Appendix A Supplementary Note) to a single model soil moisture output to quantify the variability in β and GPP_c due to the functional form of the β equation alone.

2.4 Results and Discussion

β was smallest (hereafter “strongest” water limitation) in RCP 8.5 in the desert regions. In northern and parts of southern Africa, the Arabian Peninsula, central Asia, and much of Australia, extensive portions of the land area had photosynthesis suppressed by 40% (β ~ 0.6) (Figure 2-1a). Substantial portions of Central America, the Brazilian Cerrado, Argentina, and the American West experienced β ~ 0.7. However, individual models varied significantly, and some projected much stronger β signals than others (Figure A-1).
Patterns of GPP\textsubscript{c} often differed from those of β due to spatial patterns in GPP\textsubscript{m} (Figure 2-1b). Desert regions with extremely water-stressed photosynthesis had minimal GPP\textsubscript{m}. However, grassland and savanna regions under moderate β stress had a much higher total GPP\textsubscript{m}, and in these locations GPP\textsubscript{c} exceeded 0.2 kg C m\textsuperscript{-2} yr\textsuperscript{-1} for relatively large regions and 0.8 kg C m\textsuperscript{-2} yr\textsuperscript{-1} at smaller scales (Figure 2-1b), a substantial fraction of the multi-model median global mean annual GPP\textsubscript{m} of 1.13 kg C m\textsuperscript{-2} yr\textsuperscript{-1}. Additionally, the large intermodel variation in β globally resulted in considerable variability in GPP\textsubscript{c} (Figure A-2), due to both intermodel variation in β and GPP\textsubscript{m}. 

Figure 2-1: Regions with projected drought-limitation on photosynthesis comprise a large portion of the land surface area in vegetation models. Global maps of the multi-model median (a) soil water limitation coefficient (β) and (b) GPP constrained by β (GPP\textsubscript{c}). Maps show the average annual β and GPP\textsubscript{c} (using β functions associated with their own respective model) over the years 2080-2099 for RCP 8.5 for nine model members of the CMIP5.
Plant water limitation increased globally between 2000 and 2100 in all models. Median $\beta$ decreased on average by $\sim$0.003, corresponding to a median increase in average $GPP_c$ by $\sim$0.088 kg C m$^{-2}$ yr$^{-1}$ due to both decreased soil moisture and increased $GPP_m$ from atmospheric CO$_2$ fertilization (Figure 2-2). Notably, $\beta$ increased at $\sim$20° N due to a moistening of portions of northern Africa in some models (Figure 2-2a; Figure A-3a), a response that intimates at $\beta$’s potential utility as a metric of monthly-scale drought. Much of the drought impacts literature is concerned with the appropriateness of present-day drought measures to assess future drought.
risks (Trenberth et al., 2013; Roderick et al., 2015; Milly & Dunne, 2016; Swann et al., 2016). By contrast, the estimation of $\beta$ is 1) internally consistent within each model between historical and future climates, 2) expands on soil moisture metrics of drought stress (Dai, 2012) by incorporating key feedbacks in land-atmosphere interactions (e.g. CO$_2$ effects, evapotranspiration), and 3) is directly relevant to plant water stress and simulation of global carbon and water fluxes. Nonetheless, $\beta$ alone is not a measure of drought impact: the increased $\beta$ at ~20° N did not correspond to a large decrease in GPP$_c$ (Figure 2-2b; Figure A-3b) due to the low GPP$_m$ in this region.

Both the functional form of $\beta$ and variability in soil moisture contributed to the large intermodel variation in global average $\beta$. When $\beta$ was calculated for individual models circa 2100, the global median $\beta$ ranged from ~0.6-0.9 (Figure 2-3a). However, when we applied the range of $\beta$ functional forms (Appendix A Supplementary Note) to soil moisture output from a given model, the global median $\beta$ often varied by ~0.2 and up to ~0.3 with lower values of $\beta$ corresponding to $\beta$ functions using soil moisture and higher values corresponding to $\beta$ functions using soil water potential (Figure 2-3a). We quantified how variability due solely to the functional form of $\beta$ affected GPP$_c$. In many models, we found that GPP$_c$ varied by ~0.3-0.5 kg C m$^{-2}$ yr$^{-1}$ and up to ~2 kg C m$^{-2}$ yr$^{-1}$ (Figure 2-3b). Further, we found that the functional form of $\beta$ alone explained ~40-80% of the inter-model variance in soil moisture stress on vegetation productivity (GPP$_c$).
GPP\textsubscript{c} represented a large and uncertain term relative to other components of the projected terrestrial carbon budget for all models. In the historical simulations, total GPP\textsubscript{c} ranged from 4.0 Pg C yr\textsuperscript{-1} to 353.0 Pg C yr\textsuperscript{-1} with a median of 34.7 Pg C yr\textsuperscript{-1} (Figure 2-4a-b). For context, GPP\textsubscript{c} is of the same magnitude as observation-based estimates of total GPP (123±8 Pg C yr\textsuperscript{-1})(Beer et al., 2010) and GPP\textsubscript{m} (Figure A-4a), and 0.4-36 fold larger than annual fossil fuel emissions for 2014 (9.8 Pg C yr\textsuperscript{-1})(Le Quéré et al., 2015) (Figure 2-4a). In the RCP 8.5 simulations, total GPP\textsubscript{c}
ranged from 5.56 Pg C yr\(^{-1}\) to 595.5 Pg C yr\(^{-1}\) with a median of 64.2 Pg C yr\(^{-1}\) (Figure 2-4c-d). In some cases, future projected GPP\(_c\) exceeded model-based projections of GPP (Mystakidis et al., 2016) (Figure A-4b), and was roughly equivalent to projected fossil fuel emissions (29 Pg C yr\(^{-1}\)) in the highest emissions scenario (Sanford et al., 2014) (Figure 2-4c). For both historical and future projections, GPP\(_c\) was of the same magnitude as nitrogen-constrained GPP (Thornton et al., 2007). Depending on model and time period, GPP\(_c\) was equivalent to 3-286% of GPP\(_m\) (Figure A-4b).

2.5 Conclusion

Collectively, these results illustrate that soil moisture stress on photosynthesis is a large and uncertain term affecting estimates of the terrestrial carbon cycle, comparable in magnitude to observation-based estimates of global GPP, GPP\(_m\), and the effects of nitrogen limitation on photosynthesis. These results also highlight several avenues for improving the representation of (a) soil hydraulic processes and (b) water limitation on photosynthesis. We found substantial intermodel variability in soil moisture, which resulted in a large intermodel variation in \(\beta\) globally (Figure 2-3a; Figure A-1). Models with lower soil moisture also exhibited a wider variability in \(\beta\) due to the functional form alone (Figure 2-3a). In additions to differences in precipitation, drier soils in models were associated with coarser resolution soil grids within the rooting zone (Table A-1). It has already been recognized that soil column depth and resolution is crucial in capturing permafrost dynamics (Lawrence et al., 2008). Our results indicate that increased vertical resolution of 7-10 soil layers within the top 2.85 meters may also be important in capturing drought impacts on the terrestrial carbon cycle.
Finally, these results indicate that it is necessary to pay closer consideration to the representation of water limitation on photosynthesis when projecting terrestrial carbon dynamics. Trait-driven representations of water limitation whereby leaf and stem water potential are simulated and used to solve for root zone water uptake, transport of water vertically through the sapwood, and transpiration of water into the atmosphere have already been parameterized using...
observed hydraulic thresholds and implemented in the ED2 and LM3 vegetation models (Shevliakova et al., 2009; Trugman et al., 2016; Xu et al., 2016) and incorporated into ESMs (Shevliakova et al., 2009). Recent studies also indicate that including drought-induced loss of living carbon, such as sapwood used for water transport (Shevliakova et al., 2009), may allow VMs to better capture drought legacy effects on growth (Anderegg et al., 2015). These findings highlight that a more mechanistic representation of water limitation in all VMs is fundamental to our ability to accurately capture impacts of drought on the terrestrial carbon cycle with global climate change.
Chapter 3

3  Differential declines in Alaskan boreal forest vitality related to atmospheric drought stress

3.1  Abstract

Rapid warming and changes in water availability at high latitudes alter resource abundance, tree competition, and disturbance regimes. While these changes are expected to disrupt the functioning of boreal forests, their ultimate implications for forest composition are uncertain. In particular, recent local studies of the Alaskan boreal forest have reported both increases and decreases in productivity over the past few decades. Here, we test the idea that variations in Alaskan forest growth and mortality rates are contingent on species composition. Using forest inventory measurements and climate data from plots located throughout interior and south-central Alaska, we show significant growth and mortality responses associated with competition and with partially compensating effects of midsummer drought and increased growing season length. The governing climate and competition processes differed substantially across species. Surprisingly, the most dramatic climate response occurred in the drought tolerant angiosperm species, trembling aspen, and was associated with an interaction between high midsummer potential evapotranspiration, decreased growth, and increased insect-related
mortality. Given that species composition in the Alaskan and western Canadian boreal forests is projected to shift towards early-successional angiosperm species due to fire regime, these results underscore the potential for a reduction in boreal productivity stemming from increases in midsummer evaporative demand.

3.2 Introduction

Boreal forests are rapidly changing. Increased temperatures, lengthening of the growing season, changes in water availability, and increased disturbance may disrupt the functioning, structure, and composition of these forests (Kasischke & Turetsky, 2006; Hinzman et al., 2013; Zhu & McGuire, 2016). In recent decades, different parts of the North America boreal forest have experienced different changes. In Alaska, spring tree growth can be limited by temperature (Euskirchen et al., 2006), and observational studies have reported increased vegetation productivity concurrent with warming in some locations (Welp et al., 2007). In contrast, in interior Alaska, remote sensing and tree ring studies of white spruce and black spruce trees document growth declines ascribed to warming-induced water stress (Barber et al., 2000; Beck et al., 2011; Walker & Johnstone, 2014; Verbyla, 2015; Walker et al., 2015). Canadian forest inventory analyses have disagreed on the observational trends in growth and mortality as well as the mechanisms driving the changes (Peng et al., 2011; Luo & Chen, 2013, 2015; Zhang et al., 2015; Girardin et al., 2016).

These disparate changes suggest that boreal forest responses to climate change may strongly depend on the current state of the system, including current ecosystem composition. For
example, temperature sensitivity of spring tree growth, water use, and successional strategy vary dramatically between the dominant angiosperm and gymnosperm species (Johnstone & Chapin, 2006a; Drobyshev et al., 2013; Hollingsworth et al., 2013; Euskirchen et al., 2014; Trugman et al., 2016; Young-Robertson et al., 2016). Local studies have shown that angiosperm water use far outstrips that of gymnosperm species in the Alaskan boreal forest, such that angiosperm species consume >20% of total snowmelt water in comparison to the <1% associated with gymnosperm species (Young-Robertson et al., 2016). Understanding angiosperm versus gymnosperm responses to climate change is particularly important given that recent fires in Alaska have the potential to increase angiosperm coverage by up to 20% (Barrett et al., 2011). However, few studies address how climate variability and change impact decadal-scale growth and mortality dynamics of Alaskan angiosperm species at broad spatial scales (Barber et al., 2000; Beck et al., 2011; Walker & Johnstone, 2014; Juday et al., 2015; Walker et al., 2015; Nicklen et al., 2016).

In addition to climate change, recent tree growth and mortality rates may have been affected by changes in competition and in insect disturbance. In central and western Canada, investigations using forest inventory measurements have attributed increases in tree mortality to increased competition resultant from warming temperatures (Luo & Chen, 2015; Zhang et al., 2015). Sustained insect outbreaks in British Columbia (Kurz et al., 2008) and interior Alaska (Wagner & Doak, 2013; Doak & Wagner, 2015) have also caused widespread species-specific tree mortality.

In this study, we use forest inventory measurements to evaluate the relative importance of the impacts of climate, competition, and insect disturbance on decadal-scale species-specific
growth and mortality rates in interior and south-central Alaska. We use 323 plots from the Cooperative Alaska Forest Inventory (CAFI) (Malone et al., 2009) that were repeatedly measured at five year intervals from 1994 to 2013 (Figure B-1; Figure B-2). With variance decomposition and mixed effects model analyses (Grömping, 2015), we address four questions: (i) Have there been detectable changes in Alaskan tree growth and mortality rates over the last 15 years? (ii) What is the relative importance of different climate drivers with respect to growth and mortality rates? (iii) Do gymnosperm species exhibit different climate sensitivities, in magnitude or even sign, than angiosperm species? (iv) Is insect disturbance related to growth and mortality rates, and, if so, for what species?

3.3 Methods

3.3.1 Study area and forest inventory data

Temperature in interior Alaska ranges from -40° C in the winter to >30° C in the summer and mean annual precipitation is approximately 300 mm (Van Cleve et al., 1983). In contrast, conditions in south-central Alaska are wetter with more moderate temperature changes. Throughout Alaska, the growing season is short (approximately 90 days), but up to 22 hours of sunlight are available during the summer months (Van Cleve et al., 1983).

The CAFI permanent sample plots (PSPs) are a network of fixed-sized PSPs established in 1994 to monitor growth, yield, and health of Alaskan forests (Malone et al., 2009). The layout, establishment, and maintenance of the PSPs follows conventional forest inventory procedures (Curtis, 1983). The PSPs are located in forests without evidence of human interference that
experience a range of climate conditions and include a diverse span of stem densities, stand structures, species compositions, and site conditions representative of the region. In addition to documenting growth, the CAFI records insect damage (Figure B-8) and intensity (minor (<11%), moderate (11-40%), severe (>40%), or unspecified) on individual trees for ten insect categories (unknown or unspecified, defoliators, bark beetles, sucking insects, aphids, spruce budworm, leaf roller, ants, leaf miner, ips beetle). We selected 323 PSPs in our study (Figure B-1; Figure B-2; Table B-1; Table B-2) based on the following criteria: (i) PSPs with evidence of fire, tree cutting, or other manmade damage in the census periods were excluded; (ii) PSPs had at least three complete censuses, enabling us to compare demographic rates from a minimum of two different time intervals; (iii) because individual plots were our unit of analysis, we limited analyses to PSPs containing ≥ 30 trees at the first census according to the methods of previous inventory studies to reduce random variation in plot-level demographic rates (van Mantgem et al., 2009; Peng et al., 2011; Zhang et al., 2015); (iv) only trees with diameter at breast height (DBH) > 3.8 cm were included to avoid biasing our results due to a change in the definition of minimum tree size during the study interval.

### 3.3.2 Competition indices

To evaluate the effect of competition on tree growth and mortality, we used two methods, (1) competition indices and (2) tree canopy status. First, we used two competition indices, stand basal area and the stand density index (SDI) (Zhang et al., 2015). Stand basal area is a surrogate for stand crowding in each PSP as it factors in both tree size and density. SDI is another metric used to assess the degree of crowding within a stand (Reineke, 1933):
\[ SDI = N \times \left( \frac{DBH_{\text{mean}}}{25.4} \right)^{1.605}. \]

In Equation 3-1, \( N \) represents the number of trees per hectare and \( DBH_{\text{mean}} \) represents the quadratic mean DBH in centimeters. Second, we sorted trees based on canopy status (e.g. trees with a dominant or codominant crown class versus intermediate, suppressed, or understory (Malone et al., 2009)) to isolate competition and climate effects in the absence and presence of light competition.

### 3.3.3 Climate variables

The following climate variables were selected for initial consideration based on previous studies (Barber et al., 2000; Beck et al., 2011; Peng et al., 2011; Luo & Chen, 2015; Walker et al., 2015; Zhang et al., 2015): precipitation, vapor pressure deficit (VPD), potential evapotranspiration (PET), climate moisture index (CMI), and temperature. Precipitation, PET, temperature, and vapor pressure were derived from the monthly 0.5° gridded CRU V3.23 product (Harris et al., 2014). PET was derived from temperature, vapor pressure, cloud content, and a fixed monthly climatology for wind speed using a variant of the Penman-Monteith method (Harris et al., 2014). Monthly CMI values were calculated as monthly precipitation minus PET. Annual CMI was calculated by summing monthly CMI from January through December. VPD was calculated using vapor pressure and temperature. Though there is some uncertainty in
variables such as vapor pressure and cloud cover in station-sparse regions, the CRU data has been used as one of the principal climate products by the University of Alaska Fairbanks and the International Arctic Research Center to assess climate change impacts on Alaskan ecosystems (SNAP, 2016), and has been demonstrated to perform well in other locations of the North American boreal ecosystem (Luo & Chen, 2015).

For all variables we tested both 5-year means and 5-year minimum/maximum in accordance with the inventory re-measurement interval. We did this for (i) annual, (ii) seasonal, (iii) start of the growing season (May), and (iv) midsummer (July) meteorology. Based on previous studies of biologically relevant climate drivers and sensitivity tests, we selected two metrics of drought, 5-year maximum July PET and 5-year mean July precipitation, and also 5-year mean March-May temperature. Maps of climate variables are visible in Figure B-3 - B-5.

3.3.4 Statistical Analysis: Competition, Climate, and Insects

First, we used mixed effects models to evaluate the dependence of tree growth and mortality on climate, competition, and insect drivers. We identified climate and competition effects associated with growth with the following model:

\[
\frac{\log(BA_{i,j}) - \log(BA_{i,j-1})}{5} = \beta_0 + \beta_1 CI_j + \beta_2 Gyf_j + \beta_3 PET_j + \beta_4 Prec_j + \beta_5 MAMT_j + \gamma_i. \quad \text{Equation 3-2}
\]

In Equation 3-2, \(BA_{i,j}\) represents the basal area of the \(i\)th PSP of the \(j\)th census, and includes all trees with a diameter > 3.8 cm at the previous census. \(CI_j\) is the competition index calculated
using the total number of trees in a given plot, $Gyf_j$ is a fixed effect that controls for changes in demographic rates due to forest aging and/or succession (Luo & Chen, 2015). $JPET_j$ is the July PET, $JPrec_j$ is the July precipitation, and $MAMT_j$ is the March-May temperature. The random effect of the $i$th PSP, $\gamma_i$, is assumed to follow a normal distribution with mean zero and standard deviation $\sigma_\gamma$. Each $\beta$ coefficient represents the standardized fixed effect associated with an individual model parameter.

Similarly, we identified climate and competition effects associated with mortality with the following logistic regression (van Mantgem et al., 2009; Luo & Chen, 2015):

$$
\text{logit}(p_{i,j}) = \beta_0 + \beta_1 CI_j + \beta_2 Gyf_j + \beta_3 JPET_j + \beta_4 JPrec_j + \beta_5 MAMT_j + \beta_5 insect_j + \gamma_i. 
$$

Equation 3-3

In Equation 3-3, $p_{i,j}$ is the 5-year tree mortality probability for the $i$th PSP of the $j$th census, and $insect_j$ indicates the fraction of trees infested with insects with an intensity of $>11\%$. All other parameters are identical to the growth model (Equation 3-2).

Finally, we identified climate and competition effects associated with the insect infestation fraction using with the following model:

$$
\frac{n_{insect_{i,j}}}{n_{i,j}} = \beta_0 + \beta_1 CI_j + \beta_2 Gyf_j + \beta_3 JPET_j + \beta_4 JPrec_j + \beta_5 MAMT_j + \gamma_i. 
$$

Equation 3-4
In Equation 3-4, $n_{insect,i,j}$ represents the number of trees infested with insects with an intensity >11%, and $n_{i,j}$ represents the total number of trees of the $i$th PSP of the $j$th census. All other parameters are identical to the growth model (Equation 3-2).

To further evaluate the significant effects of climate, competition, and insects, we categorized the trees in the CAFI based on canopy status, size, and species. We divided PSPs by growing season length/light (latitude), mean annual precipitation (MAP), soil drainage conditions, topography (elevation, slope, aspect), and permafrost presence. For canopy status, trees were categorized as canopy or understory trees based on tree crown category in the CAFI. Trees were divided into three size classes with the following thresholds: DBH < 9 cm, 9 cm ≤ DBH < 20, DBH ≥ 20. We also categorized trees as angiosperm, gymnosperm, trembling aspen ($Populus tremuloides$ Michx.), birch (either $Betula kenaica$ Evans and $Betula neoalaska$ Sarg.), black spruce ($Picea mariana$ Mill.), and white spruce ($Picea glauca$ Moench). Finally, insects were considered to be an infestation in an individual tree if the intensity was classified as moderate or severe (> 11% damage) (Malone et al., 2009). PSPs were divided by latitude using 62.5° N as the dividing line. PSPs were also divided into low and high precipitation groups using MAP > 500 mm as the high precipitation group. Soils were divided into two moisture classes: wet soils (encompassing peraquic, aquic, and subaquic soils) and dry soils (encompassing perhumid, humid, subhumid, subxeric, and xeric soils). PSP elevation ranged from ~16-920 m, and PSPs were divided into low elevation (< 395 m) and high elevation groups (> 395 m). PSPs were also divided by northern and southern aspect, by shallow (< 9%), intermediate (9-20%), and steep (> 20%) slope grade, and by permafrost presence or absence.
Changes in growth and mortality with age and successional status (van Mantgem et al., 2009) were accounted for with two methods. First, we included a metric in all mixed models to control for changes in forest demographic rates due to the natural aging and/or successional process (Gyf, Equation 3-2Equation 3-4) (Luo & Chen, 2015). We also categorized PSPs based on stand age: young forests (33-80 years), mature forests (80-120 years), and old growth forests (> 120 years) and examined demographic trends within each of these age groups (Luo & Chen, 2013; Zhang et al., 2015).

For our mixed models, we used both SDI and basal area for the competition index parameter and found little difference in the significance or magnitude of the fixed effect. Similarly, both age and gymnosperm fraction behaved similarly in our model when controlling for changing demographic rates due to aging and/or succession. Because plot age was not recorded for all PSPs, we used gymnosperm fraction in our final analysis. To optimize the number of independent climate, competition, and disturbance variables, we minimized the AIC for models tested on the total inventory. We found insect presence to be significantly associated with mortality but not growth (Cailleret et al., 2016) and that including it in our growth models increased the AIC, thus we used it only in our mortality models. The interactions between climate and competition variables were also considered, but were not included in our final models when AIC was minimized. We then used the mixed models to evaluate correlations between climate and competition with tree growth, mortality, and insect infestation fraction.

Third, we identified trends over time in growth, mortality, and insect infestation to evaluate possible declines in growth or increases in mortality during the study period. Trends in basal area growth were assessed using the following linear model:
\[
\frac{\log(BA_{i,j}) - \log(BA_{i,j-1})}{5} = \beta_0 + \beta_1 CI_j + \beta_2 Gyf_j + \beta_3 t_j + \gamma_i. \quad \text{Equation 3-5}
\]

In Equation 3-5, parameter \( t_j \) is the year of the \( j \)th census and all other parameters are identical to Equation 3-2.

Similarly, we modeled the 5-year probability of tree mortality using the following logistic regression:

\[
\text{logit}(p_{i,j}) = \beta_0 + \beta_1 CI_j + \beta_2 Gyf_j + \beta_3 t_j + \gamma_i. \quad \text{Equation 3-6}
\]

In Equation 3-6, all parameters are identical to those specified previously.

We estimated 5-year trend in insect infestation fraction according to the following linear model:

\[
\frac{n_{\text{insect}ij}}{n_{i,j}} = \beta_0 + \beta_1 CI_j + \beta_2 Gyf_j + \beta_3 t_j + \gamma_i. \quad \text{Equation 3-7}
\]

In Equation 3-7, all parameters are identical to those specified previously.

Finally, we estimated the relative importance of each independent variable in our growth, mortality, and insect models using variance decomposition (Chevan & Sutherland, 1991; Grömping, 2015). This method calculates goodness of fit measures for the entire hierarchy of linear (growth and insect fractions) and logistic (mortality) models using all combinations of
variables and to obtain the average independent contribution of climate, competition, and insect effects (Chevan & Sutherland, 1991).

Mixed effects model analyses were performed in MATLAB using fitglme. Our linear growth and insect models were fit assuming a normal distribution and identity link function. Our mortality models were fit using a binomial distribution and logistic link function. Standardized response coefficients in all mixed effects models were estimated using a maximum likelihood Laplace approximation. The relative importance of climate, competition, and insect factors to growth, mortality, and insect presence was calculated in R using hier.part. Our linear growth and insect models were fit assuming a normal distribution. Our mortality models were fit using a binomial distribution. Goodness of fit in all models was assessed using log likelihood. Codes are available upon request.

3.4 Results and Discussion

We found significant declines in growth in two widespread boreal tree species, trembling aspen (*Populus tremuloides*) and black spruce (*Picea mariana*), and no significant change in growth in white spruce (*Picea glauca* Moench) and birch species (*Beluta kenaica* Evans and *Beluta neoalaska* Sarg.). Contrary to expectations based on previous studies (Drobyshhev *et al.*, 2013), the relative strength of the growth decline was ~3 times stronger in trembling aspen than in black spruce (Table 3-1) and was significantly associated with high summer potential evapotranspiration (PET) (Figure 3-1A-B; Figure 3-2A-B). Though no significant climate trends occurred over the study area from 1994-2013 (Figure B-3A Figure B-5A), the variability in
summer PET increased substantially after year 2000 and the years with the highest and third highest summer PET from 1952-2014 occurred post 2000 (Figure B-3A). Increased variability in summer PET, and particularly PET during the summer of 2004 which exceeded $2\sigma$ above mean summer PET, may have caused growth declines through increased and/or compounding of drought legacy effects (Anderegg et al., 2015).

Water availability, temperature, and competition all affected tree growth and mortality, though the relative importance of different drivers differed between growth and mortality models (Figure 3-1; Figure 3-2A,D; Appendix B). Growth was negatively associated with increased competition, gymnosperm fraction, July PET, and July precipitation, and positively associated with increased spring (March-May) temperature (Figure 3-1A,B). Of the factors tested, competition was most consistently a significant effect (~90% of growth models), though multiple climate factors were significant in ~50% of our growth models (Figure 3-1B). Insect presence resulted in significant effects in fewer than 5% of our growth models and was thus excluded from our growth analysis (see Methods). Increased tree mortality was positively associated with competition, July PET, and insect presence. The effect of spring temperature and gymnosperm fraction ranged from positive to negative depending on species (Figure 3-1C,D).

Table 3-1: Changes in growth, mortality, and insect presence over the last two decades are evident but differ across species. The left column shows the relative importance (percent) determined from variance decomposition and the right column shows the standardized response coefficient determined from mixed effect model analysis. Significance level is shown in parentheses. Non-significant effects ($p > 0.05$) are indicated by ‘NS’.

<table>
<thead>
<tr>
<th>MODEL</th>
<th>Populus tremuloides</th>
<th>Beluta kenaica/neoalaska</th>
<th>Picea glauca</th>
<th>Picea mariana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth</td>
<td>19.79</td>
<td>-0.28</td>
<td>1.46</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------</td>
<td>--------</td>
<td>---------</td>
<td>-------</td>
<td>--------</td>
</tr>
<tr>
<td>Mortality</td>
<td>41.46</td>
<td>0.24</td>
<td>3.23</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt;0.0001)</td>
<td></td>
<td>(0.026)</td>
</tr>
<tr>
<td>Insect</td>
<td>40.76</td>
<td>0.014</td>
<td>3.34</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.013)</td>
<td></td>
<td></td>
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</table>

The relative importance of competition, water availability, and temperature to tree growth differed considerably between species (Figure 3-2B-C,E-F; Figure B-6). In particular trembling aspen, an early successional species adept at growing in dry conditions, recorded a strong (negative) association between growth and July PET and a slightly smaller (positive) association between growth and spring temperature (Figure 3-2B). In contrast, growth variability in white spruce was predominantly associated with competition and gymnosperm fraction, not climate effects (Figure 3-2C).
The relative importance of different climate and competitions drivers associated with tree mortality differed substantially from those that associated with growth. It was also more difficult to explain tree mortality compared to tree growth using the same climate and competition effects (the average $R^2$ for the growth models was 0.77, in contrast to an average $R^2$ of 0.55 for the mortality models). For mortality of trembling aspen, the relative importance of most drivers, including competition, climate, and insect presence, was similar (Figure 3-2E). However,
increased mortality in white spruce was primarily associated with warmer spring temperatures (Figure 3-2F). Of the other species tested, including birch and black spruce, the relative importance of climate and competition for tree growth and mortality varied along a spectrum between the responses observed for white spruce and aspen (Figure B-6).
High July PET was strongly associated with growth declines in aspen regardless of mean annual precipitation (MAP) (Figure 3-3A-B) or soil moisture classification (Figure B-7A-B), and the relative importance of July PET was much larger than that of July precipitation for all environmental conditions (Figure 3-2A; Figure 3-3A-B; Figure B-7A-B). In fact, the strong negative effect of midsummer evaporative demand was more pronounced in sites with higher
MAP and wetter soils, indicating that recorded growth declines were primarily related to a higher evaporative demand associated with warmer summer temperatures, rather than decreased soil water availability. These findings are supported by observations that tree growth is becoming increasingly limited by atmospheric vapor pressure deficit in locations across latitudes ranging from Arizona to the Pacific Northwest (Restaino et al., 2016), hypotheses that atmospheric drought is causing declines in white spruce and black spruce productivity in interior Alaska (Beck et al., 2011; Walker et al., 2015), and preliminary observations of increased aspen drought stress in interior Alaska (Juday et al., 2012). In contrast, warmer springs were associated with increased aspen growth, the relative importance of which was comparable to July PET under some conditions (Figure 3-2B; Figure 3-3A-B; Figure B-7A-B).
Significant increases in mortality were recorded only for aspen during the study period (Table 3-1). This increase corresponded with a strong increase in aspen insect pests (predominantly aspen leaf miners and defoliators), a smaller but significant decrease in white spruce and black spruce pests (primarily aphids and some spruce budworms and bark beetles), and no significant change in birch pests (predominantly defoliators and leaf rollers) (Table 3-1). There were also interactions between climate and insect presence. High July PET and low spring
temperature were associated with decreased aspen vitality (Figure 3-2B,E; Figure 3-3; Figure B-7) and increased insect presence (Figure 3-1E). Further, increased aspen mortality was more strongly associated with insect presence in locations with a higher MAP (Figure 3-3C-D).

These results have both similarities and differences with recent studies of Alaskan and Canadian forests. Previous site-level studies have recorded significant growth declines for white spruce trees in interior Alaska (Barber et al., 2000; Beck et al., 2011), however we did not find significant trends in white spruce growth during the study period (Table 3-1). This difference may be explained by differences in sample time period and spatial scales (Nicklen et al., 2016). We also found no significant growth or mortality trends for birch trees. Earlier studies have found aspen, a typical early-successional canopy species, to be more moisture limited than birch, a more shade-tolerant subcanopy species (Huang et al., 2010). This difference in microenvironment could account for the different climate responses of birch and aspen in the CAFI. Indeed, we do find the relative importance of July PET in our growth models to be a factor of two larger for canopy trees compared to the understory, like due to differences in direct radiation.
Pervasive increases in tree mortality spanning multiple species have been recorded in the lower latitude Canadian boreal forest (Peng et al., 2011; Luo & Chen, 2015; Zhang et al., 2015). Two studies attributed the increase in mortality to increased competition associated with climate change (longer growing seasons due to warming and/or possibly CO$_2$ fertilization effects) (Luo & Chen, 2015; Zhang et al., 2015). In contrast, Peng et al. (2011) attributed the increase in mortality to increasing drought conditions. Though we found no significant trends in mortality from 1994-2013 associated predominantly with climate or competition, we did document that high midsummer evaporative demand and increased competition were associated with increased

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**Figure 3-4**: The competing effects of warmer springs, drier summers, and increased insect pests will determine future boreal productivity. Outcomes for gymnosperm (left) and angiosperm (right) vitality can differ. The bottom section shows the expected effect of changes in fire on species presence (Johnstone & Chapin, 2006a; Barrett et al., 2011; Hollingsworth et al., 2013). Given that fire frequency and severity are expected to increase the prevalence of early successional angiosperm species, it is particularly important to understand how changing climate conditions impact angiosperm demographic rates.
Alaskan tree mortality. However, results differed substantially by species. We also found significant declines in growth in both aspen and black spruce; perhaps preluding elevated mortality in the coming decade (Kane & Kolb, 2014; Cailleret et al., 2016). However, contrary to the overarching theme of declining forest vitality, we found that the climate-mortality response of angiosperms and gymnosperms was negatively correlated and partially compensating (Drobysh et al., 2013). Lastly, we found significant increases in insect-driven mortality in aspen trees associated with a severe ongoing leaf miner outbreak (Wolken et al., 2011; Wagner & Doak, 2013; Doak & Wagner, 2015), and additional evidence that elevated leaf miner presence was associated with high midsummer PET and cool spring temperatures, perhaps due to decreased aspen insect defenses resulting from unfavorable climate conditions.

Collectively, these results indicate that atmospheric drought-associated declines in growth are most evident in an early-successional angiosperm species, trembling aspen. This conclusion may hold even more ecological significance in the coming century if a strengthening of the fire regime causes aspen to become more prevalent (Barrett et al., 2011). We further demonstrate that small-scale studies of declining tree growth associated with atmospheric drought stress recorded in interior Alaska scale across broad areas of the region. With projected increases in temperature and evaporative demand (Williams et al., 2012), these drought-related declines in tree productivity will likely become increasingly important. These results can help inform larger-scale projections for the western North American boreal forest by quantifying the relative importance of spring warming, summer water limitation, and insect presence to tree growth and mortality (Figure 3-4), enabling better projections of the future vitality and carbon storage in the western boreal forest of North America.
3.5 Conclusion

In conclusion, our analysis indicates that competition, climate, and insect disturbance interact to influence growth and mortality in the Alaskan boreal forest. However, the complexity of species-specific responses to spring temperature, midsummer water limitation, and insect-related mortality makes it difficult to anticipate the net effect of changes in climate on boreal forest vitality and carbon storage (Figure 3-4). The strong negative association between July PET and trembling aspen growth is particularly surprising because aspen is a widespread boreal angiosperm species that is adept at growing in dry conditions. Given that recent fires in Alaska have the potential to increase angiosperm coverage by up to 20% in the Alaskan boreal forest (Barrett et al., 2011; Zhu & McGuire, 2016), it is essential to better understand the climate drivers impacting boreal angiosperm growth and anticipate how future climate conditions may affect their growth and mortality rates.
Chapter 4

4 Climate, soil organic layer, and nitrogen jointly drive forest development after fire in the North American boreal zone

4.1 Abstract

Previous empirical work has shown that feedbacks between fire severity, soil organic layer thickness, tree recruitment, and forest growth are important factors controlling carbon accumulation after fire disturbance. However, current boreal forest models inadequately simulate this feedback. We address this deficiency by updating the ED2 model to include a dynamic feedback between soil organic layer thickness, tree recruitment, and forest growth. The model is validated against observations spanning monthly to centennial time scales and ranging from Alaska to Quebec. We then quantify differences in forest development after fire disturbance resulting from changes in soil organic layer accumulation, temperature, nitrogen availability, and atmospheric CO$_2$. First, we find that ED2 accurately reproduces observations when a dynamic soil organic layer is included. Second, simulations indicate that the presence of a thick soil organic layer after a mild fire disturbance decreases decomposition and productivity. The combination of the biological and physical effects increases or decreases total ecosystem carbon depending on local conditions. Third, with a 4°C temperature increase, some forests transition
from undergoing succession to needleleaf forests to recruiting multiple cohorts of broadleaf trees, decreasing total ecosystem carbon by ~40% after 300 years. However, the presence of a thick soil organic layer due to a persistently mild fire regime can prevent this transition and mediate carbon losses even under warmer temperatures. Fourth, nitrogen availability regulates successional dynamics; broadleaf species are less competitive with needleleaf trees under low nitrogen regimes. Fifth, the boreal forest shows additional short-term capacity for carbon sequestration as atmospheric CO$_2$ increases.

4.2 Introduction

The boreal forest has experienced significant changes in climate over the past century. Atmospheric carbon dioxide concentrations have increased by 100 ppm since 1900 and could increase to 1000 ppm by 2100 in high-emissions scenarios (IPCC, 2013). Air temperature has risen 2°C at high latitudes since 1901, and is projected to rise by an additional 2°-11°C by 2100 (IPCC, 2013). In recent decades fire frequency and severity have also increased in the western part of the North American (NA) boreal forest (Kasischke & Turetsky, 2006). Over the next century, it is projected that warming temperatures and hotter drought conditions will extend the fire season length, resulting in further increases in fire frequency and larger, more severe fires in Alaska and in many parts of Canada (Kasischke & Turetsky, 2006; Girardin et al., 2013; Hinzman et al., 2013). Projected changes in temperature and fire also have the potential to increase plant available nitrogen in the boreal forest by increasing the rate of nitrogen cycling and by changing atmospheric nitrogen deposition rates (Weber & Flannigan, 1997).
Models are useful tools for understanding how the complex changes in atmospheric CO₂, temperature, fire regime, and nitrogen cycling can affect NA boreal forest dynamics. However, current models often do not adequately represent complex soil processes that determine forest composition and carbon storage, and have yet to couple dynamic boreal vegetation to soil carbon processes (Euskirchen et al., 2009). Here we highlight how uncertainty surrounding interactions between the soil organic layer and aboveground forest growth can strongly affect projections of NA boreal forest carbon dynamics.

In the NA boreal forest, there is a biological feedback between fire severity, soil organic layer thickness, tree seedling survivorship, and aboveground forest growth (Lecomte & Bergeron, 2005; Johnstone & Chapin, 2006b; Greene et al., 2007; Drobyshev et al., 2010; Johnstone et al., 2010; Lafleur et al., 2010; Lafleur et al., 2015b). The residual soil organic layer depth left behind after a fire is important in secondary succession because recruits and suckers of both deciduous broadleaf species, such as trembling aspen (Populus tremuloides Michx.), and evergreen needleleaf species, such as black spruce (Picea mariana Mill.), grow more readily in the presence of exposed mineral soil (Johnstone & Chapin, 2006b; Greene et al., 2007; Johnstone et al., 2010; Lafleur et al., 2015b). However, larger-seeded evergreen needleleaf species, such as black spruce, are able to grow on thick organic beds, albeit with higher seedling mortality rates (Greene et al., 2007). As a result, frequent, severe fires that burn away most of the surface organic layer and expose the mineral soil increase deciduous broadleaf forest growth (Johnstone & Chapin, 2006a). In contrast, black spruce is generally the dominant canopy tree in old forests or during secondary succession when a thick organic soil layer remains present after a fire (Lecomte & Bergeron, 2005; Johnstone & Chapin, 2006b).
While soil organic layer depth affects aboveground biomass accumulation, forest growth also controls organic layer accumulation. In broadleaf aspen forests, easily decomposable litter, lack of moss growth, and warm ground conditions increase decay rates and prevent significant accumulation of surface soil carbon (Légaré et al., 2005; Laganière et al., 2010). However, due to a relatively deep rooting system (up to 100 cm), aspen forests tend to preserve some carbon in deeper layers within the mineral soil (Laganière et al., 2013). In contrast, black spruce growth promotes continual soil organic layer accumulation through inputs of slowly-decomposing, nitrogen-poor needles, understory moss growth, and cold ground conditions (La Roi & Stringer, 1976; Laganière et al., 2011). Thus, there tends to be less soil carbon associated with aspen broadleaf forests than old black spruce forests (Légaré et al., 2005).

These interacting processes have only partially been incorporated into models. Models of forests in Alaska and central Canada have incorporated dynamic organic layer accumulation (Zhuang et al., 2002; Carrasco et al., 2006; Yi et al., 2010; Bona et al., 2016), NA boreal-specific tree types, and dynamic vegetation (Euskirchen et al., 2009; Euskirchen et al., 2014). Other models have been used to study the interplay between fires (Yue et al., 2013), soil organic layer depth, and aboveground forest growth within sub-regions of Canada and Alaska (de Groot et al., 2003; Terrier et al., 2014). Yet no NA boreal forest models applied to a range of climate gradients have coupled dynamic vegetation processes and dynamic soil organic layer accumulation, or included the effect of organic layer depth on tree seedling and sucker survivorship. How these omissions impact simulations of NA boreal carbon storage is unclear.

Ideally, models should not only account for these impacts, but also demonstrate scalability, or predictive power across space and time. There are numerous regionally varying
factors that influence the response of NA boreal forests to climate change. Permafrost
distribution, soil type, nitrogen availability, temperature, precipitation, and fire frequency all
differ regionally throughout the NA boreal forest (Kasischke & Turetsky, 2006; Reay et al.,
2008) and all exert control on aboveground forest structure (Drobychev et al., 2013; Girardin et
al., 2014), and soil carbon accumulation (Lavoie et al., 2005). A scalable model accurately
captures observed spatial variations in growth dynamics due to variations in environmental and
climate factors over both short and long timescales.

This study has two overall objectives. First, we seek to develop a data-constrained model
framework for understanding NA boreal forest development after fire disturbance. Specifically,
we update the Ecosystem Demography model version 2 (ED2) to include new parameterizations
for broadleaf aspen and needleleaf black spruce species-types, a dynamic soil organic layer,
species-specific seedling survivorship dependent on the organic layer thickness, and species-
specific litter decay rates. The model is tested against observations from throughout the NA
boreal forest including eddy covariance measurements and forest inventory data in Alaska, and
multi-century basal area, leaf area index (LAI), and organic layer depth chronosequences
measured in Saskatchewan, Manitoba, and Quebec. Collectively, these observations are diverse
in terms of processes, time scales, and spatial extent. The second major objective is to use the
updated model to understand how forest structure and soil carbon storage can be expected to
change with increasing atmospheric CO₂, warming, and with changing nitrogen availability for
different climates within the NA boreal forest.

Meeting these objectives will allow us to address the following questions. (1) Is it
possible to accurately reproduce observed forest growth and soil organic layer dynamics along a
climate gradient across the NA boreal forest by incorporating feedbacks between soil organic layer thickness and aboveground forest and moss growth? (2) What are the effects of fire-driven changes in soil organic layer thickness on modeled forest composition and ecosystem carbon accumulation? How does the biological effect that the soil organic layer exerts on seedling and sucker recruitment compare to the physical effect of the soil organic layer on soil temperature and moisture, and hence organic matter decomposition? (3) How does global climate change, namely projected changes in atmospheric CO₂, temperature, and nitrogen availability, affect forest composition and ecosystem carbon accumulation and how do these changes vary across different climates within the NA boreal forest?

4.3 Methods

4.3.1 Model description

Our model simulations were carried out using ED2, a terrestrial biosphere model that explicitly scales up tree-level competition for light, water, and nutrients to the ecosystem level. Detailed descriptions of ED2 exist in the literature (Medvigy et al., 2009; Medvigy & Moorcroft, 2012). Single-grid cell simulations were carried out for the following three different climate regimes within the NA boreal forest to capture regional variability: (1) near Delta Junction, Alaska, where the mean January temperature is -19.2°C, the mean July temperature is 13.2°C, and the mean annual precipitation is 295 mm yr⁻¹; (2) near Thompson, Manitoba where the mean January temperature is -20.9°C, the mean July temperature is 18.2°C, and the mean annual precipitation is 509 mm yr⁻¹; and (3) in western Quebec where the mean January temperature is -
17.3°C, the mean July temperature is 17.2°C, and mean annual precipitation is 905 mm yr⁻¹ (Figure 4-1). We then performed regional validation simulations using forest inventory from interior and south-central Alaskan forests and Canadian boreal forests in Alberta to test the effect of regional variability on the relative importance of key climate and competition drivers in both the observations and the model.

### 4.3.2 Experimental overview

Our model experiments fell within three general categories, model evaluation, model sensitivity experiments, and regional forest inventory comparisons. First, to evaluate our model’s performance, we tested model simulations against observed net ecosystem productivity (NEP), basal area and leaf area growth, and soil organic matter accumulation. Second, we ran a series of experiments exploring the sensitivity of aspen-black spruce forest growth and carbon accumulation to environmental forcings that are projected to change with global climate change in the NA boreal forest. Each set of experiments was composed of an ensemble of simulations in order to capture the range of uncertainty associated with select ecophysiological parameters used in the model. Third, we ran regional simulations of Alaskan and Albertan forests and compared the relative importance of climate and competition to observed forest growth derived from the forest inventory over the last five decades.

### 4.3.3 North American boreal ecosystem dynamics in ED2
For our first two sets of simulations, we have included the following newly developed parameterizations specific to the NA boreal forest into ED2: (1) aspen and black spruce plant functional types; (2) species-specific seedling growth dependent on organic layer depth; (3) species-specific litter decay rates; (4) a dynamic soil organic layer that includes dynamic moss growth with moss accumulation dependent on canopy tree type; and (5) an updated nitrogen cycle including mineralized soil nitrogen leaching due to soil water drainage and nitrogen fixation by cyanobacteria associated with moss. For our regional simulations, we also included newly parameterized jack pine and white spruce plant functional types. In addition, we include other recent developments, such as a new phenology scheme parameterized using NA boreal phenology observations of aspen (Jeong & Medvigy, 2014) and an updated plant hydraulics...
module (Xu et al., 2016). We refer to our updated model as “ED2-boreal”. To our knowledge, no other terrestrial biosphere model applied to the large climate gradients within NA boreal forest couples dynamic NA boreal-specific vegetation with a dynamically accumulating soil organic layer and includes the species-specific effect of organic layer depth on seedling growth.

New plant functional types were parameterized by synthesizing measurements reported in previous studies (Table C-1). Although our species choice of aspen and black spruce for our first two sets of experiments is not fully representative of all NA boreal tree species, aspen and black spruce are some of the most abundant and widely distributed deciduous broadleaf and evergreen needleleaf species in the NA boreal forest. Spruce trees comprise 47.3% of NA boreal forest wood by volume and cover >60% of the forest land area. Aspen in particular is adept at growing in a diverse range of environmental conditions similar to those projected for the future NA boreal climate and comprise 13.1% of forest wood by volume. An aspen-black spruce two species system has the advantage of simplicity and with it we hope to achieve a first order estimate of regional trends in forest composition and ecosystem carbon storage.

Previous sensitivity studies have identified that the maximum rate of carboxylation ($V_{c_{\text{max}}}$) and leaf biomass allometry exert particular control over the simulated dynamics (White et al., 2000; Dietze et al., 2014). Substantial variation has been reported in field measurements of $V_{c_{\text{max}}}$ for aspen and black spruce (Kubiske et al., 1997; Rayment et al., 2002). However, models generally take a single value for $V_{c_{\text{max}}}$ (at reference temperature) for each plant functional type. Under this construct, it is unclear how to capture the observed variability in $V_{c_{\text{max}}}$ in terrestrial biosphere models. Likewise, the parameters linking leaf biomass to tree diameter can vary by location and tree size even for trees within the same species (Ter-Mikaelian & Korzukhin, 1997).
Our own preliminary analyses confirmed model sensitivity to these parameters. In addition, we also found that tree growth can be sensitive to the rate of nitrogen leaching, a parameter that is poorly constrained in terrestrial biosphere models. Finally, the upward bound of maximum seedling mortality fraction for black spruce in thick organic soils is poorly constrained (Greene et al., 2004). To account for these sources of parameter uncertainty, we defined normal priors representing a range of feasible parameter values. In the case of $V_{\text{emax}}$, we used a range of values measured within a single study (Kubiske et al., 1997; Rayment et al., 2002). Variations in leaf biomass allometry were derived from two site-specific allometric relations near Delta Junction, Alaska and Thompson Manitoba (Bond-Lamberty et al., 2002a; Yarie et al., 2007). We derived the range in the rate of mineralized soil nitrogen leaching based on differences between parameterizations used by Gerber and Brookshire (2014) and the CLM model [Oleson et al., 2013]. Finally, we placed uncertainty bounds on the maximum mortality fraction of black spruce seedlings based on our own sensitivity tests combined with millennial growth trends of old spruce forests (Fenton et al., 2005) and germination measurements (Greene et al., 2004). The means and standard deviations of the priors for these parameters are reported in Table C-2.

In our model, both aspen and black spruce experience increasing seedling mortality with increasing organic layer depth according to the following equation:

$$m_p = \max \left( \left( 1 - \exp(-c_1 \cdot O_L_{\text{depth}}) \right) \cdot m_{p,\text{max}}, m_{p,\text{min}} \right).$$  \hspace{1cm} \text{Equation 4-1}

In Equation 4-1, $m_p$ is the seedling and sucker mortality fraction, $m_{p,\text{max}}$ is the species-specific maximum seedling and sucker mortality fraction in deep organic layers, $c_1$ is a positive species-
specific shape parameter, $OL_{\text{depth}}$ is the organic layer depth in centimeters, and $m_{p,\text{min}}$ is the background seedling and sucker mortality fraction characteristic of shallow organic layers (Table C-1; Table C-2). In ED2-boreal, aspen seedlings experience mortality rates greater than $m_{p,\text{min}}$ in organic layers thicker than 2 cm and 100% mortality in organic layers thicker than 5 cm in accordance with observations by Johnstone and Chapin (2006b). In contrast, black spruce seedlings experience mortality rates greater than $m_{p,\text{min}}$ in organic layers thicker than 10 cm, and significantly elevated mortality in organic layers thicker than 40 cm (Fenton & Bergeron, 2006; Fenton et al., 2006; Drobyshev et al., 2010).

Greene et al. (2007) and Lafleur et al. (2015b) also find differential survivorship of aspen and black spruce seedlings in thick organic layers, although they reported different organic layer intervals over which mortality changes. Specifically, Greene et al. (2007) find that aspen seedling survivorship is 8000 times higher on an organic layer 0.5 cm than on one of 6 cm. In contrast, black spruce trees have a seedling survivorship ratio of 30 at these depths in absence of interspecies competition (Greene et al., 2007). Lafleur et al. (2015b) find that aspen seedling survivorship is relatively uninhibited in organic layers shallower than 10 cm, but seedling survivorship decreases linearly to 0% in organic layers greater than 25 cm (Lafleur et al., 2015b). Our uncertainty analysis of the maximum seedling mortality fraction for black spruce partially addresses this uncertainty in the literature.

For the purposes of this paper, we define fire severity in accordance with our parameterization of organic layer-induced seedling mortality. A severe fire is defined as any fire that reduces the soil organic layer to less than 4 cm, allowing regeneration of aspen seedlings. A moderate fire is defined as a fire event that reduces the soil organic layer to 4 - 40 cm such that
aspen seedlings are unable to grow and black spruce seedlings grow with elevated mortality. Finally, we define a mild fire as any fire event with a residual soil organic layer greater than 40 cm, allowing very little regeneration of spruce seedlings (Van Bogaert et al., 2015). All of our simulations are classified as developing after a mild, moderate, or severe burn, with the classification determined by the organic layer depth with which the simulation was initialized.

The model’s surface litter inputs are composed of leaves, dead seeds, and black spruce fine roots. We assume that fine roots from aspen trees are present in the mineral soil and the structural tree litter is heterogeneously scattered on top of the soil organic layer, and so they are not included when calculating the organic layer depth. Litter loss occurs at a species-specific characteristic decay rate that is applied to an entire species’ litter pool (leaves, fine roots, and seeds) as specified in Table C-1. This characteristic rate is modified by temperature and moisture. The soil organic layer accumulates dynamically above the mineral soil and the soil organic layer depth is calculated as the sum of aspen litter (excluding fine roots), black spruce litter, and moss growth. Different bulk densities are assigned to the litter and moss pools due to the proximity of moss to the surface of the soil organic layer (Table C-1) (Trumbore & Harden, 1997; Carrasco et al., 2006). For the purposes of calculating temperature and water content, all components of the soil organic layer (both moss and litter) are assumed to have physical properties given in Table C-3 (McCumber & Pielke, 1981). Depending on thickness, the organic layer is discretized into one or more vertical layers so that gradients in temperature and soil moisture are resolved. Temperature and water content are calculated for each layer according to Walko et al. (2000).
Moss accumulation is observed in black spruce forests when the canopy begins to close and where deciduous leaf litter does not shade moss in the sub-canopy (Natalia et al., 2008). The net accumulation rate has been found to be mainly a function of forest age and canopy species-type such that moss is present in black spruce forests but not aspen forests (Zackrisson et al., 2004). Here we model net moss biomass accumulation using the following equation:

\[
\frac{ds}{dt} = \begin{cases} 
  a \cdot s^b, & l_a < 0.05 \\
  0, & l_a \geq 0.05 
\end{cases} \tag{4-2}
\]

In Equation 4-2, \(s\) is moss biomass in kg C m\(^{-2}\), \(dt\) is a monthly time step, and \(l_a\) is the amount of aspen litter present in kg C m\(^{-2}\). We set a threshold for moss growth of 0.05 kg C m\(^{-2}\) of aspen litter, above which moss does not accumulate, preventing moss growth in aspen-dominated stands. We parameterized the constants \(a\) and \(b\) using a percent Sphagnum moss cover chronosequence measured in the Abitibi clay belt region of Quebec (Fenton et al., 2005). Similar to Bona et al. (2016), in our analysis we found Sphagnum percent cover to be proportional to moss biomass in chronosequence points with \(^{14}\)C ages younger than 750 years. With this parameterization, net moss accumulation is dependent only on aspen litter and previous month’s moss biomass; it is not affected by changes in the temperature or moisture regime. In ED2-boreal, moss biomass is included as part of the soil organic layer for the purposes of calculating seedling survivorship, resolving the soil energy and water balance and calculating total ecosystem carbon.

In the updated nitrogen cycle in ED2-boreal, when a tree dies or sheds its fine roots, needles, or leaves, both the aboveground carbon and nitrogen pools are transferred to the soil
system. Soil organic matter decomposition rate is modified by species litter type, soil temperature, and soil moisture (Moorcroft et al., 2001). As carbon is mineralized, the associated nitrogen from the decomposing structure is released into a bioavailable mineralized soil nitrogen pool. Each day, tree demand for nitrogen is calculated and the amount of nitrogen removed from the bioavailable soil nitrogen pool is the minimum of either the soil nitrogen available to the plant or the nitrogen required for growth. Any remaining mineralized soil nitrogen after plant nitrogen uptake is subjected to leaching loss with the assumption that a small fraction (see Table C-2) is in soluble form and loss occurs as a function of soil water drainage out of the rooting zone (Thornton & Rosenbloom, 2005). Additional mineralized soil nitrogen inputs include atmospheric nitrogen deposition and, in older spruce forests, nitrogen fixation by cyanobacteria associated with Sphagnum moss. Here we model nitrogen fixation as increasing with the amount of Sphagnum moss according to the following relationship:

\[ N_{\text{fix}} = \begin{cases} f \cdot s, & s \geq 2.5 \\ 0, & s < 2.5 \end{cases} \]  

Equation 4-3

In Equation 4-3, \( N_{\text{fix}} \) is the nitrogen fixation rate in kg N day\(^{-1}\) and \( f \) is a constant. When moss biomass accumulates to approximately 2.5 kg C m\(^{-2}\), an increasing presence of Sphagnum moss that associates with nitrogen-fixing cyanobacteria results in a linear increase in nitrogen fixation with moss biomass (Fenton et al., unpublished data 2015). Because in this study we focus on forest recovery from fire and do not include dynamic fire disturbance, we do not specifically address how combustion losses affect the long-term mass balance of forest nitrogen. Post-fire nitrogen fertilization depends on the fire severity scenario and the nitrogen available in the residual soil organic layer.
4.3.4 Model Evaluation

We assessed whether our model could accurately simulate aspen and black spruce forest growth and soil organic layer accumulation over long time scales in addition to capturing monthly net ecosystem productivity (NEP). For this assessment we utilized observations that varied with respect to both measurement type and measurement location in order to scale up to different climate regimes within the NA boreal forest (Figure 4-1). None of the observations used to evaluate the model performance were used during model calibration. To our knowledge, no previous studies have challenged models in the NA boreal zone with such diverse observations in terms of time scale, measurement type, and range of climate gradients. Unless otherwise specified, all of our simulations were forced with 1.0°, 3-hourly meteorology from the Princeton Global Forcing (PGF) dataset (Sheffield et al., 2006), atmospheric CO₂ levels were held constant at 370 ppm, and nitrogen deposition rates were held constant at 0.5 g N m⁻² yr⁻¹ for simulations in Canada and 0.1 g N m⁻² yr⁻¹ for simulations in Alaska (Reay et al., 2008).

Each model evaluation was composed of a 20-member ensemble of simulations that captured the range of uncertainty associated with select ecophysiological parameters used in the model (Table C-2). In a preliminary analysis, we tested ensemble sizes ranging from 1 to 30 and determined that the ensemble mean and standard deviation stabilized at around 15-20 members. Each ensemble member was initialized with a random draw from the joint prior probability distribution for $V_{\text{max}}$, leaf allometry, maximum seedling mortality fraction, and soil nitrogen leaching rate. The same 20 parameter sets were used in all of our analyses. Additional details on simulations and model evaluations are available in Table C-4.
To assess our model’s ability to reproduce monthly NEP in both aspen and black spruce forests, we compared two 3-year (2002-2004) eddy covariance records from an aspen and black spruce forests situated near Delta Junction, Alaska (Welp et al., 2007) to simulated NEP for the same locations. Inventory data were not available at the sites so we carried out preliminary spin-up runs to initialize the model forest cover so that modeled leaf area index (LAI) was similar to that of the observed forest LAI during the measurement years (Liu et al., 2005). Each model forest was grown from a seedling density of 0.2 m\(^{-2}\). For the model spin up, we used PGF meteorology looped over years 2002-2004. The aspen forest soil organic layer was initialized to 3 cm in depth (typical of a secondary successional aspen forest in Alaska). The black spruce forest was initialized with a 15 cm soil organic layer (a typical organic layer that would allow black spruce trees to be the primary species growing during secondary succession). Both forests were grown on a mineral soil of silty clay loam texture according to observations. Following the spin-up, we compared simulated and observed NEP. To assess performance, we computed the ensemble mean and percent error between ensemble mean and observations for each month in the growing season (May-August).

To validate ED2-boreal for decadal-scale forest growth in Alaska, we compared successive forest inventories from Cooperative Alaska Forest Inventory (CAFI) (Malone et al., 2009) with simulated forest growth. First, we grouped inventory plots based on their composition (pure aspen, pure black spruce, mixed aspen-black spruce) and location (northern or southern) so that we could assess model performance in both monoculture and mixed stands along a climate gradient within interior Alaska. The grouping by climate was determined based on the 1° PGF meteorology. Grid boxes associated with each grouping are detailed in Table C-4. This grouping resulted in five categories of simulations: northern and southern simulations initialized with pure
aspen (TA-north-CAFI-AK; TA-south-CAFI-AK), northern and southern simulations initialized with pure black spruce (BS-north-CAFI-AK; BS-south-CAFI-AK), and a southern simulation initialized with mixed forest (Mixed-CAFI-AK). The CAFI did not include any mixed stands in the northern region. Three to six inventory plots were present within each category, and each plot was simulated separately with a 20-member ensemble.

Because ED2-boreal tracks the size and density of cohorts of trees, it is possible to initialize ED2-boreal with inventory data of tree diameter at breast height (DBH) and soil carbon from CAFI. Nitrogen data were not available, so we initialized the soil nitrogen as proportional to basal area in forests with aspen and inversely proportional to the basal area in forests with only black spruce (Jerabkova et al., 2006). Each plot was initialized with a mineral soil of silty clay loam texture. In our assessment of model performance, we calculated average percent error in basal area between the observed and simulated category mean.

We also validated ED2-boreal with basal area, LAI, and soil carbon chronosequences for aspen forests and black spruce forests in locations in Saskatchewan and Manitoba measured as part of the BOREAS campaign (Sellers et al., 1997). In the BOREAS Northern Study Area (NSA) in Manitoba, we compared simulated forest growth to the dry black spruce chronosequence and the old aspen forest (Bond-Lamberty et al., 2002b) and we compared the simulated soil carbon accumulation in black spruce forests after 150 years to observed carbon storage in shallow organics (Harden et al., 2012). In Southern Study Area (SSA) in Saskatchewan, we compared simulated forest growth to both the old aspen and black spruce forests. This evaluation involved four sets of 20 ensembles members each: one set for an aspen-only seeded forest (TA-chrono-MB) and one set for a black spruce-only seeded forest (BS-
chrono-MB) at the NSA, and one set for an aspen-only seeded forest (TA-chrono-SK) and one set for a black spruce-only seeded forest (BS-chrono-SK) at the SSA. Each black spruce and aspen forest was spun up from seedlings at a density of 0.2 m$^{-2}$. The aspen forest soil organic layer was initialized to 3 cm in depth and the black spruce forest was initialized with a 15 cm thick soil organic layer. Forests were grown on a mineral soil of clay texture according to observations. Simulations were forced with PGF meteorology looped over years 1990 - 2008. We assessed model performance by computing the ensemble mean and percent error between simulated mean and measured basal area and LAI.

Several factors complicate comparison of simulated forest growth to chronosequences. Each point measured in a forest chronosequence grew under different atmospheric CO$_2$ conditions and under a different climate forcing, depending on the age of the chronosequence point. To determine whether this was important for our analysis, we performed separate model simulations for each chronosequence point, forcing the model with dynamic atmospheric CO$_2$ corresponding to the levels seen by each forest throughout its lifetime. From these tests, we found that the forest adjustment to increasing atmospheric CO$_2$ is sufficiently rapid that it is unnecessary to include separate simulations for each chronosequence point. We also found that the overall growth trends of the forest were not very sensitive to the interval over which we looped the meteorology, provided that the interval was longer than 5 years and was not composed mainly of anomalous years.

In the eastern NA boreal forest, we compared our model simulations to two black spruce basal area and organic layer depth chronosequences measured after a moderate fire disturbance and a mild fire disturbance in the Clay Belt region of Quebec (Fenton et al., 2005). Accurately
capturing differing growth dynamics of black spruce in diverse initial conditions is particularly important in eastern Canada because the fire return interval is long, old black spruce forests of multiple generations are common, and the structure of the forest changes significantly as the forest ages and the soil organic layer accumulates (Bergeron & Fenton, 2012). We limit the scope of our analysis to the $^{14}$C-dated forest age and chronosequence points less than 500 years old. The current fire cycle in eastern Canada is approximately 500 years, and the long term average was previously around 140 years, ensuring that the majority of stands present in this region are younger than 500 years (Bergeron et al., 2004). Each evaluation was composed of 20 ensemble members with meteorology looped over years 1990-2008 and stands initialized with a seedling density of 0.2 m$^{-2}$. The soil organic layer was initialized to 20 cm with no moss present in the moderate burn simulation (BS-mod-chrono-QC). The mild burn simulation (BS-mild-chrono-QC) was initialized with a 45 cm soil organic layer composed of litter and moss. Forests were grown on a mineral soil of clay texture according to observations.

4.3.5 Model Sensitivity Experiments

We performed 5 sensitivity experiments exploring the sensitivity of forest composition and ecosystem carbon accumulation to changes in organic layer conditions and increased temperature, nitrogen availability, and atmospheric CO$_2$. The motivation for these experiments was two-fold. First, changes in fire regime and increases in temperature, nitrogen deposition, and atmospheric CO$_2$ are likely to happen over the next century. Second, both increases in temperature and changes in nitrogen are directly linked to NA boreal forest soil organic matter accumulation; the soil organic layer accumulation rate is highly dependent on temperature-
regulated decomposition and the rate of organic matter decomposition directly controls the rate of nitrogen cycling. Though whole-plant response to increases in atmospheric CO$_2$ is poorly understood (Nowak et al., 2004), NA boreal forest carbon accumulation rates may be increasing in response to increasing atmospheric CO$_2$ and could potentially store CO$_2$ in plant biomass or soil organic matter, at least in the proximate future (Trumbore & Harden, 1997). As such, leaf-level carbon assimilation rates calculated by ED2-boreal could be used as an upper bound for the carbon drawdown sensitivity of the NA boreal forest under elevated atmospheric CO$_2$. Changes in precipitation were not included in our simulations because climate models give conflicting projections (Allen & Ingram, 2002). Because our simulations do not include changes in the full set of environmental forcings, they should be viewed as sensitivity studies rather than future projections.

In our sensitivity experiments, the 20 ensemble members used the same 20 parameter sets as in the model evaluations. Each experiment included ensembles of a hypothetical mixed aspen and black spruce forests simulated with the climate of Delta Junction, Alaska; Thompson, Manitoba; and in the Abitibi, on the Clay Belt of Quebec and Ontario. This spatial distribution was designed so that we could (1) identify the unifying processes occurring throughout the NA boreal forest and (2) resolve the differing regional responses due to a climate gradient. All ensembles were initialized with aspen and black spruce seedlings, each at a density of 0.2 m$^{-2}$ and were forced with meteorology looped over years 1990-2008. We assessed (1) the effect of fire severity, (2) the biological and physical effect of the soil organic layer, (3) the effect of projected mean annual temperature increases, (4) the effect of projected changes in nitrogen deposition, and (5) the effect of projected increases in atmospheric CO$_2$ on forest composition and total ecosystem carbon accumulation. In our experiments, total ecosystem carbon was
computed as the sum of plant carbon, coarse woody debris carbon, dead seeds, discarded fine roots, discarded leaves, and moss carbon. Forest composition was assessed based on the ratio of aspen biomass to total tree biomass (aspen plus black spruce). Simulations are described in detail below and summarized in Table C-5.

To examine the effect of fire severity on forest composition and total ecosystem carbon accumulation, we ran two sets of 500-year ensembles for each site along the regional climate gradient, one representing forest development after a severe fire where the soil organic layer was mostly burned (burn-severe) and one representing forest development after a mild fire (burn-mild) where a thick organic layer remained (Table C-5).

To disentangle the biological and physical effects of the soil organic layer, we ran six sets of 300-year ensembles. The first ensemble corresponds to the standard ED2-boreal configuration in which the dynamic organic layer and seedling mortality module are active (OLon-SMon). For the second ensemble, the dependence of seedling mortality on organic layer depth was turned off (OLon-SMoff). For the third ensemble, both the dependence of seedling mortality on organic layer depth and the dynamic organic layer were turned off (OLoff-SMoff). Our next three experiments (OLon-SMon-warm, OLon-SMoff-warm, OLoff-SMoff-warm) replicated the first three experiments but also included with a uniform increase in temperature of 4°C to isolate possible changes in the biological and physical effects of the soil organic layer with warming temperature. Other meteorology, including precipitation, solar radiation, and relative humidity, were not changed. All ensembles were initialized as if developing after a mild fire disturbance with an organic layer depth of 60 cm (Table C-5). The initial organic layer depth was chosen to highlight conditions in which including the seedling mortality module and dynamic soil organic
layer would most affect the outcome of forest composition and total ecosystem carbon accumulation.

In our third set of experiments, to examine the effect of warming temperatures, ensembles were forced with current meteorological conditions (T-0C\text{warm}), with a uniform increase in temperature of 2°C (T-2C\text{warm}), and with a uniform increase in temperature of 4°C (T-4C\text{warm}). Other meteorology, including precipitation, solar radiation and relative humidity, were unchanged. Forests in these simulations were initialized to represent stand development after fire disturbance in the upcoming century near Delta Junction, Alaska, Thompson, Manitoba, and the Clay Belt of Quebec. Fire severity is projected to increase in both Manitoba and Alaska in the upcoming century resulting from longer fire seasons and higher atmospheric vapor pressure deficits (Kasischke & Turetsky, 2006; Girardin et al., 2013; Hinzman et al., 2013); however, in the Clay Belt in Quebec, fire severity is not projected to increase leading up to year 2100 (Terrier et al., 2014). Thus, we initialized the forests in Alaska and Manitoba with a thin organic layer of 3 cm and the forest in Quebec with a thick organic layer of 60 cm.

In our fourth set of experiments, we examined the effect of changes in nitrogen with four different nitrogen deposition scenarios for all locations: annual nitrogen deposition rates of (1) 0.1 g N m\textsuperscript{-2} yr\textsuperscript{-1}, comparable to deposition rates currently seen in Alaska (Ndep-0.1); (2) 0.5 g N m\textsuperscript{-2} yr\textsuperscript{-1}, comparable to rates seen in many parts of Canada (Ndep-0.5); (3) 2 g N m\textsuperscript{-2} yr\textsuperscript{-1}, projected for the year 2030 in some areas in southern Quebec (Ndep-2) (Reay et al., 2008); and (4) 20 g N m\textsuperscript{-2} yr\textsuperscript{-1} (Ndep-20). All simulations were initialized to represent stand development after fire disturbance in the upcoming century near Delta Junction, Alaska, Thompson, Manitoba, and the Clay Belt of Quebec (Table C-5).
In our final set of experiments, we examined the effect of atmospheric CO$_2$ fertilization. In ED2-boreal, the effect of atmospheric CO$_2$ fertilization on leaf-level carbon assimilation and water fluxes is computed using the model developed by Farquhar, Ball, Berry and others, described in detail in Appendix B of Medvigy et al. (2009). We ran two sets of 300-year ensembles with atmospheric CO$_2$ fixed at 370 ppm (CO2-370) and with atmospheric CO$_2$ fixed at 1000 ppm (CO2-1000), a high-emissions scenario for the year 2100 [IPCC, 2013]. Meteorology including temperature, precipitation, solar radiation and relative humidity, were unchanged. All simulations were initialized to represent stand development after a fire disturbance in the upcoming century near Delta Junction, Alaska, Thompson, Manitoba, and the Clay Belt of Quebec (Table C-5).

4.3.6 Regional Simulations

We performed 2 sets of regional simulations to assess (1) the model’s ability to reproduce the species-specific relative importance of key climate drivers of forest growth, (2) the difference in relative importance of different climate drivers within species but across regions, and (3) how vegetation hydraulics feeds back into local environmental drivers. The motivation for these regional simulations was to understand (a) how current climate has been influencing boreal forest growth over a period of warming and increasing atmospheric CO$_2$ ranging from 1960-present, (b) if models are able to capture the relative importance of key climate drivers, and (c) how vegetation hydraulics affects model performance.
In our regional experiments, in addition to our aspen and black spruce PFT, we included newly parameterized jack pine and white spruce PFTs. Regional simulations were run with one ensemble member using the mean ecophysiological parameters values for aspen and black spruce. Each simulation was initialized with forest inventory data from either the CAFI (Malone et al., 2009) or the Alberta forest inventory. In each inventory, permanent sample plots were binned by survey start year (within a five year window) and half degree latitude/longitude grid cell in accordance with the meteorological forcing (Sheffield et al., 2006). Different plots were included as different patches within a given grid cell (Medvigy et al., 2009). The initial organic layer depth was not provided for some of the inventory plots, so all plots were initialized with an average organic layer depth associated with a given species composition. Because these were decadal-scale simulations of predominantly mature trees, sensitivity tests indicated that forest growth dynamics were not particularly sensitive to the initial organic layer conditions. These regional simulations additionally included both dynamic atmospheric CO$_2$ forcing and spatially explicit nitrogen deposition.

For both Alaska and Alberta, we ran two sets of simulations, one with a mechanistic hydraulic scheme from Xu et al. (2016) with a trait-driven representations of water limitation whereby leaf and stem water potential are simulated and used to solve for root zone water uptake, transport of water vertically through the sapwood, and transpiration of water into the atmosphere, and one with an empirical soil moisture limitation factor based on Medvigy et al. (2009) to understand how vegetation hydraulics feeds back to local environmental drivers and surface energy partitioning. At the end of each simulation, we compared the simulated growth to the observed tree growth and calculated the relative importance of competition, midsummer precipitation, midsummer vapor pressure deficit (VPD), and spring temperature using on
variance decomposition (Grömping, 2015). Analyses were performed using the hier.part function in R. Climate data associated with the model simulations was derived from the Sheffield et al. (2006) meteorological forcing, however some properties, such as canopy VPD, were model emergent. Climate data associated with the observations was derived from the monthly 0.5° gridded CRU V3.23 product (Harris et al., 2014). Average midsummer (July) or spring (May) values were calculated by averaging over the entire inventory period for a given grid cell.

4.4 Results

4.4.1 Model-data comparison

When compared to measured NEP near Delta Junction, Alaska, the simulated ensemble mean captured the seasonal and interannual trends for both aspen (Figure 4-2a,c,e) and black spruce (Figure 4-2b,d,f) forests for years 2002-2004. In the aspen forest, both simulated and observed total growing season (May-August) NEP increased each year between 2002-2004. In the black spruce forest, total growing season NEP increased between 2002 and 2003 and decreased between 2003 and 2004. This initial increase in growing season NEP followed by a decline in 2004 was also captured in the model simulations. We found that the model best reproduced carbon fluxes in the aspen forest in June and July, where the simulated ensemble mean was within 17.5% of the observed NEP (Figure 4-2c,e; Table C-6). In May, the absolute difference between observed and simulated ensemble-mean NEP was not large, but the small denominator in the percent error calculation resulted in a large percent error (Figure 4-2a,c,e; Table C-6). The poor performance of the model in the aspen forest in August was caused by a
discrepancy between observed and simulated NEP in 2004 (Figure 4-2a). During 2004, a major drought occurred in central Alaska, so it is possible that the simulated NEP was not as sensitive to the drought conditions. In contrast, the simulated NEP at the black spruce forest did respond to the drought conditions of 2004 with a dip in NEP that was more pronounced than in the observations (Figure 4-2b). For all growing season months except for August, the ensemble mean for the black spruce forest was within 23% of the observed NEP. However, in August, the ensemble mean under-predicted NEP relative to the observations by 69% (Figure 4-2b,d,f; Table C-6).
We found that the model was able to capture patterns in forest basal area growth when compared to the CAFI across a climate gradient within central Alaska (Figure 4-3). For aspen trees in both monoculture and mixed stand categories, the combined ensemble and category mean came within 10% of the observed category mean basal area growth and the range in simulated basal area fell within the range of observations (Table C-6; Figure 4-3a,c,e). In the black spruce monocultures, the combined ensemble and category mean came within 5.5% of the observed category mean and the simulated range in basal area generated by the different ensembles was nearly identical to the CAFI range (Figure 4-3b,d; Table C-6). However, in the
mixed stand category, the model over-predicted black spruce basal area growth by an average of 45.3% (Table C-6, Figure 4-3f).

When compared to the century-long chronosequences in central Canada, the simulated ensemble mean captured initial forest growth and maximum basal area and LAI for both black spruce and aspen forests (Figure 4-4; Figure 4-5). In the black spruce forests near Thompson, Manitoba, the average percent error between the simulated ensemble mean and measured LAI and basal area was 4.5% and 26%, respectively (Figure 4-4a-b; Table C-6). In this particular simulation set, the maximum black spruce forest basal area was controlled by the nitrogen availability and ensemble members with a lower nitrogen leaching efficiency simulated forest basal area values within 13% of the observations (Figure 4-4b). After 150 years, we found that the simulated spruce forests accumulated an average of 5.36 kg C m$^{-2}$ in the soil organic layer, well within the observed range of ~1.8 – 12 kg C m$^{-2}$ (Harden et al., 2012). In Saskatchewan, the average percent error between the simulated ensemble mean and observed basal area in the old black spruce forest was 4.2% (Figure 4-4c; Table C-6). In the 53-year-old aspen forest in Manitoba, the simulated ensemble mean came within 0.4% and 21.2% of the observed basal area and LAI, respectively (Figure 4-5a-b; Table C-6). Finally, in the 67-year-old aspen forest in Saskatchewan, the simulated ensemble mean came within 0.7% and 1.5% of the observed basal area and LAI, respectively (Figure 4-5c-d; Table C-6).
In the Clay Belt region of Quebec, the model was able to reproduce the distinct growth response of black spruce in different fire disturbance scenarios (Figure 4-6). Here, the difference in simulated forest growth was due mainly to changes in spruce seedling establishment. In the mild burn chronosequence (Figure 4-6a-b), the average percent error between the simulated
ensemble mean and observed basal area and organic layer thickness was 32% and 10%, respectively (Figure 4-6a-b; Table C-6). The ensemble mean and almost all of the ensemble members fell well within the upper and lower decile bounds of the observed basal area (Figure 4-6a) and all ensemble members fell within the bounds of observed organic layer depths (Figure 4-6b).
Figure 4-4: Comparison of simulated and observed black spruce basal area (BA) and leaf area index (LAI) growth in central Canada. For BA and LAI, simulated ensemble members are indicated in grey, the ensemble mean is indicated in black, and measured forest chronosequence points are indicated in red. Error bars, available for only a subset of the observations, indicate the upper and lower decile bounds of the observations. Measurements of LAI and BA were taken in the BOREAS Northern Study Area near Thompson, Manitoba (a-b) and the BOREAS Southern Study Area near Prince Albert (c).

In the moderately burned Quebec chronosequence, the average percent error between the simulated ensemble mean and observed basal area and organic layer thickness was 40.4% and 17.5%, respectively. The high percent error in basal area growth was due to an under-prediction of the initial forest growth rate (Figure 4-6c) such that the ensemble mean underestimated forest basal area in the first 100 years (Figure 4-6c). This could be due to uncertainty in the initial organic layer depth at the beginning of the chronosequence; an initial overestimation of the
organic layer thickness in our simulation would have decreased the black spruce basal accumulation rate in the first 100 years. However, around year 90, the simulated ensemble mean fell within the observed basal area range and after year 100, the ensemble mean and the majority of ensemble members fell within the observational range (Figure 4-6c). All ensemble members fell within the upper and lower decile bounds of observed organic layer depths in the moderately burned Quebec chronosequence (Figure 4-6d).

The overall range of uncertainty depicted by the different ensemble members was large in all of the forest chronosequences. For example, in the moderately burned Quebec chronosequence, individual ensemble members ranged from 6.0 to 45.4 m² ha⁻¹ in basal area after 365 years. A similarly large spread was observed in many of the other basal area and LAI
chronosequence validations in Table C-6 despite the good agreement between the ensemble mean and the observations. Interestingly, the percent range in simulated organic layer depth chronosequences was much smaller than the percent range in aboveground forest growth metrics (Table C-6). The large range in basal area and LAI of individual ensemble members was due mainly to model sensitivity to the range of measured values for $V_{cmax}$ for both aspen and black spruce. The black spruce chronosequence in Manitoba was an exception; the maximum basal area and LAI were controlled mainly by the efficiency of nitrogen leaching. Uncertainty in the maximum seedling mortality rate of black spruce trees had little effect in the central Canada chronosequence validations. However, in the longer chronosequence validations in Quebec, the maximum seedling mortality exerted control over the slope of the decline in basal area in older black spruce forests (Figure 4-6c).

4.4.2 Model experiments

4.4.2.1 Forest development after fire disturbance: interactions between fire severity, forest composition, and ecosystem carbon storage

In our model, simulated post-fire soil organic layer thickness controlled secondary succession after a fire disturbance event such that a thick organic layer prohibited aspen from establishing and increased black spruce seedling mortality. In thin organic layers, the time to succession between aspen and black spruce was controlled by the temperature regime and the availability of nutrients. In cooler regions such as Alaska, a shorter growing season and less productivity during the early and late growing season resulted in a maximum aspen biomass fraction of less than 0.5 and a shorter period of aspen presence (Figure 4-7a). In contrast, the
longer growing season and increased precipitation in Manitoba and Quebec allowed for a longer duration of plant productivity and increased productivity during the early and late growing season. Increased growing season length and warmer summers favored aspen over black spruce growth, and resulted in a maximum aspen biomass fraction that was twice of that of Alaska (Figure 4-7b-c). However, because the total precipitation in Quebec was ~65% greater than in Manitoba, the simulated rate of nitrogen leaching was approximately ten times greater in Quebec. This difference in nitrogen regimes shifted the competitive balance between aspen and black spruce, resulting in a shorter period of aspen dominance in Quebec relative to Manitoba (Figure 4-7b-c). When nitrogen leaching was excluded from the Quebec site, the period of aspen dominance became comparable to that of Manitoba.
Burn severity also had implications for total ecosystem carbon storage. Because simulations in the burn-severe experiment started out with very little residual soil organic layer, the difference in total ecosystem carbon between burn-severe (Figure 4-7d-f) and burn-mild (Figure 4-7g-i) was initially large. However, rapid secondary succession in the burn-severe simulation resulted in significant carbon accumulation during the first 350 years post-disturbance (Figure 4-7d-f). In the burn-mild simulations (Figure 4-7g-i), the initial ecosystem carbon was high due to a significant amount of soil carbon, but subsequent carbon accumulation was minimal or slightly negative due to low aboveground productivity and litter inputs into the soil organic layer. Despite the decreased aboveground productivity and litter inputs, some soil carbon lost through decomposition was compensated for through moss growth. Independent of initial soil organic layer depth, older forests (> 350 years) converged into unproductive black spruce stands with roughly equivalent rates in organic layer accumulation constrained mainly by moss biomass accumulation (Figure 4-7d-i). The range in the amount of carbon accumulated after 500 years between ensemble pairs was large in some cases. This variation was dependent mainly on model sensitivity to parameter values used for $V_{cmax}$.

4.4.2.2 Direct effects of soil organic layer on forest growth ecosystem carbon

We used six sets of simulations to disaggregate the biological and physical effects of the soil organic layer on forest structure and total ecosystem carbon in a forest developing after a mild burn. Because we expected that a thicker soil organic layer would affect forest outcome more strongly than a thinner soil organic layer, we adopt a mild burn disturbance scenario in this experiment. First, we ran one experiment using our standard parameterization that included both
the dynamic organic layer and seedling mortality module (OLon-SMon). In this experiment, aspen trees were unable to grow owing to the thick soil organic layer (resulting in an aspen biomass fraction of zero) and slow ecosystem carbon accumulation owing to few litter inputs but steady moss accumulation (Figure 4-8). In our next experiment, we turned off the dependence of seedling mortality on organic layer depth to remove the biological effect of the soil organic layer (OLon-SMoff). In our third experiment, we turned off both dependence of seedling mortality on organic layer depth and the dynamic organic layer to remove both the biological and physical effects of the soil organic layer (OLoff-SMoff).
When comparing the ensemble mean difference between OLoff-SMoff and OLon-SMon, we found that neglecting the biological effect of the organic layer resulted in an over-prediction of the presence of aspen in young forests in all locations (Figure 4-8a-c) and in total ecosystem
carbon throughout the simulation (Figure 4-8d-f, blue line). This occurred because a higher rate of seedling survivorship (and subsequently more litter inputs) but a more rapid organic matter decomposition in OLoff-SMoff partially compensated for the lower seedling survivorship but slower decomposition and moss accumulation in OLon-SMon.

We illustrated these errors by disaggregating the biological and physical effects of the soil organic layer in OLon-SMoff, an experiment that did not include the biological effect of the organic layer but did include the physical effects of the soil organic layer on soil temperature, moisture, and organic matter decomposition. When we compared the ensemble mean difference between OLon-SMoff and OLon-SMon after 300 years, we found that total ecosystem carbon was a factor of two greater in OLon-SMoff compared to OLon-SMon at all locations (Figure 4-8d-f). Total carbon accumulated much more rapidly in OLon-SMoff when compared to OLoff-SMoff because the dynamically accumulating soil organic layer in OLon-SMoff included increased soil insulation, which significantly decreased the temperature at which decomposition occurred.
Figure 4-8: Simulated biological and physical effects of the soil organic layer on forest growth and ecosystem carbon storage. Here we simulated sets of ensembles to separate out the biological and physical effects of the soil organic layer on forest growth and ecosystem carbon storage in forests developing after a mild burn with an initial soil organic layer depth of 60 cm. We simulated one group of ensembles with a fully dynamic soil organic layer and organic layer dependent seedling mortality (simulation OLon-SMon), one without the biological effect of the soil organic layer where we turned off organic layer dependent seedling mortality (OLon-SMoff), and one without both the physical and biological effect of the soil organic layer where we turned off dynamically accumulating soil organic layer and organic layer dependent seedling mortality (OLoff-SMoff), further eliminating the impact of the soil organic layer on the soil thermal and moisture regimes. The left column (a-c) shows the change (either OLon-SMoff – OLon-SMon or Oloff-SMoff – OLon-SMon) in the ratio of aspen biomass to total plant biomass (aspen plus black spruce). The center column (d-f) shows the change in total ecosystem carbon. The right column (g-i) shows the change in total ecosystem carbon expected with a 4°C mean temperature increase. Individual ensemble members are shown with thin, light lines and the ensemble mean is shown with a thicker, darker line. All simulations were performed for locations near Delta Junction, Alaska (a,d,g), near Thompson, Manitoba (b,e), and near Abitibi, Quebec (c,f,i) for a 300-year forest lifetime.
In our next three sets of simulations, we compounded the effect of a 4°C mean increase in temperature with our experiments examining the biological and physical effects of the soil organic layer. This set of experiments was designated as OLon-SMon-warm, OLon-SMoff-warm, and OLOff-SMoff-warm. Interestingly, compared to the suite of similar experiments without warming, we found a slightly negative ensemble mean difference in total ecosystem carbon storage between OLOff-SMoff-warm and OLon-SMon-warm in Quebec and Manitoba (Figure 4-8g-i) due to the more rapid rate of soil organic matter decomposition in OLOff-SMoff-warm relative to OLon-SMon-warm. When compared to Figure 4-8d-f, in Figure 4-8g-i, we simulated a decreased biological effect of the soil organic layer because more rapid organic layer decomposition decreased the depth of the organic layer rapidly.

4.4.2.3 Effects of projected warming

In the T-2Cwarm and T-4Cwarm experiments, we found that an increase in the mean temperature changed forest composition in Alaska and Manitoba and ecosystem carbon accumulation at all locations. However, the magnitude and sign of the effect was location specific and depended on the age of the forest. In Alaska and Manitoba, increased temperature increased the period of aspen dominance relative to T-0Cwarm (Figure 4-9a-b). This was due to two factors. First, increased temperature resulted in a longer growing season with increased productivity during the growing season (Figure 4-9g-i). Second, warmer temperatures increased the rate of nitrogen cycling between T-0Cwarm and T-4Cwarm thereby increasing mineralized soil nitrogen. As a result, aspen were able to grow and prevent black spruce seedlings from recruiting into the canopy for a longer period. In Alaska, the maximum aspen biomass fraction
increased by ~0.4 in the T-4Cwarm experiment relative to T-0Cwarm and the period of aspen dominance increased from 0 to ~100 years (Figure 4-9a). However, because the growing season was still relatively short despite warming, black spruce recruitment was not fully inhibited and the forest eventually underwent succession to black spruce. In contrast, in the T-4Cwarm experiment in Manitoba, aspen productivity increased, particularly in the early spring (Figure 4-9h), to the point that it became difficult for black spruce to recruit seedlings and aspen produce multiple new cohorts. Depending on the value of $V_{cmax}$ used for aspen and black spruce in an ensemble member, succession to black spruce might not have occurred or was delayed significantly (Figure 4-9b). Despite increased temperatures and nitrogen availability, a thick soil organic layer in Quebec prevented aspen from recruiting and black spruce perennially dominated (Figure 4-9c).
Simulated changes in forest composition with warming resulted in an initial (slight) increase in ecosystem carbon storage relative to T-0Cwarm in younger forests in Alaska and Manitoba due to increased aspen productivity (Figure 4-9d-e). No increase in storage was simulated in the spruce forests in Quebec (Figure 4-9f). After ~100 years, there was a decrease in
ecosystem carbon storage relative to T-0Cwarm at all locations due to slower soil carbon accumulation. The decrease in carbon storage in older forests was caused by increased temperature-dependent decomposition, and, to varying degrees, increased aspen litter inputs which decomposed more rapidly than black spruce litter and which also prevented moss carbon accumulation. These factors resulted in warmer soils (due to less insulation from a thinner soil organic layer) and faster organic matter decomposition. Particularly large losses in ecosystem carbon storage, on the order of 40%, were seen in Manitoba in T-4Cwarm due to the persistence of multiple cohorts of aspen (Figure 4-9e). In contrast, in Alaska and Quebec the simulated drop in ecosystem carbon between the T-0Cwarm and T-4Cwarm was <15% because black spruce was still able to recruit in the first century of forest growth.

4.4.2.4 Effects of changing nitrogen deposition rates

In our simulations, increased nitrogen deposition increased the period of aspen dominance in Manitoba (Figure 4-10b) and Alaska (Figure 4-10a). Interestingly, the effect of increasing nitrogen had a nonlinear effect on total ecosystem carbon accumulation in older forests depending on the location (Figure 4-10c-d). In Alaska and Manitoba, increased nitrogen deposition increased the productivity and carbon accumulation in young forests. However, in Manitoba, increased persistence of multiple aspen cohorts due to increased nitrogen availability resulted in a decreased ability to accumulate carbon in older forests relative to Alaska. In Quebec, nitrogen deposition had no effect on forest growth or carbon accumulation because the forest was not nitrogen limited as a result of the thick soil organic layer, underlying clay mineral soil, and low nitrogen demand of black spruce trees.
4.4.2.5. **Effects of atmospheric CO$_2$ fertilization**

We found that an increase in atmospheric CO$_2$ from 370 ppm to 1000 ppm changed forest composition in Alaska and Manitoba and increased ecosystem carbon accumulation at all locations. In Alaska and Manitoba, increased atmospheric CO$_2$ initially had a small positive effect on the aspen biomass fraction due to increased productivity from CO$_2$ fertilization (Figure 4-10): Simulated effects of increasing atmospheric CO$_2$ on forest growth and ecosystem carbon storage for forests developing in the 21$^{st}$ century. Here we show the effects of an increase in atmospheric CO$_2$ from 370 ppm to 1000 ppm. The left column (a-c) shows change (simulations CO2-1000 – CO2-370) in ratio of aspen biomass to total plant biomass (aspen plus black spruce). The right column (d-f) shows change in total ecosystem carbon. Individual ensemble members are shown with thin, light lines and the ensemble mean is shown with a thicker, dark line. Simulations were performed for locations near Delta Junction, Alaska (a,d), near Thompson, Manitoba (b,e), and near Abitibi, Quebec (c,f) over a 300-year forest lifetime.
4-11a-b). This positive effect on aspen growth was followed by a stronger negative effect due to progressive nitrogen limitation (Figure 4-11a-b). No aspen growth was simulated in Quebec as a result of the prohibitively thick soil organic layer (Figure 4-11c). At all locations, we simulated increased aboveground growth and litter inputs, which resulted in an increase in carbon accumulation by a factor of 2 or more after 300 years in experiment CO2-1000 relative to CO2-370.
Figure 4-11: Simulated effects of increasing atmospheric CO$_2$ on forest growth and ecosystem carbon storage for forests developing in the 21st century. Here we show the effects of an increase in atmospheric CO$_2$ from 370 ppm to 1000 ppm. The left column (a-c) shows change (simulations CO2-1000 – CO2-370) in ratio of aspen biomass to total plant biomass (aspen plus black spruce). The right column (d-f) shows change in total ecosystem carbon. Individual ensemble members are shown with thin, light lines and the ensemble mean is shown with a thicker, dark line. Simulations were performed for locations near Delta Junction, Alaska (a,d), near Thompson, Manitoba (b,e), and near Abitibi, Quebec (c,f) over a 300-year forest lifetime.
4.4.3 Regional Simulations

4.4.3.1 Relative importance of competition, precipitation, vapor pressure deficit, and temperature to forest growth

We found that the relative importance of forest basal area, midsummer precipitation, midsummer VPD, and spring temperature varied by species and that the model was able to capture this variation (Figure 4-12). In particular, different gymnosperm species seemed to be affected by distinct climate and competition drivers: the relative importance of precipitation was largest for black spruce growth, the relative importance of competition was largest for white spruce, and the relative importance of temperature was largest for jack pine (Figure 4-12). We performed several sets of simulations to determine whether ecophysiological traits were responsible for the
observed and simulated difference in relative importance among gymnosperm species, including varying tree hydraulic parameters, maximum photosynthetic capacity, and trait swapping between black spruce and white spruce PFTs. The trait manipulations had a relatively small effect on the relative importance of climate and competition on black spruce growth (Figure C-1), indicating that the differences in relative importance between gymnosperm species were predominantly due to environmental forcing not ecophysiological traits. Specifically, black spruce forest growth was highest in central Alberta where the midsummer precipitation rate was highest (Figure 4-13). Jack pine was most prevalent along the border of the northern Rocky Mountains, resulting in cooler temperatures throughout much of the jack pine range. White spruce stands had a higher basal area and were prevalent throughout the inventory, increasing the
relative importance of competition to white spruce growth. For the aspen/angiosperm PFT, both competition and temperature, followed by VPD, were important. However, the distribution of and growth of aspen stands was most correlated with higher burn frequency in the northern part of the Province (Parisien et al., 2006).

Additionally, the mechanistic hydraulic model using the trait-based hydraulic scheme minimized the root mean square difference between observed and predicted growth rates when compared to the empirical model (Figure 4-14). Further, the mechanistic hydraulic model outperformed the empirical model in predicting the relative importance of all competition and
climate drivers compared to the Alberta forest inventory 70% of the time (Table C-7). Compared to the Alaska inventory, the mechanistic hydraulic model outperformed the empirical model in assigning the relative importance of VPD for all PFT groups and temperature for three out of four PFT groups, but performed worse in assigning the relative importance of basal area in all instances and precipitation in three out of four instances (Table C-7). Predictions for tree growth from the mechanistic hydraulic scheme had a slightly lower correlation coefficient with the observed growth rates compared with predictions from the empirical hydraulic scheme (Figure 4-14).
Regional differences

We found noticeable differences in the relative importance of climate and competition within species between Alaska (Figure 4-15) and Alberta (Figure 4-12). In particular, the relative importance of competition was minimal in Alaska and the relative importance of VPD ranged between 20-60%, in contrast to Alberta where the relative importance of competition was > 60% for both angiosperm and gymnosperm and the relative importance of VPD was minimal. Despite

4.4.3.2 Regional differences

We found noticeable differences in the relative importance of climate and competition within species between Alaska (Figure 4-15) and Alberta (Figure 4-12). In particular, the relative importance of competition was minimal in Alaska and the relative importance of VPD ranged between 20-60%, in contrast to Alberta where the relative importance of competition was > 60% for both angiosperm and gymnosperm and the relative importance of VPD was minimal. Despite

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the wide ranging differences in topography and climate between Alaska and Alberta, the mechanistic hydraulic model did a reasonable job capturing the relative importance for the majority of species and drivers with the exception of under predicting the importance of competition for aspen/angiosperm in Alaska and over predicting the importance of competition for black spruce in both Alaska and Alberta (Figure 4-12; Figure 4-15).

4.4.3.3 Feedbacks between model hydraulic scheme and surface environmental conditions

Compared to the empirical soil water limitation scheme, the mechanistic trait-based water limitation scheme predicted significantly higher canopy vapor pressure deficit, significantly lower soil moisture, and a significantly higher Bowen ratio (Figure 4-16). The stronger water limitation predicted by the mechanistic hydraulic model resulted in growth constraints consistent with observations from the forest inventory (Figure 4-14), and better predicted the relative importance of key climate drivers (Figure 4-12; Figure 4-15)
Figure 4-16: Model hydraulic scheme impacts local environmental conditions and surface energy fluxes. Simulated model emergent (a) vapor pressure deficit, (b) soil moisture, and Bowen ratio (c) for the mechanistic hydraulic scheme (y-axis) versus the empirical water limitation scheme (x-axis). Black dashed line denotes the 1:1 line.
4.5 Discussion

The new model formulation presented here can inform Earth System Model (ESM) development in several ways. Most importantly, the species-specific effect of the soil organic layer on seedling recruitment and growth represents a critical step towards achieving an accurate North American boreal forest vegetation distribution as an emergent property of ESMs. We also find that the physical effects of the soil organic layer are important, and that our inclusion of a dynamic soil organic layer allows for a better simulation of the thermal and hydrological properties of the soil and the subsequent effects on decomposition and plant growth. Additionally, the new model formulation serves to improve the representation boreal of functional diversity in ESMs. Though it is not possible to include all individual NA boreal species in a global ESM, some species are sufficiently unique and important to warrant their own PFT. We argue that this is the case for black spruce, and maybe also for aspen because both are ecologically prevalent over a large geographic region in the NA boreal forest. Finally, our parameterization of moss growth, while empirical, highlights an important North American boreal ecosystem process that is neglected in many ESMs. Further implications and limitations of our analysis are discussed in the remainder of this section.

4.5.1 Uncertainty in model parameterizations

In this study, new modules related to soil organic matter accumulation and seedling mortality within ED2 were developed, parameterized, and tested against observations of NEP, inventory measurements of forest basal area, and chronosequences of forest basal area, LAI, soil
organic layer depth, and soil carbon. As our simulation results show, incorporation of key feedbacks between soil organic layer thickness and aboveground forest growth (Lecomte & Bergeron, 2005; Johnstone & Chapin, 2006b; Drobyshev et al., 2010; Johnstone et al., 2010; Lafleur et al., 2010; Lafleur et al., 2015b) within our new NA boreal forest model enabled us to capture observed patterns of ecosystem dynamics on seasonal to multi-century timescales in different fire disturbance regimes.

Though the overall effect of the soil organic layer on seedling establishment is robustly observed, there is some debate in the literature about possible regional variations in the feedbacks between soil organic layer thickness and aboveground forest growth. Greene et al. (2007) and Lafleur et al. (2015b) each found a different organic layer depth interval over which aspen and black spruce seedling mortality increased when compared to the Johnstone and Chapin (2006b). Additional measurements would be useful for model validations.

Moss has been shown to be an important component of the carbon balance in some boreal forests (Goulden & Crill, 1997). However, it is not included in many boreal forest models (Zhuang et al., 2002). Our model includes an empirical moss growth scheme based on a multi-century moss cover chronosequence. Our parameterization includes moss sensitivity to tree cover type (aspen versus black spruce), however our model was parameterized using data only from one region in eastern Quebec and we do not explicitly treat the short timescale responses of moss growth to temperature and moisture regimes (Williams & Flanagan, 1996). Therefore, our moss parameterization is not intended to represent interannual and shorter timescale variations in moss accumulation and should be further developed for other locations throughout the NA boreal
forest. Moss physiological models are an active area of research (Launiainen et al., 2015; Bona et al., 2016), and we plan to include these dynamics into ED2-boreal in the future.

Chronosequences, which we employed as space-for-time substitution, were useful for evaluating the model’s ability to simulate long-term forest growth. However, controlling for site-to-site variability in the chronosequences can be difficult (Bond-Lamberty et al., 2002b). Immediate post-fire forest conditions such as seedling density, soil nitrogen content, soil organic layer depth, and moss content were unknown. We handled this ambiguity by initializing all chronosequences for the same species-type (aspen or black spruce) with the same initial parameters, except in Quebec where data was available from which we could extrapolate the approximate initial soil organic layer depth. Given the uncertainty in the initial conditions of our simulations, uncertainty in model parameters, and uncertainty in the observations themselves, it is expected that some discrepancies would exist between simulated and observed forest growth (Table C-6).

We quantified the uncertainty associated with key model parameters by running ensembles composed of 20 members for each model validation and model experiment. These parameters included 2 parameters that the model is particularly sensitive to (Dietze et al., 2014) and two parameters that were important to our simulations but poorly constrained by experimental data. Each ensemble member featured a random draw from the joint prior probability density function defined from the literature or our own sensitivity tests (Table C-2) for leaf biomass accumulation, $V_{cmax}$, maximum seedling mortality fraction, and nitrogen leaching efficiency. We found that tree growth was most affected by the variation in $V_{cmax}$. The spread among ensemble members was large when simulating long-term forest growth.
Nevertheless, we found that the simulated ensemble mean did an overall realistic job of capturing forest basal area growth (Figure 4-4b-c; Figure 4-5a-c; Figure 4-6a-c), LAI (Figure 4-4a; Figure 4-5b,d), and soil organic layer accumulation (Figure 4-6b,d), as well as the age-related decline in LAI in older forests (Figure 4-4a; Figure 4-5b,d). Based on the model’s satisfactory performance against a diverse set of observations in multiple climate zones within the NA boreal forest, we argue that ED2-boreal is a useful tool in examining the ecosystem carbon budget in the NA boreal region.

4.5.2 Implications for forest composition

Over the next century, fire frequency, burn extent, and mean temperature are all projected to increase throughout the NA boreal forest (Kasischke & Turetsky, 2006; Girardin et al., 2013; Hinzman et al., 2013). The increase in fire activity will likely correspond with a decrease in mean organic layer depth in most of the NA boreal forest (Greene et al., 2007; Genet et al., 2013), an increase in aspen seedling survivorship and a decrease in the mean forest age (Kasischke & Turetsky, 2006). However, a decrease in the mean organic layer thickness is not likely to be uniform throughout the NA boreal forest due additional environmental factors. In the Clay Belt of Ontario and Quebec, all scenarios indicate that up to year 2100, low severity fires will be more common because paludification will likely be maintained under a warmer climate (Lafleur et al., 2015a). This will generate more stands with thick soil organic layers that have a low probability of burning at high severity due to the waterlogging, poorly drained clay soils and Sphagnum moss growth (Terrier et al., 2014).
In our simulations, increased mean temperature resulted in a longer growing season for deciduous forests with increased productivity during the growing season at all locations (Figure 4-9a-c). However, trends in growing season productivity were not uniform throughout the climate gradient. In Manitoba, increased productivity was particularly noticeable in the early spring (May), but marginal when compared to the current temperature regime throughout the rest of the growing season (Figure 4-9h). In contrast, in Alaska, productivity increased significantly throughout the entire growing season with warming temperature (Figure 4-9g). Recent work quantifying possible effects of future climate scenarios on forest management strategies in eastern Canada similarly found a slight increase in aspen productivity, but a distinct decline in black spruce growth with warming (Dhital et al., 2015). Our simulations showed only a marginal increase in black spruce productivity with warming in Quebec (Figure 4-9i), but this increase was significantly more pronounced in aspen forests in Alaska and Manitoba. In our simulations, younger forests with thinner post-fire soil organic layers and longer/warmer growing seasons with more rapid nitrogen cycling were heavily populated with aspen. This indicates the possibility of a shift in forest composition towards increased aspen presence that can prevent black spruce recruitment. Such a regime shift has been suggested as a possible future trajectory based on both paleoforest analysis and changing climate conditions (Edwards et al., 2005; Bonan, 2008). Interestingly, this shift to aspen dominance with changing climate seems to be more attributable to increasing temperature rather than CO₂ fertilization; we simulated that increasing CO₂ alone resulted in progressive nitrogen limitation (Liu et al., 2004) in aspen forests early on in during forest growth, ultimately resulting in a decline in aspen productivity (Figure 4-11a-c). This possible shift to more broadleaf-dominated forest cover has implications not only for soil carbon storage, but could also feed back into the climate system through
changes in energy partitioning between sensible and latent heat fluxes (Hogg et al., 2000) and changes in both summertime and wintertime surface albedo (Liu et al., 2005; Lyons et al., 2008), as well as reducing fire frequency and fire burn severity.

We also simulated significant diversity in regional responses to warmer temperatures, nitrogen limitation, and atmospheric CO2. A mean warming of 4°C had the potential to decrease recruitment of black spruce seedlings and shift forest composition so that multiple cohorts of aspen recruited in succession in Manitoba (Figure 4-9b). In Alaska, a shift to complete aspen dominance was not simulated in the 4°C warming scenario because the growing season remained sufficiently short and evergreen black spruce trees retained a competitive advantage against aspen trees. However, we did simulate an increased aspen presence in younger Alaskan forests (Figure 4-9a). With a fire return interval in Alaska of less than 100 years (Kasischke & Turetsky, 2006), a similar effect of persistent aspen presence could occur in Alaska, at least in the short term before the increased presence of aspen forest exerted a negative feedback on fire frequency.

In Quebec, our simulations indicated that black spruce forests were less sensitive to changes in atmospheric CO2, temperature, nitrogen, and fire activity than in western NA boreal forest. This difference was due to the robust presence of a thick soil organic layer projected to last throughout the 21st century (Terrier et al., 2014). The presence of this thick soil organic layer allowed for black spruce recruitment in the absence of competition with aspen even with warmer conditions. Interestingly, our simulations also indicated that nitrogen limitation strongly regulated aspen forest growth (Vadeboncoeur, 2010). This effect was particularly apparent in our atmospheric CO2 fertilization experiments where increased aspen productivity due to higher atmospheric CO2 was rapidly countered by progressive nitrogen limitation associated with the increased aspen nitrogen demand (Figure 4-11a-b).
Finally, both simulations and observations indicated that the relative importance of key climate drivers was distinct both between species within the same region (Figure 4-12) and within species between regions (Figure 4-12; Figure 4-15). This difference appears to be due predominantly to differences in environmental drivers rather than diversity in ecophysiological traits (Figure C-1). In particular, the drier climate of Alaska elicited a much stronger VPD response from a majority of species (Chapter 3) compared with Alberta where relatively warmer temperatures, higher moisture conditions, and a longer growing season supported a higher forest basal area and increased competition for resources. Though ED2-boreal can accurately predict forest growth and the relative importance of climate and competition given a mature forest distribution, more work is necessary to understand the mechanisms controlling emergent species distributions within the forest inventory.

4.5.3 Implications for ecosystem carbon budgets

In our severe burn experiment, total ecosystem carbon accumulated rapidly after succession from aspen to black spruce and before the ecosystem became an unproductive old black spruce forest (Figure 4-7d-f). These simulated middle-aged forests accumulated carbon at a rate of ~0.25 kg C m$^{-2}$ yr$^{-1}$. Using $^{14}$C dating, a previous study has reported water-logged black spruce stands accumulating 6-11 kg C m$^{-2}$ over the period from ~1960-1995 (~0.17-0.31 kg C m$^{-2}$ yr$^{-1}$) (Trumbore & Harden, 1997). In upland black spruce stands, soil carbon has been observed to accumulate more slowly (~0.086 kg C m$^{-2}$ yr$^{-1}$) but still at the same order of magnitude as our simulated accumulation rate (Trumbore & Harden, 1997). These accumulation rates are remarkably large. If scaled to the area of the circumpolar boreal forest ($1.2 \times 10^7$ km$^2$), the
resulting rate would be about 3 Pg C yr\(^{-1}\) with further CO\(_2\) fertilization over the 21\(^{st}\) century potentially increasing this rate, depending on ecosystem response to changes in climate and nitrogen availability (Figure 4-11d-f). This rate is comparable to the annual global carbon emissions resulting from the burning of fossil fuels (~9 Pg C yr\(^{-1}\)), underscoring the carbon mitigation potential of boreal forests.

However, our simulated ecosystem carbon accumulation should be interpreted as an upper bound for current boreal forest carbon accumulation potential for the following reasons. First, carbon accumulation rates slow with time since fire due to slower aboveground tree growth and fewer litter inputs (Figure 4-7d-i), making it difficult to integrate values simulated or measured at an individual site to an entire region because of the heterogeneous spatial extent of forest age. Second, the NA boreal forest contains species other than black spruce and aspen, many of which accumulate significantly less soil carbon than black spruce stands (Trumbore & Harden, 1997). Third, such an estimate does not include carbon released during forest disturbance events such as fire or insect attack which have the potential to change the behavior of the boreal forest from a carbon sink to a carbon source (Kurz \textit{et al.}, 2013). Fourth, an implicit assumption of static environmental conditions is made. However, climate and disturbance event frequency and severity are both projected to change rapidly in the NA boreal forest and will affect the boreal forest carbon balance (Kurz \textit{et al.}, 2013). Nevertheless, the impressive carbon storage capacity of middle-aged black spruce forests highlights the link between carbon management and forest management practices and emphasizes the need for proper forest management to preserve the NA boreal carbon sink with a changing fire cycle and warming temperatures in the 21\(^{st}\) century.
With increasing temperature, we simulated a shift to more broadleaf-dominant forests where aspen was able to recruit multiple cohorts and prevent black spruce seedlings from recruiting. Such a change in NA boreal forest successional dynamics has the potential to decrease ecosystem carbon storage through increasing litter decay rates and decreasing moss accumulation (Légaré et al., 2005; Laganière et al., 2010); the effect this shift would have on ecosystem carbon storage is dependent on the age of the forest. In warmer temperatures in younger forests (<100 years), we simulated that deciduous tree growth increased ecosystem carbon relative to black spruce growth due to increased aboveground productivity (Cavard et al., 2010). In contrast, we simulated older forests that transition from black spruce-dominated to deciduous stands lost approximately 40% of their carbon storage potential (Figure 4-7e-f; Figure 4-9e-f). This reduction occurred because aspen forests, as simulated, had less soil carbon accumulation due to more decomposable organic litter inputs, more rapid nitrogen cycling, and warmer soils that lacked insulating moss growth when compared to black spruce forests. However, recent work indicates that aspen forests tend to preserve more carbon than previously thought in deeper layers of the mineral soil due to fine root turnover and the relatively deep rooting system of aspen clones (Laganière et al., 2013). In addition to potentially increasing the amount of soil carbon thought to be associated with aspen stands, soil carbon residing deep within the mineral soil layer would be more resistant to decomposition with warming temperatures. Nevertheless, an increase in aspen cover would have a major impact on the soil thermal regime (Zhuang et al., 2002), and could potentially increase soil temperatures in the top 20 cm by up to 7°C (Jiang et al., 2015). Such a large temperature increase would significantly increase the rate of soil organic matter decomposition and carbon loss. In our experiments, we
found that an increase in soil temperature associated with loss of the soil and moss organic layer resulted in a decrease of ~15 - 20 kg C m$^{-2}$ at all locations (Figure 4-8d-f).

### 4.5.4 Implications for land-atmosphere feedbacks

In our simulations contrasting the mechanistic and empirical water limitation schemes within ED2-boreal, we found that a trait-driven representations of water limitation whereby leaf and stem water potential were simulated and used to solve for root zone water uptake, transport of water vertically through the sapwood, and transpiration of water into the atmosphere resulted in significantly drier soil and atmospheric conditions, constraining tree growth (Figure 4-14; Figure 4-16). Given that the majority of global terrestrial biosphere models represent water limitation empirically (Chapter 2), these results indicate that models may underestimate the extent to which growth is water limited under both current and future conditions.

### 4.5.5 Comparison to other boreal fire disturbance modeling studies

Other terrestrial ecosystem modeling studies have previously recognized the necessity of integrating feedbacks between fire disturbance and the soil organic layer to capture soil thermal, hydrological, and biogeochemical dynamics in boreal forest ecosystems (Zhuang et al., 2002; Carrasco et al., 2006; Yi et al., 2010). In work with a dynamic soil organic layer formulation of the Terrestrial Ecosystem Model (TEM), a new empirically parameterized moss layer and multiple soil carbon pools each with distinct porosity, bulk density, and decomposition rates are included (Zhuang et al., 2002; Carrasco et al., 2006; Yi et al., 2010). With this implementation
of TEM, Carrasco et al. (2006) and Yi et al. (2010) find that temperature and the soil thermal properties of the organic layer are important for preserving boreal forest soil carbon, citing a temperature gradient between surface and deep soils exceeding 10°C during the summer, which facilitates a 50 - 300% difference in mid-summer decomposition between surface and deep soils of similar recalcitrance. Bona et al. (2016) further include 6 moss sub pools divided into live, labile, and recalcitrant components for both feather and Sphagnum moss types with growth and decay rates empirically parameterized using various field sites throughout Canada. By including the moss submodel, Bona et al. (2016) find significant improvements in model-predicted soil carbon that are biased low by 40 Mg ha\(^{-1}\) when the moss submodel was not included. In ED2-boreal, we implement a comparable soil organic layer scheme, dividing the soil organic layer into an empirically parameterized moss layer and multiple soil carbon pools each with a different recalcitrance and bulk density. In our experiments, we similarly find that gradient in temperature between the surface and the base of soil organic layer can reach up to 15°C, doubling the temperature gradient between the surface and equivalent soil depth when compared to simulations with no insulating soil organic layer. Further, we find that the physical effect of the soil organic layer on the temperature of soil carbon decomposition results in approximately a 20 - 50% more carbon accumulation after 300 years when compared to simulations without the physical effect of the soil organic layer (Figure 4-8d-f, difference between red and blue curves).

With this implementation of ED2-boreal we found the biological effect of the soil organic layer on aboveground tree growth to also be important in projecting carbon storage capacity under warming temperatures because of the ability of the soil organic layer to mediate successional dynamics between early successional deciduous species and black spruce forests. Yue et al. (2013) similarly address boreal carbon dynamics after stand-replacing fire
disturbances using the terrestrial biosphere model ORCHIDEE at multiple NA boreal forest sites. Despite the lack of some important features in their model such as the physical and biological effects of the soil organic layer and species types other than black spruce, Yue et al. (2013) were roughly able to capture postfire forest carbon dynamics when errors were upscaled across multiple sites. We build on the work by Yue et al. (2013) by further examining post-fire successional dynamics between multiple forest species during different fire disturbance scenarios, and by capturing site-level carbon dynamics through our inclusion of interspecies competition and soil organic layer dynamics.

4.5.6 Limitations and areas for future work

The primary purpose of this study was to examine the terrestrial carbon accumulation dynamics in the NA boreal forest. We did this for three different climate regimes within the NA boreal forests and looked at how changes with fire regime, temperature, nitrogen availability, and atmospheric CO$_2$ might affect ecosystem carbon storage potential. To isolate fire, temperature, nutrient, and CO$_2$ effects, we chose to use a simple two-species system with only aspen and black spruce species-types. Though aspen and black spruce provide a reasonable and parsimonious representation of NA boreal forest species composition, they are not representative of the full species diversity present in the NA boreal forest which includes trees such as birch, jack pine, white spruce, balsam fir, tamarack, and alder, as well as various shrubs, graminoids, and mosses. Furthermore, our two-species set up does not allow for new species to migrate or replace aspen or black spruce as the dominant type of land cover. Rather, we are only able to examine the competitive dynamics between aspen and black spruce species-types with changes
in environmental forcing. Additionally, some observations indicate that a number of boreal species are able to uptake organic nitrogen, alleviating some of the nitrogen stress due to a lack of available mineralized nitrogen (Näsholm et al., 1998; Zhu & Zhuang, 2013). However, in the interest of parsimony, we did not include this process in our model. Finally, though we have extensively parameterized and tested our model with observations of near-surface soil organic layer processes in aspen and black spruce forests, our model has not been developed to capture dynamics of deep soil carbon formation and loss or the peat water-table feedback (Ise et al., 2008). Accounting for some or all of these processes may be important when projecting changes in the carbon storage capacity in the NA boreal zone with warming temperatures, receding permafrost, and changing moisture regimes.

Some of our parameterizations, especially those related to moss, remain predominantly empirical. We see our empirical parameterizations of as an intermediate step between “no representation” and “full mechanistic representation” in models.

We are also working to improve the representations of functional diversity and fire in ED2-boreal. Though it will not be possible to include all individual NA boreal species in a global ESM, it has become apparent the increased functional diversity over current levels in global models is necessary to accurately capture forest carbon dynamics (Pavlick et al., 2013; Fisher et al., 2015). We are currently carrying out modeling experiments of the NA boreal with increased numbers of plant functional types. We are also working on explicitly incorporating fire into our model. Multiple dynamic fire models with the necessary capabilities already exist (Pfeiffer et al., 2013), but it will be essential to evaluate model simulations of the interactions
between fire severity, fire return interval, and long-term forest nitrogen dynamics (Harden et al., 2002).

4.6 Conclusions

We implemented new seedling survivorship and organic layer accumulation modules within an existing terrestrial biosphere model, allowing us to simulate the interdependence of seedling growth on soil organic layer thickness and the effects that the soil organic layer has on soil thermal and moisture regimes. By incorporating this interdependence, we were able to accurately simulate observed forest growth, ecosystem-level carbon fluxes, and soil organic layer dynamics after different fire disturbance scenarios along a climate gradient within the NA boreal forest.

Our study simulated surprisingly rapid carbon accumulation rates in middle-aged black spruce forests. These simulated rates were similar to previously measured carbon accumulation rates in water-logged black spruce stands, indicating the strong atmospheric CO$_2$ mitigation potential of the boreal black spruce forests and underscoring the need for proper forest management practices moving into the 21st century to preserve the NA boreal carbon sink with changing climate and fire regimes. In addition, our simulations linked a decrease in carbon accumulation with warming to a transition in forest cover that was ~3 times greater than would be expected based on increased decomposition rates alone. Deciduous broadleaf forests, though initially more productive than evergreen needleleaf forests, did not promote surface organic layer accumulation in our model as a result of their decomposable litter inputs, lack of moss
accumulation, and warm soils, which resulted in a significant decrease in carbon accumulation potential over the forest’s lifetime. In contrast, evergreen needleleaf forests promoted significant surface organic layer accumulation in our model as a result of their slowly decomposing litter inputs, moss accumulation, and cool, moist soil conditions. This resulted in a ~40% decrease in forest carbon accumulation over a 300-year forest lifetime in boreal forests that recruited multiple cohorts of broadleaf trees compared to boreal forests that underwent succession to needleleaf trees. Interestingly, nitrogen limitation potentially acted to increase boreal forest carbon accumulation by promoting succession from aspen forests (relatively poor in soil carbon) to black spruce forests (relatively rich in soil carbon) rather than allowing persistent aspen dominance with warmer temperatures.

Currently, global terrestrial biosphere models feature generic broadleaf and evergreen species-types in the NA boreal region and do not fully incorporate the observed dynamics between aboveground forest composition and soil carbon accumulation. Regional models do incorporate some of the important processes to varying degrees, but have generally been run at a much smaller scale than the NA boreal forest. The new model feedbacks reported here have the potential to significantly improve projections of future carbon storage in the NA boreal forest when compared to previous model schemes because of the important link between carbon accumulation and forest cover. Continued assessment of the impacts that climate change will have on aboveground forest composition and soil organic layer accumulation using species-types specific to the NA boreal zone remains an important task for our understanding of short- and long-term behavior of the forest growth and terrestrial carbon dynamics in the boreal forest.
Chapter 5

5 Changes in fire-driven ecosystem carbon loss and tree-grass balance in Neotropical savannas and forests modulated by tree bark investment strategy

5.1 Abstract

Forest fragmentation and increasing drought occurrence resulting from global change has the potential to increase fire frequency in Neotropical savannas and forests. Such changes in fire regime and climate are hypothesized to decrease the stability of tropical carbon storage, but there has been little consideration for variability in tree fire tolerance strategies. To test how carbon stocks change with fire frequency and community composition, we update the ED2 model with (i) a fire survivorship module based on tree bark thickness (a key fire-tolerance trait), and (ii) plant functional types representative of trees found in Neotropical savannas and forests. When a growth tradeoff associated with bark investment is incorporated into the model, differential growth rates for savanna and forest trees are accurately predicted without further parameter adjustment. Observations of tree demography and ecosystem carbon are also accurately simulated. Simulations illustrate that the high survival rate of thick-barked, large trees is key in
the resistance of ecosystem carbon stocks to increasing fire at all levels of precipitation, but that bark investment particularly increases resistance at higher precipitation. Additionally, in landscapes that experience relatively frequent fire, tree bark investment strategy can broaden the range of climate and fire conditions under which savannas occur and reduce the range of conditions leading to zero tree cover. These results highlight that tropical carbon vulnerability depends not only on changing environmental drivers, but also on tree fire survival strategy. Critically, incorporation of a bark investment strategy in vegetation models holds promise for improving predictions of ecosystem-level carbon dynamics and tree-grass competition in the context of global anthropogenic climate change.

5.2 Introduction

Tropical savannas and forests are important components of the land carbon sink (Pan et al., 2011). However, the magnitude (Wright, 2013) and future changes in this sink are unclear due in part to projected increases in drought frequency and changes in fire regime (Malhi et al., 2008; Brando et al., 2014). Globally, tropical forests, savannas, and grasslands comprise ~60% of total terrestrial gross primary productivity (Beer et al., 2010), but are also responsible for over 65% of global carbon emissions stemming from fire and tropical deforestation (van der Werf et al., 2009; van der Werf et al., 2010). The balance between biological carbon uptake through photosynthesis and carbon emissions from respiration and biomass burning determine whether tropical savannas and forests are a net carbon sink or source (van der Werf et al., 2010; Ahlström et al., 2015).
Fire is particularly important in defining the vegetation structure and distribution of tropical savannas and forests (Bond et al., 2005; Staver et al., 2011a; Hoffmann et al., 2012b), with a dynamic positive feedback between fire and flammable grass presence in open canopies being an important mechanism in maintaining savanna regions (Archibald et al., 2009; Staver et al., 2011b; Hoffmann et al., 2012a). Some trees persist, despite high fire frequencies in many savannas, because they invest heavily in building thick bark (Pellegrini et al., 2017). Thick bark insulates the xylem and phloem from fire damage, increasing the probability of surviving a fire (Brando et al., 2012; Hoffmann et al., 2012b), and potentially decreasing ecosystem carbon vulnerability to increasing fire frequency with global climate change (Pellegrini et al., 2016b). However, this increase in bark investment comes at a growth cost in that thicker-barked species of savanna grow more slowly than thinner-barked forest species under similar growing conditions (Rossatto et al., 2009; Hoffmann et al., 2012b). Though many savanna trees have growth strategies that employ thick bark as a fire survival mechanism, species vary greatly in their investment in bark (Pausas, 2015; Rosell, 2016; Pellegrini et al., 2017).

Climate, particularly precipitation, has the potential to interact with fire frequency and tree growth strategy (Brando et al., 2014). In locations with low precipitation, tree growth rates are much slower than in locations with high precipitation (Baker et al., 2003). Slower growth rates result in a population of smaller trees with relatively thinner bark than their larger counterparts, making it more difficult for trees to grow and survive in high frequency fire regimes in dry regions. In addition to climate, physiology can play a role because some trees grow more rapidly than others due to differences in maximum photosynthetic capacity or specific leaf area (Rossatto et al., 2009). The resulting growth rate of the vegetation is critical for
determining the ability of trees to recover from fire, and consequently the fire frequency necessary to maintain savanna.

Simulating savanna vegetation dynamics is notoriously difficult, and many models fail to predict coexistence of trees and grasses over the broad geographic extents (Cramer et al., 2001; Bonan et al., 2003; Hely et al., 2006; Hickler et al., 2006; Schaphoff et al., 2006; Sato et al., 2007). Progress has recently been made in identifying some key mechanisms needed to stabilize savannas in dynamic global vegetation models (DGVMs) (Higgins et al., 2000; Scheiter & Higgins, 2009; Haverd et al., 2013; Baudena et al., 2015; Lasslop et al., 2016). However, DVGMs are still unable to fully capture global savanna extent as emergent features, generally over-predicting the scope of either grasslands or tropical forests (Cramer et al., 2001). This makes it difficult to quantify the impacts of projected climate change on tropical carbon storage because both carbon storage capacity and the resistance of ecosystem carbon to changes in precipitation and fire regime vary across tropical biomes. Consequently, additional mechanisms observed to be important for maintaining tree-grass coexistence, such as variability in tree fire survival strategy, still need to be incorporated in DVGMs.

To better understand the sensitivity of tropical carbon to changes in rainfall regime and fire frequency, we updated the Ecosystem Demography model 2 (ED2) to include distinct tropical savanna and forest plant functional types (PFT), each with a different bark investment strategy and considered two hypotheses. (1) Including bark investment as a tree fire survival strategy decreases projected Neotropical carbon vulnerability to increasing fire frequency with global change under all precipitation regimes due to the higher probability of survival for thicker-barked, larger trees, which comprise a substantial ecosystem carbon reservoir. (2)
Including bark thickness as a fire survival strategy expands the environmental conditions under which tree-grass coexistence is emergent by allowing for increased tree survival in frequently burned savannas. To test these hypotheses, we evaluated our model’s emergent dynamics against observations of savanna and forest tree growth rates, tree inventories, and total aboveground carbon (AGB) for different fire frequencies using field data from savannas and forests in the Cerrado region of Brazil. We then considered the effects of changing fire frequency and fire survival strategy on ecosystem structure and aboveground carbon vulnerability along a rainfall gradient in the Neotropics.

5.3 Materials and Methods

5.3.1 Model description

Our model simulations were carried out in a cohort-based terrestrial biosphere model, ED2. ED2 explicitly scales up tree-level competition for light, water, and nutrients to the ecosystem level (Medvigy et al., 2009; Medvigy & Moorcroft, 2012). One novel aspect of the version of ED2 used in this study is the mechanistic representation of water-limited photosynthesis whereby leaf and stem water potential are tracked and used to solve for root zone water uptake, transport of water vertically through the sapwood, and transpiration of water into the atmosphere (Xu et al., 2016). Variability in hydraulic traits such as turgor loss point, xylem water conductivity, and marginal water use efficiency determine PFT-specific responses to changes in leaf and stem water potential.
We have incorporated in ED2 the following new processes important to ecosystem fire resistance in the Neotropics: (1) updated tropical PFTs that include a PFT-specific bark investment strategy; (2) a carbon tradeoff between bark production and tree height, canopy area, sapwood area, rooting depth, and leaf carbon; (3) a fire survivorship function dependent on individual tree bark thickness; and (4) a dynamic feedback between tree size, survivorship probability, and grass biomass availability. Model codes are available upon request. Our two new PFTs represent a generic tropical forest tree PFT and tropical savanna tree PFT. Both are based on the tropical brevideciduous PFT from Xu et al. (2016). The brevideciduous PFT was chosen because its intermediate wood density and specific leaf area represent a drought survival strategy incorporating both drought avoidance and resistance. This intermediate strategy is utilized by a broad array of tropical tree species (Xu et al., 2016). The savanna and forest PFTs differ only in their bark investment strategy and the associated trade-offs. In the model, individual tree bark thickness is calculated according to the following equation (Thonicke et al., 2010):

\[ bt(PFT, \text{dbh}) = \beta(PFT) \times \text{dbh} . \]

Equation 5-1

In Equation 5-1, \( bt \) is tree bark thickness in cm, \( \beta \) is the bark thickness slope coefficient that varies with PFT, and \( \text{dbh} \) is tree diameter at breast height in cm. In the Cerrado, \( \beta \) ranges from \(-0.068 - 0.087\) for trees of the forest functional guild and from \(-0.087 - 0.142\) for trees of the savanna functional guild (Pellegrini et al., 2016a). We assigned \( \beta = 0.077 \) and \( \beta = 0.110 \) to our forest and savanna PFTs, respectively, based on the average of the observed ranges in bark thickness and simulation sensitivity tests.
The carbon cost of a tree investing in bark is incorporated through the tree allometric relations. Ordinarily in cohort- or individual-based models, tree diameter at breast height (dbh) is allometrically related to woody biomass, leaf biomass, crown height, crown area, rooting depth, and sapwood area. Our model also uses a standard dbh-woody biomass allometric relationship. However, our model relates the other derived properties to the dbh with bark excluded (denoted dbh’). Thus, for a given dbh, a PFT with a large $\beta$ will have a smaller dbh’, fewer leaves, a shorter height, a shallower rooting depth, a smaller crown, and a smaller sapwood area for water transport than a PFT with a small $\beta$.

The advantage of a tree having thicker bark is incorporated through our fire survivorship function. This function prescribes that trees with thicker bark are more likely to survive a fire event than trees with thinner bark. Thus, large trees and trees with a large $\beta$ at a given height are more likely to survive than small trees and trees with a small $\beta$. Survivorship is also dependent on the amount of grass biomass present. This grass dependence comports with observations that an abundance of grass biomass results in higher ecosystem flammability and hotter fires that cause increased tree mortality (Hoffmann et al., 2012a). These ideas are incorporated in the following equation based on Pellegrini et al. (2016a) derived from data in (Hoffmann et al., 2009):

$$\text{survivorship} = \begin{cases} 
\min(1, 0.618 \ast BT + 0.0383) & \text{for } g_b > 25 \\
\min(1, 0.602 \ast BT + 0.1484) & \text{for } g_b \leq 25
\end{cases}$$

Equation 5-2

In Equation 5-2, $\text{survivorship}$ is the tree survivorship fraction of a given tree size class and functional guild, $g_b$ is grass biomass (in g C m$^{-2}$), and 25 is the threshold for increased fire
intensity based on grass biomass curves of savanna flammability from Hoffmann et al. (2012a). We used the updated model to assess: (1) the accuracy of the bark investment-growth tradeoff when simulating differential emergent tree growth rates between savanna and forest functional guilds; (2) the joint effects of precipitation, fire disturbance, and bark investment strategy on tree demography and AGB; and (3) the impacts of bark investment strategy on the emergence of tree-grass coexistence.

5.3.2 Simulations

We conducted four classes of single-grid cell simulations designed to evaluate the influence of bark investment strategy on emergent vegetation dynamics across a rainfall and fire gradient in the Cerrado. In these simulations, the costs and benefits of bark were introduced factorially to evaluate the influence of each on model performance. First, we performed a control simulation that included C₄ grass and our updated savanna and forest PFTs, but no investment in bark or fire survival benefit (nBT). The second class of simulation included C₄ grass and our updated savanna and forest PFTs with a fire survival strategy based on bark investment but with no investment tradeoff (BT). The third class of simulation included C₄ grass and our updated savanna and forest PFTs with a bark investment tradeoff but no fire survival benefit (tradeoff). The fourth class of simulation included C₄ grass and our updated savanna and forest tree PFTs with a fire survival strategy and allometric tradeoffs based on bark investment (BT + tradeoff).

In our simulations, ecosystems were spun up from tree seedlings initialized at a density of 1.0 seedlings m⁻². C₄ grass was able to seed in at a rate of 0.001 kg C month⁻¹ m⁻². Simulations
were forced with 0.5°, 3-hourly meteorology from the Princeton Global Forcing dataset (Sheffield \textit{et al.}, 2006). To isolate the effects of precipitation and fire frequency, all simulations were forced with a constant 370 ppm atmospheric CO$_2$ and meteorology looped over the same 20-year period (1980-2000). Median fire frequency was prescribed at the beginning of a simulation and fire frequency varied stochastically within ± 3 years of the user input value. Fire disturbance occurred only once per year on January 1. The minimum fire return interval was constrained to one year, and the fraction of the landscape that burned was kept constant at 30% during a given fire event. Thus, there were no climate feedbacks on fire, and grass biomass only affected fire intensity (i.e. tree fire survival probability), but not the frequency or burned area fraction. Windthrow disturbance affected 1% of the landscape each year, resulting in 100% mortality of trees taller than 5 m and 20% mortality of trees smaller than 5 m.

5.3.3 Model Evaluation

We evaluated model performance using two levels of ecosystem measurements: (1) individual tree growth rates and (2) ecosystem-level tree size class inventories and AGB in patches of forests with different fire-disturbance histories (Table 5-1). The study sites were located in IBGE and the adjacent JBB Ecological Reserves within the Cerrado region of Brazil located at approximately 15.95° S and 47.85° W with a mean annual temperature of ~22.5 °C. At the study sites, mean annual precipitation (MAP) totals ~1460 mm with a distinct dry season from May to September. From the 1910s until reserve formation in the 1970s, the whole landscape was subject to frequent fire at ~2 year intervals (Pellegrini \textit{et al.}, 2014). Since reserve formation, the initiation of fire management strategies has provided a landscape with diverse
disturbance histories: fire return interval ranges from a few years in savannas to half a century in some adjacent forest patches (Pellegrini et al., 2014).

Table 5-1: Model evaluations at IBGE Ecological Reserve

<table>
<thead>
<tr>
<th>Metric</th>
<th>Fire frequency</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Annual diameter increments of twelve paired savanna and forest species</td>
<td>(1) No fire</td>
<td>Rossatto et al. (2009)</td>
</tr>
<tr>
<td>(2) Inventory tree size class</td>
<td>(1) 2-8, (2) 9-15, and (3) 57-63 years</td>
<td>Pellegrini et al. (2014) plots 3, 4-5, and 6</td>
</tr>
<tr>
<td>(3) Inventory above ground biomass</td>
<td>(1) 2-8, (2) 9-15, and (3) 57-63 years</td>
<td>Pellegrini et al. (2014) plots 3, 4-5, and 6</td>
</tr>
</tbody>
</table>

To evaluate whether the carbon cost of growing thicker bark results in a realistic tradeoff with tree growth in the model, we compared emergent annual diameter increments in a simulation where bark is fully represented ($BT + \text{tradeoff}$) without fire disturbance to annual diameter increments of twelve paired savanna and forest species measured over the years 2006-2007 (Rossatto et al., 2009). We performed a 35-year model spin up and then examined the range of average annual diameter increments of our savanna and forest PFTs over a 20-year period to the range of observed annual diameter increments. In our simulations, the dbh size classes included in the calculation for the savanna PFT ranged from 5-9 cm with a mean of ~7 cm and from 6-10 cm with a mean of ~8 cm for the forest PFT in accordance with the Rossatto et al. (2009) observations.
Next, we assessed the ability of the model to predict observed tree size class distributions and measurements of AGB at sites with different fire frequencies to evaluate if the updated model could more accurately capture ecosystem-level carbon dynamics and demography compared to the null model. We compared model simulations to inventories of trees with dbh > 2 cm along 200-300 m² transects made in July 2012 within the IBGE and JBB Ecological Reserves. Total AGB was calculated from diameter inventories using the allometric relations from Xu et al. (2016) and accounting for bark carbon investment assuming $\beta = 0.077$. We performed a 35-year model spin up in accordance with the disturbance history of the reserves after 1970 (Pellegrini et al., 2014) and then compared the range in simulated AGB over the next 10-year period in a simulation with bark fully included ($BT + \text{tradeoff}$) and a control simulation without bark investment ($nBT$) to observed AGB estimates and tree size class distributions. In our simulations, our high fire frequency scenario was forced with a fire return interval that ranged from 2-8 years, our intermediate fire frequency scenario was forced with a return interval that ranged from 9-15 years, and our low fire frequency scenario was forced with a return interval that ranged from 57-63 years, in accordance with the disturbance regimes of Pellegrini et al. (2014) plots 3, 4-5, and 6, respectively.

5.3.4 Model Experiments

To assess the outcome of including bark investment as a fire survival strategy on carbon vulnerability and tree-grass coexistence, we conducted experiments along a rainfall gradient within the Cerrado, one with a low MAP of ~820 mm, one with an intermediate MAP of ~1150 mm, and one with a high MAP of ~1660 mm. At each location, we included factorial simulations
with bark fully included \((BT + \text{tradeoff})\), with only the fire survivorship benefit of bark \((BT)\), with only the growth tradeoff associated with bark \((\text{tradeoff})\), and with no bark benefit or tradeoff \((nBT)\) at four forced fire return intervals ranging from 1-6, 5-11, 9-15, and 22-28 years. Additionally, we included a control simulation with no fire (Table 5-2). For each simulation, we performed a 100-year model spin up from seedlings and then analyzed the subsequent 20-year average total AGB, AGB by tree size, and tree crown area fraction. Tree crown area fraction ranged from zero, corresponding to open grassland, to one, corresponding to closed canopy forest. Savanna regions were defined as regions having a crown area fraction of 0.2-0.8.

### Table 5-2: Model experiments along a rainfall gradient

<table>
<thead>
<tr>
<th>Precipitation gradient (lat/lon)</th>
<th>Simulated fire frequency at each location</th>
<th>Experiments at each fire frequency</th>
<th>Ecosystem metrics from each experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) 820 mm (-15.25/-42.25);</td>
<td>(1) 1-6 years</td>
<td>(1) nBT: no bark benefit or cost</td>
<td>(1) Total AGB</td>
</tr>
<tr>
<td>(2) 1150 mm (-18.25/-44.25);</td>
<td>(2) 5-11 years</td>
<td>(2) BT: bark benefit but no cost</td>
<td>(2) AGB by size class</td>
</tr>
<tr>
<td>(3) 1660 mm (-22.25/-46.25)</td>
<td>(3) 9-12 years</td>
<td>(3) tradeoff: bark cost but no benefit</td>
<td>(3) Tree crown area fraction</td>
</tr>
<tr>
<td>(4) 22-28 years</td>
<td></td>
<td>(4) BT + tradeoff: bark benefit and cost</td>
<td></td>
</tr>
<tr>
<td>(5) no fire</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 5-1: Observed and model-simulated tree diameter at breast height (dbh) size class distributions under (a) high, (b) intermediate, and (c) low frequency fire regimes. Model simulations included a 35-year model spin up in accordance with the disturbance history of the observations (Pellegrini et al., 2014). Simulated tree size was compared over the subsequent 10-year period for the following models: bark fully included ($BT + trade$) and no bark benefit or tradeoff ($nBT$). The red line denotes the median tree size, the blue box denotes the interquartile range, and the dotted error bars denote $\pm 2.7\sigma$. 
5.4 Results

5.4.1 Agreement between emergent tree growth in simulations and observations

Simulated growth rates for both the savanna and forest PFTs fell well within the observed range for Cerrado species when the allometric growth tradeoff with bark thickness was included (Figure D-1). The median growth rate for the savanna PFT was < 0.1% different from the observed median savanna species growth rate (Figure D-1a). Additionally, both observed and simulated savanna species had similar minimum diameter increments. However, the model did not capture the upper limit of faster growing savanna species. The model overestimated the median growth rate for the forest species by ~23%, but could capture a wide range of the variability in growth rates seen in the observations (Figure D-1b). Further, the interquartile range of observed and simulated diameter increments overlapped broadly.

Including a bark investment strategy in the model resulted in higher fire survival of large trees compared to small and intermediate-sized trees during a fire event. For higher fire frequencies, simulations where bark was fully represented \((BT + \text{tradeoff})\) better estimated the observed maximum tree size compared to the original model \((nBT)\) (Figure 5-1). Further, at high fire frequencies, simulations where bark was fully represented \((BT + \text{tradeoff})\) had the smallest percent difference in predictions of the median size class (23.0% compared to 25.9% for \(nBT\)) (Figure 5-1a). At intermediate fire frequencies, simulations where bark was fully represented \((BT + \text{tradeoff})\) also had the smallest percent difference in predictions of the median size class (27.0% compared to 51.7% for \(nBT\)) (Figure 5-1b). For low fire frequencies, including a bark investment strategy \((BT + \text{tradeoff})\) did not improve predictions of maximum tree size, however
a better prediction for median tree size was achieved (38.6% for BT + tradeoff compared to 44.1% for nBT) (Figure 5-1c).

Size-specific survivorship affected predictions of ecosystem AGB under different fire frequencies. At high fire frequencies, simulations where bark was fully represented (BT + tradeoff) captured the observed AGB within its predicted range and had the lower percent error between simulated mean AGB and observed (an overestimation by 36.2% compared to an underestimation by 38.8% for nBT) (Figure 5-2a). Under intermediate fire frequencies, simulations where bark was fully represented (BT + tradeoff) overestimated mean AGB by 0.8%, and the observed AGB was fully within the simulated interquartile range, whereas the original model (nBT) underestimated mean AGB by 20.2% and did not capture the observed AGB within the range of predicted values (Figure 5-2b). At low frequency fire, the original model (nBT) predicted the observed AGB marginally more accurately than the model where bark was fully represented (BT + tradeoff) (percent errors of +4% and -6.7%, respectively) (Figure 5-2c).
Figure 5-2: Observed (Obs) and model-simulated above ground biomass (AGB) under (a) high, (b) intermediate, and (c) low frequency fire regimes. Model simulations included a 35-year model spin up in accordance with the disturbance history of the observations (Pellegrini et al., 2014). Simulated AGB was compared over the subsequent 10-year period for the following models: bark fully included (BT + trade) and no bark benefit or tradeoff (nBT). The red line denotes the median AGB, the blue box denotes the interquartile range, and the dotted error bars denote ± 2.7σ.
5.4.2 Bark investment increases carbon resistance at high fire frequencies

We found striking differences in the fraction of AGB present in different tree size classes between the original model ($nBT$) and the model where bark was fully represented ($BT + tradeoff$) at high to intermediate fire frequencies and for intermediate to high levels of MAP (Figure 5-3; Figure D-2). While the original model without a bark investment strategy ($nBT$) and the model with only the growth tradeoff associated with bark investment ($tradeoff$) predicted the presence of substantially more small and intermediate-sized trees, both the model where bark was fully represented ($BT + tradeoff$) and the model with bark but no growth tradeoff ($BT$) predicted almost no biomass in the smaller tree size classes (Figure 5-3a and to a lesser extent Figure 5-3c,e; Figure D-2b,c) This was due to the much lower probability of mortality during a fire disturbance for larger trees owing to the fire survival strategy and the relationship between tree size and bark thickness (Equation 5-1). As would be expected, the difference in tree size distributions between $nBT$, $tradeoff$, $BT$, and $BT + tradeoff$ decreased substantially when fire disturbance was eliminated (Figure 5-3b,d,f).
We also found that the tree size was largely unaffected by MAP when simulations were forced with frequent fire in both simulations where bark was fully represented ($BT + tradeoff$) and simulations with bark but no growth tradeoff ($BT$) (Figure 5-3a,c,e), and only minor impacts were found at intermediate fire frequency and high MAP (Figure D-2c). In contrast, small size
classes were prevalent, particularly at low MAP, for high frequency fire simulations using the original model without bark investment \((nBT)\) and the model with only the growth tradeoff associated with bark investment \((tradeoff)\) (Figure 5-3a,c,e).

Incorporating bark thickness decreased predicted carbon losses with increasing fire frequency because larger, thick-barked trees made up the majority of AGB and had a very low probability of mortality during a fire (Figure 5-4). When bark was fully represented \((BT + tradeoff)\), fire caused almost no reduction in biomass in the wettest site, (Figure 5-4a). When bark was not represented \((nBT)\), trees were highly vulnerable to fire, so burning at 3-year intervals resulted in a 73% reduction in biomass (Figure 5-4b). However, the difference in simulated carbon loss between \(nBT\) and \(BT + tradeoff\) decreased as MAP decreased. At an intermediate MAP, relative to a >40 year fire interval, a 3-year fire interval caused a 36% reduction in AGB when bark was fully represented \((BT + tradeoff)\) and an 81.2% reduction in AGB using the original model without bark investment \((nBT)\). At the driest site, a 3-year fire interval, relative to a >40 year fire interval, caused a 70% reduction in AGB in \(BT + tradeoff\) and a 76% reduction in AGB for \(nBT\).

There was a strong interaction between precipitation, fire, and bark investment strategy. When no bark investment strategy was included, both fire frequency and precipitation exerted an equivalently strong control on total AGB, and the range in AGB after 100 years of growth increased substantially with increasing precipitation depending on fire frequency (Figure 5-4b,d). However, when bark investment was included as a fire survival strategy, MAP exerted a much stronger control than fire on the total AGB (Figure 5-4a,c).
Figure 5-4: Model-simulated total above ground carbon (AGB) present at different MAP and forced fire regimes for the following models: (a) bark fully included (\(BT + \text{trade}\)), (b) no bark benefit or tradeoff (\(nBT\)), (c) only the fire survivorship benefit of bark (\(BT\)), (d) only the growth tradeoff associated with bark (\(\text{tradeoff}\)). Simulations were initialized with tropical tree and C\(_4\) grass plant functional types and included a 100-year model spin up from seedlings. The subsequent 20-year average AGB for each disturbance and precipitation regime is shown.
5.4.3 Environment and biological traits jointly affect simulated tree-grass coexistence

Both fire frequency and precipitation were important in maintaining tree-grass coexistence and controlling the distribution of grasslands, savannas, and tropical forests (Figure 5-5). At high fire frequencies and low precipitation, we simulated grasslands with minimal tree cover regardless of the model scheme (Figure 5-5a,c,e,g). At intermediate MAP we simulated savannas in both the original model with no bark investment strategy (nBT) and the model with bark fully incorporated (BT + tradeoff). However, at fire return intervals exceeding 5-11 years or at high MAP and more frequent fire, we simulate closed canopy forests in all but the model with bark fully incorporated (BT + tradeoff), where tree-grass coexistence was still observed (Figure 5-5 a-b). Thus, including bark investment as a fire survival strategy and a corresponding growth tradeoff affect the model’s ability to capture tree-grass coexistence as an emergent property (i) at high MAP (Figure 5-5 a) and (ii) at lower fire frequency (Figure 5-5 b). It is also apparent that both MAP and fire strongly affect the balance between tree and grass presence.

5.5 Discussion

Tree bark investment and the corresponding growth tradeoffs were critical for accurately modeling vegetation dynamics in savannas and forests. Furthermore, bark investment strategy interacted with precipitation and fire frequency to determine both (i) the stability of ecosystem carbon to fire and (ii) the coexistence of grasses and trees. The protection afforded by bark increased the stability of the substantial carbon stock in large trees, decreasing ecosystem carbon losses with increased fire frequency. This mechanism was especially critical in wetter savannas
and forests, illustrating that the distribution of functional traits is fundamental to the resilience of wet forests to increased fire and changing rainfall regimes.
5.5.1 Implications for carbon resistance

Our simulations provided evidence that tree bark thickness as a fire survival mechanism substantially decreases fire-driven carbon losses, however the magnitude of the effect is strongly dependent on precipitation regime (Figure 5-4a-b). We found that bark investment was particularly important at stabilizing ecosystem carbon at higher fire frequencies in locations with a high MAP where trees had ample water availability, enabling them to grow rapidly and decreasing the probability of fire mortality to near zero, even with the growth penalty associated with bark investment. In contrast, very little increase in carbon resistance with bark investment was seen at the lowest MAP and highest fire frequency because trees were not able to invest in bark and grow rapidly enough to escape fire mortality. Taken together, these results suggest that current models that do not account for bark thickness may under predict Neotropical carbon resistance to fire in both savannas and forests. Such models would over-predict mortality of large thick-barked trees that make up much of aboveground ecosystem biomass (Hanan et al., 2008; Slik et al., 2013). However, further work understanding the spatial distribution of tree species and their corresponding bark thickness traits is also critical (Dantas et al., 2013; Pausas, 2015; Rosell, 2016; Pellegrini et al., 2017), because observations show that most trees in wet forests have thin enough bark that they suffer substantial fire mortality, even at large size classes (Uhl & Kauffman, 1990).
5.5.2 Implications for tree-grass coexistence

Capturing savanna distributions globally has long been difficult for vegetation models, which over-predicted the extent of either tropical forests or grasslands (Cramer et al., 2001; Bonan et al., 2003; Hely et al., 2006; Hickler et al., 2006; Schaphoff et al., 2006; Sato et al., 2007). A number of recent studies have focused on this issue: the adaptive dynamic global vegetation model (aDGVM) was able to capture savanna extent in Africa by including (i) trees with a higher fire mortality rate in small tree size classes, (ii) regenerative tree resprouting after fire events, and (iii) grass as super individuals (Scheiter & Higgins, 2009). The individual-based Populations-Order-Physiology model also included size-dependent tree mortality and was able to reproduce key vegetation structure and function along a rainfall and fire gradient in Australia (Haverd et al., 2013). Studies by Baudena et al. (2015) and Lasslop et al. (2016) have proposed several key mechanisms for capturing savannas in models: (1) water limitation on tree growth, (2) competition for water between grasses and trees, and (3) a grass-fire feedback.

The results from this study showing a strong dependence of savannas on precipitation and fire frequency are in agreement with observations (Brando et al., 2014) and other modeling studies (Baudena et al., 2015). However, we also found additional potential to maintain tree-grass coexistence in wetter environments forced with frequent fire when a fire survival mechanism based on tree bark thickness was included. Thus, both environmental factors and species-specific bark thickness traits have the potential to affect tree and grass coexistence. In the broader context of the global carbon cycle, these results indicate that the interaction between the tree bark thickness traits and environmental conditions should be considered, particularly in mesic locations, to accurately capture savannas emergent ecosystems. Inclusion of the bark
thickness trait has the potential to substantially enhance our ability to accurately project changes in the tropical carbon sink with changes in fire and rainfall over the upcoming century.

5.5.3 Limitations and future work

Several avenues exist for future model improvement. Tree resprouting after fire has been shown to be essential in predicting the range of conditions for which tree-grass coexistence is possible (Higgins et al., 2000). Currently in our model, trees reproduce only through seedling recruitment. This has the potential to affect simulation outcomes because initial aboveground growth rates of resprouts are substantially higher compared to seedlings due to (a) access to belowground carbohydrate stores and (b) elimination of the need to allocate carbon for roots. Thus, resprouting may allow for better agreement between model predictions at higher growth rates and fire frequencies (Figure 5-1; Figure 5-2; Figure D-1). Enabling tree resprouting may also stabilize savannas under frequent fire and low precipitation where the model is currently simulating grasslands (Figure 5-5).

Additionally, the current fire model does not interact dynamically with climate or the nitrogen cycle. ED2 is capable of resolving nitrogen dynamics (Trugman et al., 2016) and we anticipate that coupling nitrogen and climate feedbacks to fire will be an important step in projecting future distributions of tropical biomes. Despite these current limitations, the updated model accurately predicts growth, demographics, and AGB. We believe that these results can provide important insight into tree-grass coexistence and carbon resistance with changing fire frequency in the Neotropics with global change.
5.6 Conclusions

Our results highlight that tropical carbon vulnerability depends not only on changing environmental drivers with global change, but also on tree fire survival strategy. Thus, both enhancing our understanding of the distribution of bark functional traits and incorporating this knowledge of bark investment into future vegetation models is important to improve projections of the tropical carbon sink with global climate change. Further, an increased understanding of the interaction between bark investment strategy and environmental drivers promises to increase our ability to project savannas distributions in regions previously simulated as grasslands through increased tree survival. Finally, these results motivate further work understanding the distribution of trees with different fire survival strategies, including both bark investment and resprouting, in future projections so that we can develop a better understanding of how diversity in fire survival strategies across tropical biomes affects ecosystem carbon vulnerability to changes in rainfall and fire regime with global climate change.
Chapter 6

6 Conclusions

Overall this thesis presents the case that diversity in plant functional strategy, in processes ranging from seedling recruitment strategy, to maximum photosynthetic capacity, vegetation hydraulic efficiency, nitrogen use, and fire survival strategy, significantly impacts the outcome of climate change on the terrestrial carbon cycle. From my research on the North American boreal forest, I have learned first that both competition and climate interact to influence forest dynamics and carbon accumulation. Second, because the growing season is short due to cool spring temperatures, warming has the potential to increase productivity. However, warmer temperatures can also increase the atmospheric moisture demand, resulting in decreased forest growth and increased mortality. Third, the complexity of species-specific responses to fire frequency, nitrogen limitation, climate, and insect disturbance makes it difficult to anticipate the net effect of changes in climate on boreal carbon accumulation. Specifically speaking to this complexity, I found that aspen, a typical early successional species expected to become more abundant in the future, is more sensitive to high VPD compared to other prominent boreal species (Chapter 3). However, warming temperatures increased the ability of aspen trees to recruit multiple cohorts (Chapter 4). Thus, it is unclear what the net effect of climate change will be on aspen growth. Fifth, though warming has the potential to increase vegetation productivity (Chapter 4), this can result in large declines in boreal carbon storage due to loss of soil carbon
associated with slow growing black spruce forests (Chapter 4). The net effect of these changes makes it difficult to predict the future carbon status of the North American boreal forest.

From a modeling perspective, I have found that both variability in traits and functional strategy can strongly impact carbon cycle projections (Chapter 5). However, in some cases environmental variability, rather than species-specific growth strategy is the main cause of differential importance of climate and competition (Chapter 4). Second, that representation of vegetation processes can feedback into the emergent environmental dynamics of the land surface by affecting the soil moisture, vapor pressure, and the Bowen ratio (Chapter 4). Third, I have highlighted that this vegetation hydraulic feedback is cause for concern when considering carbon cycle projections of global Earth system models because numerous models have not methodically considered how to represent vegetation physiology associated with plant water limitation.

Through this work, I have come to appreciate that understanding the ramifications of climate change on ecosystems globally is a gargantuan task, and I look forward to continuing to contribute to this effort in the future.
Appendix A

Supplement to Chapter 2

Supplementary Methods

S1. Validation of inversion approach for calculating soil water stress factor (β)

Several key assumptions were made in our calculation of β. First, the β values used in this study are not the β values used in the model projections, as β is not a standard model output. Instead, β was calculated via inversion using model output soil moisture, assumed root biomass curves (for all models except the MIROC model), assumed soil hydraulic parameters, and assumed soil moisture variability at a monthly time scale. However, for the CESM model only (model #5 in Table A-1), we output monthly-average β calculated online in the model. We used this information to assess whether our inversion approach to obtaining β is a reasonable proxy in estimating β strength and spatial distribution ca. 2000 and 2100.

We calculated three variations of inverted β as sensitivity tests to our assumptions of rooting depth and soil hydraulic parameters. Inversion 1 was calculated using the standard CESM β function (Function 4, Supplementary Note) and using spatially varying maps of Ψ_e in place of Ψ_o and Ψ_w in place of Ψ_c (Table A-2) to account for some spatial variability in hydraulic parameters, given that variability in parameters due to PFT distribution was unknown (see main methods section for additional details on the soil hydraulic datasets). Inversion 2 was calculated assuming shallow roots globally distributed in only the top soil layer, given that the globally
simulated root distribution was unknown. Inversion 3 was calculated using the standard CESM \( \beta \) function and the least negative, average, and most negative PFT specific water potential thresholds globally. We used global maps of \( \beta \) (Figure A-5) and calculated the Pearson’s correlation coefficients for all grid cells < 58 ° latitude (excluded due to dynamics associated with frozen soil layers), as one metric to assess the performance (Table A-3). Next, we look at the impact of the inversion approach on global estimates of constrained GPP (GPP\(_c\))(Figure A-6; Figure A-7).

We found that in using the inversion approach, we were able to capture both the spatial variability and strength of \( \beta \). However, the performance of the \( \beta \) inversion method depended somewhat on the soil hydraulic parameters used (Figure A-5). The calculated \( \beta \) using gridded soil hydraulic parameters (Inversion 1) and the calculated \( \beta \) using only the soil moisture of the top soil layer (Inversion 2) performed the best when compared to the model output beta (Table A-3, Figure A-5a-c). The ‘top soil’ model (Inversion 2) had a higher correlation coefficient and did a better job capturing the strong beta regulation in Northern Africa, the Middle East, Chile, and Northern South America. However, it predicted an overly strong (small) \( \beta \) in key locations of relatively high productivity (Figure A-6; Figure A-7). This resulted in a very large overestimate of GPP\(_c\) (Figure A-7b). Though the ‘spatially variable’ model (Inversion 1) had a slightly lower correlation coefficient and did not predict the \( \beta \) strength as well in the regions with a strong \( \beta \) compared to the ‘top soil’ model (Inversion 2), it did a much better job in projecting \( \beta \) in key regions of higher productivity, and correspondingly estimated GPP\(_c\) with a high accuracy (Figure A-7b).
Based on these results, we use Inversion 1 in our main analysis and calculated $\beta$ using gridded soil hydraulic parameters, replacing constant threshold parameters in Functions 1-7 (Supplementary Note) with spatial maps from the GSWP2. These substitutions are referenced in Table A-2. Overall, the results from this validation showed that a reasonable approximation of $\beta$ globally could be obtained based on the inversion approach. However, the average $\beta$ estimated using inversion represented an upper limit for the model output $\beta$ for CESM, indicating that the standard inversion approach underestimated realized drought stress in some locations, and thus provided a lower bound estimate of $GPP_c$. Importantly, this validation provided strong support for the idea that there is remarkable uncertainty in carbon cycle estimates when using an empirical soil moisture parameterization because simulated GPP is heavily regulated based on a non-mechanistic, untested function.

S2. Sensitivity of calculations to plant rooting depth, soil database, and soil hydraulic parameters

Both assumed root biomass curves and soil hydraulic parameters have the potential to impact estimates of $\beta$ and $GPP_c$. Though root biomass is sometimes available as a model output, $\beta$ depends on the fraction of root biomass available in each soil layer with depth, which is not routinely available. We used global maps of rooting depth at 1° resolution from the GSWP2 database (Dirmeyer et al., 2002). We calculated the root biomass fraction in each soil layer by fitting an established rooting depth curve (Jackson et al., 1996) to the 50% root biomass depth:

$$F = 1 - \beta_r^d.$$  

Equation A-1
In Equation A-1, \( d \) is depth, \( F \) is the proportion of roots up to depth \( d \) (0.5 in the case of our fitting procedure), and \( \beta_r \) is the fitted parameter dependent on rooting depth of the grid cell which determines how root biomass tapers with soil depth. Additionally, we performed sensitivity tests of our calculations of \( \text{GPP}_c \) using globally constant root distributions with \( \beta_r = 0.976 \), which corresponds to the deep roots of temperate conifers, and \( \beta_r = 0.943 \) which corresponds to shallow roots in boreal and agricultural systems (Jackson et al., 1996). We also looked at the sensitivity of \( \text{GPP}_c \) to soil database by downloading clay, sand, and organic matter fractions from Harmonized World Soil Database v1.2 (Wieder et al., 2014), and re-gridding the soil texture databases in the same manner as the CMIP5 model output. Using the soil texture databases, we calculated all hydraulic parameters based on the methods of Oleson et al. (2010). Finally, we examined the sensitivity of \( \text{GPP}_c \) to the use of constant soil hydraulic thresholds specified in the \( \beta \) Functions (Supplementary Note) compared this to the spatially varying thresholds from the GWSP2 database. Though there are some minor differences depending on our choice of rooting depth, soil database, and hydraulic parameters (Figure A-5; Figure A-6; Figure A-7; Figure A-8), the differences do not impact the major conclusions of our analysis.

S3. Sensitivity of calculations to the time scale of analysis

In this study, we focused on examining long-term trends in prevalence and magnitude of \( \beta \) use between historical and future projections rather than interannual variability in drought conditions. To avoid confounding signals of short-term variability in soil moisture, we computed an average monthly soil moisture from 1981-2000 and 2080-2099 for both the historical and RCP 8.5, respectively. In reality, plant water stress varies on the sub-daily scale and computing a
monthly average value could bias estimates due to nonlinearities when up-scaling from the sub-daily to monthly level. However, it has already been shown that $\beta$ is unable to capture observed short-term variations in plant water limitation (Powell et al., 2013). Additionally, a recent study of temporal variability in root zone soil moisture at subtropical and temperate forest sites found a soil moisture memory effect of 25-38 days observed across sites (Nakai et al., 2014), well in line with our monthly time-scale analysis of $\beta$. As a final justification of our use of monthly-level soil moisture data in our calculations of $\beta$ and $\text{GPP}_c$, we performed a site-level sensitivity test using a vegetation model, the Ecosystem Demography model 2 (ED2)(Medvigy et al., 2009).

S4. Site-level sensitivity test: quantifying the impacts of timescale on estimates of $\text{GPP}_c$

We ran a site-level experiment using ED2 to quantify potential biases in our monthly-level analysis of $\beta$. In ED2, we directly output $\beta$ at both the daily and monthly level. Detailed descriptions of the water limitation scheme in ED2 are available in the literature (Medvigy et al., 2009). We ran a simulation with an 80-year vegetation and soil moisture spin up in a relative dry location in Cerrado region of Brazil where mean annual precipitation was $\sim$800 mm yr$^{-1}$. This location was chosen with the reasoning that $\beta$ was likely to be used frequently to limit photosynthesis given the aridity of the region, thus highlighting any biases in our use of monthly-level calculations. In our analysis, we compared $\beta$ for 14 different years of meteorology. We output both monthly and daily mean $\beta$, calculated $\text{GPP}_c$, and integrated this value over the year to get the total annual $\text{GPP}_c$. We found that utilizing the monthly level $\beta$ positively biased our calculations of annual $\text{GPP}_c$ relative to the daily-level calculation with a median bias of +4.85%. Results ranged from 1.56-7.33% depending on the year. This analysis demonstrated that the
calculations we present using the monthly-level soil moisture can be interpreted as an upper bound for estimates of GPP\(_c\), but provide a reasonable first-order estimate given the small percent error between the daily and monthly-level values and previous literature on soil moisture memory and \(\beta\) temporal dynamics\(^2,3\).

**Supplementary Note**

*Soil moisture limitation functions in vegetation models*

All \(\beta\) functions range from one when the soil is wet to near zero when the soil is dry and depend on the soil water according to the following relationships. Parameter values are listed in Table A-2.

Function 1: \(\beta = \sum_{l=1}^{N_l} r(l) \times \min \left( \max \left( \frac{\Psi_{\text{max}} - \Psi_s(l)}{\Psi_{\text{max}} - \Psi_{\text{sat}}}, 1 \times 10^{-10} \right), 1 \right) \), where \(\Psi_{\text{max}}\) is a spatially-fixed constant describing the wilting point potential of leaves. \(\Psi_s\) is the soil water matric potential of layer \(l\) calculated from the CMIP5 soil moisture model output, \(\Psi_{\text{sat}}\) is the spatially-varying saturated soil matric potential from soil texture database, \(r\) is the root fraction in layer \(l\), and \(N_l\) is the number of soil layers. \(\beta\) is used to scale maximum photosynthetic capacity.
Function 2: \( \beta = \sum_{l=1}^{N_l} r(l) \times \min \left( \frac{\Psi_{\text{max}} - \Psi_s(l)}{\Psi_{\text{max}} - \Psi_{fc}}, 1 \right), \) where \( \Psi_{\text{max}} \) is a spatially-fixed constant describing the wilting point potential of leaves, \( \Psi_s \) is the soil water matric potential of layer \( l \) calculated from the CMIP5 soil moisture model output, \( \Psi_{fc} \) is the spatially-varying soil matric potential at field capacity from the soil texture database, \( r \) is the root fraction in layer \( l \), and \( N_l \) is the number of soil layers. \( \beta \) is used to scale maximum photosynthetic capacity.

Function 3: \( \beta = 2 \delta - \delta^2 \) where \( \delta = \sum_{l=1}^{N_l} r(l) \times \max \left( 0, \min \left( \frac{\theta_s(l) - \theta_w}{\theta_{fc} - \theta_w}, 1 \right) \right), \) where \( \theta_{fc} \) and \( \theta_w \) are the spatially-varying soil water content at field capacity and wilting point, respectively, from the soil texture database, \( \theta_s \) is the soil water content of layer \( l \) from the CMIP5 model output, \( r \) is the root fraction in layer \( l \), and \( N_l \) is the number of soil layers. \( \beta \) is used to scale maximum photosynthetic capacity.

Function 4: \( \beta = \sum_{l=1}^{N_l} r(l) \times \min \left( \frac{\Psi_{\text{c}} - \Psi_s(l)}{\Psi_{\text{c}} - \Psi_{\text{o}}}, 1 \right) \left( \frac{\theta_{\text{sat}}(l) - \theta_{\text{ice}}(l)}{\theta_{\text{sat}}(l)} \right), \) where \( \Psi_{\text{c}} \) are spatially-fixed, plant functional type-specific constants describing the soil water potential when stomata are fully closed or fully open, respectively (Table A-2), \( \Psi_s \) is the soil water matric potential of layer \( l \) calculated from the CMIP5 soil moisture model output, \( \theta_{\text{sat}} \) is the soil water content of layer \( l \), \( \theta_{\text{ice}} \) is the ice content of layer \( l \), \( r \) is the root fraction in layer \( l \), and \( N_l \) is the number of soil layers. Because we masked out locations when the minimum temperature decreased below freezing, and
because soil ice content was not available by layer, we neglected the term \( \frac{\theta_{sat}(l) - \theta_{ice}(l)}{\theta_{sat}(l)} \).

Though some locations in our analysis could have permafrost during the growing season and may be impacted by this simplification, we do not anticipate that this simplification had major effects on our estimates of GPP. \( \beta \) is used to scale maximum photosynthetic capacity.

**Function 5:**\[ \beta = \sum_{l=1}^{N_l} r(l) \times \min \left( \frac{\max (\theta_s(l) - \theta_{sw}, 0)}{\theta_{s} - \theta_{sw}}, 1 \right), \] where \( S_* \) and \( s_w \) are spatially-fixed, plant functional type specific constants describing the soil water content at moisture stress onset and wilting point, respectively, \( \theta_s \) is the soil water content of layer \( l \) from the CMIP5 model output, \( r \) is the root fraction in layer \( l \), and \( N_l \) is the number of soil layers. \( \beta \) is used to scale canopy conductance.

**Function 6:**\[ \beta = \sum_{l=1}^{N_l} r(l) \times \min \left( \frac{\max (\theta_s(l) - \theta_{sw}, 0)}{\theta_{fc} - \theta_{sw}}, 1 \right), \] where \( \theta_w \) and \( \theta_{fc} \) are spatially-varying and describe the soil water content at wilting point and field capacity, respectively, from the soil texture database, \( \theta_s \) is the soil water content of layer \( l \) from the CMIP5 model output, \( r \) is the root fraction in layer \( l \), and \( N_l \) is the number of soil layers. \( \beta \) is used to scale maximum photosynthetic capacity.
Function 7: $\beta = \min \left( \max \left( \frac{\theta_s(l) - \theta_w}{\theta_{fc} - \theta_w} \right), 1 \right)^{0.5}$ for $l \in N_l < 0.5$ meters, where $\theta_w$ and $\theta_{fc}$ are spatially-varying and describing the wilting point and field capacity soil water content, respectively, which are taken from the soil texture database, $\theta_s$ is the soil water content of layer $l$ from the CMIP5 model output, and $N_l$ is the number of soil layers. $\beta$ is used to scale maximum photosynthetic capacity.
Table A-1: CMIP5 models included in analysis.

<table>
<thead>
<tr>
<th>Model</th>
<th>Resolution</th>
<th>Soil depth*</th>
<th>Soil layers (#)*</th>
<th>β function*</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCC-CSM1-1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>128x64</td>
<td>2.86</td>
<td>10</td>
<td>1</td>
<td>(Oleson et al., 2004)</td>
</tr>
<tr>
<td>BNU-ESM&lt;sup&gt;b&lt;/sup&gt;</td>
<td>128x64</td>
<td>2.86</td>
<td>10</td>
<td>2</td>
<td>(Dai et al., 2004b)</td>
</tr>
<tr>
<td>CanESM2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>128x64</td>
<td>2.25</td>
<td>3</td>
<td>3</td>
<td>(Arora, 2003)</td>
</tr>
<tr>
<td>CCSM4&lt;sup&gt;d&lt;/sup&gt;</td>
<td>288x192</td>
<td>2.86</td>
<td>10</td>
<td>4</td>
<td>(Oleson et al., 2010)</td>
</tr>
<tr>
<td>CESM1-BGC&lt;sup&gt;e&lt;/sup&gt;</td>
<td>288x192</td>
<td>2.86</td>
<td>10</td>
<td>4</td>
<td>(Oleson et al., 2010)</td>
</tr>
<tr>
<td>GISS-E2-R-CC&lt;sup&gt;f&lt;/sup&gt;</td>
<td>144x90</td>
<td>2.73</td>
<td>6</td>
<td>5</td>
<td>(Kim et al., 2015)</td>
</tr>
<tr>
<td>HadGEM2-ES&lt;sup&gt;g&lt;/sup&gt;</td>
<td>192x145</td>
<td>2.0</td>
<td>4</td>
<td>6</td>
<td>(Cox, 2001)</td>
</tr>
<tr>
<td>MIROC-ESM&lt;sup&gt;h&lt;/sup&gt;</td>
<td>128x64</td>
<td>14.0</td>
<td>6</td>
<td>7</td>
<td>(Sato et al., 2007)</td>
</tr>
<tr>
<td>NorESM1-ME&lt;sup&gt;i&lt;/sup&gt;</td>
<td>144x96</td>
<td>2.86</td>
<td>10</td>
<td>4</td>
<td>(Oleson et al., 2010)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Beijing Climate Center, Climate System Model, version 1.1  
<sup>b</sup>Beijing Normal University, Earth System Model version 1  
<sup>c</sup>Second Generation Canadian Earth System Model  
<sup>d</sup>Community Climate System Model version 4.0  
<sup>e</sup>Community Earth System Model, version 1 with Biogeochemistry
NASA Goddard Institute for Space Studies Model E, version 2, coupled with the Russel ocean model with an interactive carbon cycle

Hadley Global Environment model, version 2 – Earth System

Model for Interdisciplinary Research on Climate, Earth System Model

Norwegian Earth System Model, intermediate resolution with biogeochemical cycling

See Text S1 for details of the soil moisture limitation functions

Refers to hydrologically active soil layers only
Table A-2: Parameter values used in the soil moisture (β) limitation functions.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
<th>GWSP2 substitution</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Psi_o$</td>
<td>-35000 to -74000 mm</td>
<td></td>
<td>$\Psi_{fc}$</td>
</tr>
<tr>
<td>$\Psi_c$</td>
<td>-255000 to -428000 mm</td>
<td></td>
<td>$\Psi_{w}$</td>
</tr>
<tr>
<td>$\Psi_{max}$</td>
<td>-150000 mm</td>
<td></td>
<td>$\Psi_{w}$</td>
</tr>
<tr>
<td>$\theta_w$</td>
<td>GSWP2 database</td>
<td>m$^3$/m$^3$</td>
<td>n/a</td>
</tr>
<tr>
<td>$\theta_{fc}$</td>
<td>GSWP2 database</td>
<td>m$^3$/m$^3$</td>
<td>n/a</td>
</tr>
<tr>
<td>$\theta_{sat}$</td>
<td>GSWP2 database</td>
<td>m$^3$/m$^3$</td>
<td>n/a</td>
</tr>
<tr>
<td>$\Psi_w$</td>
<td>GSWP2 database</td>
<td>mm</td>
<td>n/a</td>
</tr>
<tr>
<td>$\Psi_{fc}$</td>
<td>GSWP2 database</td>
<td>mm</td>
<td>n/a</td>
</tr>
<tr>
<td>$\Psi_{sat}$</td>
<td>GSWP2 database</td>
<td>mm</td>
<td>n/a</td>
</tr>
<tr>
<td>$s_w$</td>
<td>0.25 to 0.27 m$^3$/m$^3$</td>
<td></td>
<td>$\theta_w$</td>
</tr>
<tr>
<td>$S^*$</td>
<td>0.34 to 0.65 m$^3$/m$^3$</td>
<td></td>
<td>$\theta_{fc}$</td>
</tr>
</tbody>
</table>

*See Supplementary Note for details of the soil moisture limitation functions*
Table A-3: Correlation coefficient (Pearson’s) for the inversion approach used in calculating the soil water stress factor ($\beta$).

<table>
<thead>
<tr>
<th>$\beta$ inversion method</th>
<th>Correlation Coefficient (historical)</th>
<th>Correlation Coefficient (RCP 8.5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top soil layer only, spatially varying soil water potential</td>
<td>0.7495*</td>
<td>0.7743*</td>
</tr>
<tr>
<td>Calculated according to $\beta$ function$^1$, spatially varying soil water potential$^2$</td>
<td>0.6206*</td>
<td>0.6204*</td>
</tr>
<tr>
<td>Calculated according to $\beta$ function$^1$, spatially fixed soil water potential (average of all model PFTs)$^3$</td>
<td>0.5116*</td>
<td>0.4897*</td>
</tr>
<tr>
<td>Calculated according to $\beta$ function$^1$, spatially fixed soil water potential (least negative of all model PFTs)$^3$</td>
<td>0.5506*</td>
<td>0.5318*</td>
</tr>
<tr>
<td>Calculated according to $\beta$ function$^1$, spatially fixed soil water potential (most negative of all model PFTs)$^3$</td>
<td>0.4821*</td>
<td>0.4584*</td>
</tr>
</tbody>
</table>

*Significant at $p << 0.0001$

$^1$See $\beta$ function in Table A-1 associated with CESM1-BGC

$^2$See details on for $\Psi_f$ in place of $\Psi_o$ and $\Psi_w$ in place of $\Psi_c$ in the $\beta$ function in Table A-2

$^3$See values for $\Psi_o$ and $\Psi_c$ in Table A-2 for parameter ranges
Figure A-1: Regions with projected drought-limitation comprise a large portion of the land surface in all models but vary significantly between individual vegetation models. Global maps of individual model soil water limitation coefficients ($\beta$). Maps show the average annual $\beta$ over the years 2080-2099 for RCP 8.5 for nine model members of the CMIP5.
Figure A-2: Regions with projected photosynthesis limitation due to drought comprise a large portion of the land surface in all models but vary significantly between individual vegetation models. Global maps of individual model GPP constrained by soil water limitation (GPP\textsubscript{c}). Maps show the total annual GPP\textsubscript{c} over the years 2080-2099 for RCP 8.5 for nine model members of the CMIP5.
Figure A-3: Drought-limitation on photosynthesis is projected to increase in the future, however substantial spatial variability in the strength and extent is apparent. Global maps of the multi-model median difference in (a) soil water limitation coefficient ($\beta$) and (b) GPP constrained by $\beta$ ($\text{GPP}_c$). Maps show the median annual $\beta$ and $\text{GPP}_c$ over the years 2080-2099 for RCP 8.5 minus the median for years 1981-2000 in historical simulations for nine model members of the CMIP5.
Figure A-4: GPP constrained by soil water limitation is comparable in magnitude to simulated GPP and represents a large uncertain term in the projected terrestrial carbon budget for all models. Intermodel variability in (a) global GPP and (b) the ratio of GPP constrained by soil water limitation ($GPP_c$) compared to simulated GPP for historical (blue) and future (cyan) projections.
Figure A-5: The inversion approximation for calculating $\beta$ captures both the spatial variability and strength of $\beta$ in the CESM model. Model output $\beta$ (a) compared to $\beta$ calculated from Inversion 1 where the standard $\beta$ function and spatially varying maps of hydraulic thresholds were used (b), Inversion 2 where only the soil moisture of the top soil layer was used (c), and Inversion 3 where the standard $\beta$ function and the average, spatially constant PFT-specific water potential thresholds were used globally (d). Maps show the average annual $\beta$ over the years 2080-2099 for an RCP 8.5 emissions scenario.
Figure A-6: The inversion approximation for calculating constrained GPP (GPP\textsubscript{c}) captures both the spatial variability and magnitude of GPP\textsubscript{c} in the CESM model. GPP\textsubscript{c} calculated from model output $\beta$ (a) compared to GPP\textsubscript{c} calculated from $\beta$ obtained from Inversion 1 where the standard $\beta$ function and spatially varying maps of hydraulic thresholds were used (b), Inversion 2 where only the soil moisture of the top soil layer was used (c), and Inversion 3 where the standard $\beta$ function and the average, spatially constant PFT-specific water potential thresholds were used globally (d). Maps show the total annual GPP\textsubscript{c} over the years 2080-2099 for an RCP 8.5 emissions scenario.
Figure A-7: Constrained GPP (GPP\(_c\)) can be reasonably estimated using model output soil moisture and assumed rooting depth and soil hydraulic parameters. Annual average simulated GPP (GPP\(_m\)) for the CESM model over the years 2080-2099 for an RCP 8.5 emissions scenario (a), and the global fraction of GPP\(_c\)/GPP\(_m\) for each inversion approach compared to the fraction calculated using the model output \(\beta\) (Sim) (b).
Figure A-8: Global GPP constrained by soil water limitation varies depending on rooting depth profiles, soil hydraulic parameters, and soil database, but qualitative patterns remain robust. Intermodel variability in global constrained GPP (GPP_c) for RCP 8.5 future projections averaged over years 2080-2099 for our standard calculation of GPP_c using globally variable gridded hydraulic parameters and rooting depth estimates from the GSWP2, a deep constant global root distribution (R_β = 0.976), a shallow constant global root distribution (R_β = 0.943), globally constant soil hydraulic parameters specified for select β functions (Const Hyd, see Supplementary Note), and a different soil texture database (HWSD).
### Appendix B

**Supplement to Chapter 3**

**Supplementary Tables**

Tables of relative importance and standardized response coefficients are available upon request as separate excel files.

Table B-1: Numbers of plots, trees, and observations for all tree species combined and for four major Alaskan boreal tree species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of plots</th>
<th>Number of trees</th>
<th>Total trees</th>
<th>Dead trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>All tree species</td>
<td>323</td>
<td>27057</td>
<td>1759</td>
<td></td>
</tr>
<tr>
<td><em>Picea glauca</em></td>
<td>286</td>
<td>10057</td>
<td>276</td>
<td></td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>143</td>
<td>5908</td>
<td>762</td>
<td></td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td>110</td>
<td>3341</td>
<td>87</td>
<td></td>
</tr>
<tr>
<td><em>Beulata kenaica</em></td>
<td>183</td>
<td>6900</td>
<td>561</td>
<td></td>
</tr>
<tr>
<td><em>Beulata neoalaska</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table B-2: Data descriptions for the first and final census periods.

<table>
<thead>
<tr>
<th>Species</th>
<th>First census period</th>
<th>Final census period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of trees</td>
<td>Number of dead trees</td>
</tr>
<tr>
<td><strong>Picea glauca</strong></td>
<td>10057</td>
<td>276</td>
</tr>
<tr>
<td></td>
<td>10369</td>
<td>249</td>
</tr>
<tr>
<td><strong>Populus tremuloides</strong></td>
<td>5908</td>
<td>762</td>
</tr>
<tr>
<td></td>
<td>4715</td>
<td>915</td>
</tr>
<tr>
<td><strong>Picea mariana</strong></td>
<td>3341</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td>3827</td>
<td>99</td>
</tr>
<tr>
<td><strong>Belula kenaica/</strong></td>
<td>6900</td>
<td>561</td>
</tr>
<tr>
<td></td>
<td>6344</td>
<td>472</td>
</tr>
<tr>
<td><strong>Belula neoalaska</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure B-1: Spatial locations of the permanent sample plots in the Cooperative Alaska Forest Inventory. Plots are binned by half degree according to meteorological forcing. The number of plots in each half-degree grid cell is indicated by the color map.
Figure B-2: Distribution histograms of the 323 selected permanent sample plots for calendar year of first (A) and final census (B), number of censuses per plot (C), plot basal area at first census (D), stand age at first census (E), and number of trees per plot at first census (F).
Figure B-3: Time series and spatial maps of potential evapotranspiration (PET) in boreal North America from 1951-2014. Time series of summer (June-August) PET over the study region (A) and regions with significant trends in summer PET over the 1951-2014 period (B). Time series of total annual PET over the study region (C) and absolute annual PET for year 2010 (D). Time series points were computed as the average over all grid cells containing permanent sample plots. Significant trends were assessed using Spearman’s rho with a significance threshold of $p < 0.1$. 
Figure B-4: Time series and spatial maps of temperature (T) in boreal North America from 1951-2014. Time series of spring (March-May) temperature over the study region (A) and regions with significant trends in spring temperature over the 1951-2014 period (B). Time series of mean annual temperature (MAT) over the study region (C) and MAT for year 2010 (D). Time series points were computed as the average over all grid cells containing permanent sample plots. Significant trends were assessed using Spearman’s rho with a significance threshold of p < 0.1.
Figure B-5: Time series and spatial maps of precipitation (P) in boreal North America from 1951-2014. Time series of summer (June-August) precipitation over the study region (A) and regions with significant trends in summer precipitation over the 1951-2014 period (B). Time series of mean annual precipitation (MAP) over the study region (C) and MAP for year 2010 (D). Time series points were computed as the average over all grid cells containing permanent sample plots. Significant trends were assessed using Spearman’s rho with a significance threshold of p < 0.1.
Figure B-6: The relative importance of climate, competition, and insect disturbance differs substantially depending on species. Relative importance (%) of plot-specific location effects (Loc), competition index (CI), forest gymnosperm fraction (Gyf), March-May temperature (MAMt), July precipitation (Jpre), July potential evapotranspiration (Jpet), and insect presence (ins, mortality models only) to the total explained variance in growth (A-B) and mortality (C-D) for birch (A,C) and black spruce (B,D).
Figure B-7: Midsummer evaporative demand strongly affects trembling aspen growth regardless of soil moisture classification. Relative importance (%) of plot-specific location effects (Loc), competition index (CI), forest gymnosperm fraction (Gyf), March-May temperature (MAMt), July precipitation (Jpre), July potential evapotranspiration (Jpet), and insect presence (ins, mortality model only) to the total explained variance in growth and mortality for aspen trees in plots grouped by wet soils (encompassing peraquic, aquic, and subaquic soils) (A,C) and dry soils (encompassing perhumid, humid, subhumid, subxeric, and xeric soils) (B,D).
Figure B-8: Distribution histograms of the average plot-level fraction of trees infested with insects at moderate intensity or greater (>11%) over the entire 10-15 year inventory measurement period for trembling aspen (TA) (A), two species of birch (PB) (B), white spruce (WS) (C), and black spruce (BS) (D).
Appendix C
Supplement to Chapter 4

Figure C-1: Relative importance of stand basal area (BA), average July precipitation (pcp), average July vapor pressure deficit (vpd), and average May temperature (tmp) to tree growth for the black spruce PFT. Results are shown for the standard black spruce parameters (Original), a trait swap with the white spruce PFT (Trait swap), an increase in black spruce sapwood area to that corresponding to the white spruce PFT (Sapwood), and an increase in black rooting depth to 1 meter (Root depth).
Table C-1: Ecophysiological and life history parameters for aspen and black spruce

<table>
<thead>
<tr>
<th>Parameter</th>
<th>For Aspen</th>
<th>For Black Spruce</th>
<th>Unit</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allometric relation of diameter at breast height (dbh) to stem biomass</td>
<td>$b_1 = 0.0255$</td>
<td>$b_1 = 0.0404$</td>
<td>kg C</td>
<td>Adapted from Bond-Lamberty et al. (2002a) and Yarie et al. (2007)</td>
</tr>
<tr>
<td>Allometric relation of dbh to tree height</td>
<td>$h_{ref} = 0.2$</td>
<td>$h_{ref} = 0.5$</td>
<td>m</td>
<td>Adapted from Bond-Lamberty et al. (2002a) and Yarie et al. (2007)</td>
</tr>
<tr>
<td>Maximum tree height ($h_{max}$)</td>
<td>22.5</td>
<td>18.0</td>
<td>m</td>
<td>Adapted from Bond-Lamberty et al. (2002a) and Yarie et al. (2007)</td>
</tr>
<tr>
<td>Maximum rooting depth</td>
<td>1.0</td>
<td>0.3</td>
<td>m</td>
<td>Strong and la Roi (1983)</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>34.8</td>
<td>9.96</td>
<td>m$^2$ leaf kg$^{-1}$C</td>
<td>Bond-Lamberty et al. (2002b)</td>
</tr>
<tr>
<td>Specific root area</td>
<td>66.9</td>
<td>100.</td>
<td>m$^2$ root kg$^{-1}$C</td>
<td>Steele et al. (1997)</td>
</tr>
<tr>
<td>Ratio of fine roots to leaves</td>
<td>1.89</td>
<td>0.61</td>
<td>kg fine roots kg$^{-1}$ leaves</td>
<td>Ryan et al. (1997)</td>
</tr>
<tr>
<td>Fine root turnover rate</td>
<td>0.65</td>
<td>1.56</td>
<td>yr$^{-1}$</td>
<td>Pinno et al. (2010) and Ruess et al. (2003)</td>
</tr>
<tr>
<td>Leaf turnover rate</td>
<td>end of growing season</td>
<td>0.14</td>
<td>yr$^{-1}$</td>
<td>Hom and Oechel (1983)</td>
</tr>
<tr>
<td>Density independent mortality</td>
<td>$5.9 \times 10^{-2}$</td>
<td>$1.4 \times 10^{-2}$</td>
<td>yr$^{-1}$</td>
<td>Adapted from Bond-Lamberty et al. (2014)</td>
</tr>
<tr>
<td>Sapwood area</td>
<td>0.62</td>
<td>0.45</td>
<td>stem cross section fraction</td>
<td>Yarie et al. (2007)</td>
</tr>
<tr>
<td>Turgor loss point</td>
<td>-1.45</td>
<td>-4.35</td>
<td>MPa</td>
<td>Way et al. (2013) and Abidine et al. (1994)</td>
</tr>
<tr>
<td>Parameter</td>
<td>Value</td>
<td>Unit</td>
<td>Source</td>
<td></td>
</tr>
<tr>
<td>---------------------------------------------------------------------------</td>
<td>---------------</td>
<td>-----------</td>
<td>---------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Psi 50</td>
<td>-2.80 - 4.26</td>
<td>MPa</td>
<td>Sperry et al. (1994) and Balducci et al. (2015)</td>
<td></td>
</tr>
<tr>
<td>Litter decomposition rate</td>
<td>$1.8 \times 10^{-4} - 3.0 \times 10^{-3}$</td>
<td>day$^{-1}$</td>
<td>Adapted from Euskirchen et al. (2009) and Prescott et al. (2000)</td>
<td></td>
</tr>
<tr>
<td>Moss accumulation depth</td>
<td>$a = 0 - 0.0043$</td>
<td>cm</td>
<td>Equation (2)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$b = -0.28$</td>
<td></td>
<td>Based on Fenton et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>Organic layer depth at which seedling mortality starts increasing (ol_min)</td>
<td>2.0 - 10.0</td>
<td>cm</td>
<td>Based on Johnstone and Chapin (2006b)</td>
<td></td>
</tr>
<tr>
<td>Organic layer depth at which seedling mortality stops increasing (ol_max)</td>
<td>5.0 - 40.0</td>
<td>cm</td>
<td>Based on Johnstone and Chapin (2006b) and Fenton and Bergeron (2006)</td>
<td></td>
</tr>
<tr>
<td>Background seedling mortality rate ($m_{p,\text{min}}$)</td>
<td>0.95 - 0.95</td>
<td>fraction</td>
<td>Standard survivorship rate</td>
<td></td>
</tr>
<tr>
<td>Mortality shape parameter ($c_1$)</td>
<td>1.7 - 0.27</td>
<td></td>
<td>Fit to ol_min and ol_max</td>
<td></td>
</tr>
<tr>
<td>Treefall disturbance survivorship for trees smaller/larger that 12 m</td>
<td>0.30/0.0 - 0.45/0.0</td>
<td>fraction</td>
<td>Rich et al. (2007)</td>
<td></td>
</tr>
<tr>
<td>Carbon to nitrogen ratio for leaves and fine roots</td>
<td>33 - 63</td>
<td>ratio</td>
<td>Adapted from Bond-Lamberty et al. (2006)</td>
<td></td>
</tr>
<tr>
<td>Nitrogen fixation Associated with moss biomass</td>
<td>0.0 $f = 7.73 \times 10^{-9}$</td>
<td>kg N day$^{-1}$</td>
<td>Adapted from nitrogen fixation data, Quebec clay belt, Fenton et al., [unpublished, 2015]</td>
<td></td>
</tr>
</tbody>
</table>
Moss bulk density 25 kg C m⁻² Adapted from Trumbore and Harden (1997) shallow organic layer bulk density

Litter bulk density 200 kg C m⁻² 200 kg C m⁻² Adapted from Trumbore and Harden (1997) deep organic layer bulk density

¹All other parameters are defined in Table C-2 or we take as the default values for early successional hardwoods (aspen) and late successional conifers (black spruce) (Medvigy et al., 2009).

²Based on biomass (b) to diameter at breast height (dbh) allometric equations of the form:

\[ b = b_1 \times \text{dbh}^{b_2} \]. Details can be found in Medvigy et al. (2009).

³Based on height (h) to diameter at breast height (dbh) allometric equations of the form:

\[ h = h_{\text{ref}} + h_{\text{max}} \times [1 - \exp(h_1 \times \text{dbh})]. \] Details can be found in Medvigy et al. (2009)
Table C-2: Mean and standard deviation for the prior probability density functions for select ecophysiological and hydrological parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>For Aspen</th>
<th>For Black Spruce</th>
<th>Unit</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allometric relation of dbh to leaf biomass +</td>
<td>b1 = 0.0018 ( \times 10^{-4} ) *</td>
<td>b1 = 0.033 ( \times 0.0033 )</td>
<td>kg C</td>
<td>Adapted from Bond-Lamberty <em>et al.</em> (2002a) and Yarie <em>et al.</em> (2007)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>b2 = 2.506</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum photosynthetic capacity at 15°C</td>
<td>18.4 (1.6) *</td>
<td>8.07 (1.3) *</td>
<td>µmol m(^{-2}) s(^{-1})</td>
<td>Kubiske <em>et al.</em> (1997) and Rayment <em>et al.</em> (2002)</td>
</tr>
<tr>
<td>Maximum seedling mortality rate ( (m_{p,\text{max}}) )</td>
<td>1.0</td>
<td>0.9997 ( \times 0.0002 ) *</td>
<td>fraction</td>
<td>Aspen from Johnstone and Chapin (2006b), black spruce adapted from (Greene <em>et al.</em>, 2004) and taking into account slow basal area decline in old (&gt;500 year) black spruce forests</td>
</tr>
<tr>
<td>Soil nitrogen leaching efficiency</td>
<td>0.04 ( \times 0.015 ) *</td>
<td>0.04 ( \times 0.015 ) *</td>
<td>fraction</td>
<td>Adapted from (Gerber &amp; Brookshire, 2014)</td>
</tr>
</tbody>
</table>

+ Based on biomass \( b \) to diameter at breast height (dbh) allometric equations of the form:

\[ b = b_1 \times \text{dbh}^{b_2} \]. Details can be found in (Medvigy *et al.*, 2009).

* Mean (standard deviation) of the normal prior probability density function defined to encompass the range of uncertainty of the parameter values. In the case of leaf biomass allometric coefficients, \( b_2 \) was refit based on the value of \( b_1 \). In the table we only list the value of \( b_2 \) corresponding to the mean parameter value used for \( b_1 \).
Table C-3: Physical properties of the soil organic layer

<table>
<thead>
<tr>
<th>Soil organic layer property</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil moisture potential at saturation</td>
<td>m</td>
<td>-0.535</td>
</tr>
<tr>
<td>Soil moisture at saturation</td>
<td>m³ m⁻³</td>
<td>0.469</td>
</tr>
<tr>
<td>Specific heat of dry soil</td>
<td>J m⁻³ K⁻¹</td>
<td>8.740 x 10⁵</td>
</tr>
<tr>
<td>Hydraulic conductivity at saturation</td>
<td>m s⁻¹</td>
<td>2.358 x 10⁻⁶</td>
</tr>
<tr>
<td>Soil field capacity</td>
<td>m³ m⁻³</td>
<td>0.286</td>
</tr>
<tr>
<td>Wet soil albedo</td>
<td>fraction</td>
<td>0.070</td>
</tr>
<tr>
<td>Dry soil albedo</td>
<td>fraction</td>
<td>0.140</td>
</tr>
<tr>
<td>Bulk density</td>
<td>kg m⁻³</td>
<td>500</td>
</tr>
<tr>
<td>Simulation name (subject)- (type)- (location)</td>
<td>Location (lat/lon)</td>
<td>Observational Data set (reference)</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>-------------------</td>
<td>-----------------------------------</td>
</tr>
<tr>
<td>BS-chrono-MB 55.5/-98.5</td>
<td>BOREAS Northern Study Area dry chronosequence (Bond-Lamberty et al., 2002b)</td>
<td>0.2 m² black spruce seedling density; initial organic layer depth = 15 cm; looped over 1990-2008 meteorology and CO₂ = 370 ppm; nitrogen deposition rate = 0.5 g N m⁻² yr⁻¹</td>
</tr>
<tr>
<td>TA-chrono-MB 55.5/-98.5</td>
<td>BOREAS Northern Study Area old aspen forest</td>
<td>0.2 m² aspen seedling density; initial organic layer depth = 3 cm; looped over 1990-2008 meteorology and CO₂ = 370 ppm; nitrogen deposition rate = 0.5 g N m⁻² yr⁻¹</td>
</tr>
<tr>
<td>BS-chrono-SK 53.5/-104.5</td>
<td>BOREAS Southern Study Area old black spruce forest</td>
<td>0.2 m² black spruce seedling density; initial organic layer depth = 15 cm; looped over 1990-2008 meteorology and CO₂ = 370 ppm; nitrogen deposition rate = 0.5 g N m⁻² yr⁻¹</td>
</tr>
<tr>
<td>TA-chrono-SK 53.5/-104.5</td>
<td>BOREAS Southern Study Area old aspen forest</td>
<td>0.2 m² aspen seedling density; initial organic layer depth = 3 cm; looped over 1990-2008 meteorology and CO₂ = 370 ppm; nitrogen deposition rate = 0.5 g N m⁻² yr⁻¹</td>
</tr>
<tr>
<td>BS-moder chrono-QC 49.0/-79.0</td>
<td>Moderately burned black spruce and organic layer depth chronosequence, (Fenton et al., 2005)</td>
<td>0.2 m² black spruce seedling density; initial organic layer depth = 20 cm; looped over 1990-2008 meteorology and CO₂ = 370 ppm; nitrogen deposition rate = 0.5 g N m⁻² yr⁻¹</td>
</tr>
<tr>
<td>BS-mild chrono-QC 49.0/-79.0</td>
<td>Mildly burned black spruce and organic layer depth chronosequence, (Fenton et al., 2005)</td>
<td>0.2 m² black spruce seedling density; initial organic layer depth = 45 cm; looped over 1990-2008 meteorology and CO₂ = 370 ppm; nitrogen deposition rate = 0.5 g N m⁻² yr⁻¹</td>
</tr>
<tr>
<td>Area</td>
<td>Latitude/Longitude</td>
<td>Forest Inventory Source</td>
</tr>
<tr>
<td>-----------------</td>
<td>--------------------</td>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td>BS-north-CAFI-AK</td>
<td>65.0/-148.0</td>
<td>Cooperative Alaska Forest Inventory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Malone et al., 2009)</td>
</tr>
<tr>
<td>BS-south-CAFI-AK</td>
<td>61.0/-151.0</td>
<td>Cooperative Alaska Forest Inventory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Malone et al., 2009)</td>
</tr>
<tr>
<td>TA-north-CAFI-AK</td>
<td>65.0/-150.0</td>
<td>Cooperative Alaska Forest Inventory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Malone et al., 2009)</td>
</tr>
<tr>
<td>TA-south-CAFI-AK</td>
<td>62.0/-149.0</td>
<td>Cooperative Alaska Forest Inventory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Malone et al., 2009)</td>
</tr>
<tr>
<td>Mixed-CAFI-AK</td>
<td>60.0/-150.0</td>
<td>Cooperative Alaska Forest Inventory</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Malone et al., 2009)</td>
</tr>
<tr>
<td>TA-EC-AK</td>
<td>63.5/-145.5</td>
<td>Eddy Flux measurements near Delta Junction, AK</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Welp et al., 2007)</td>
</tr>
<tr>
<td>BS-EC-AK</td>
<td>63.5/-145.5</td>
<td>Eddy Flux measurements near Delta Junction, AK</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Welp et al., 2007)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 black spruce (BS); aspen (TA); mixed aspen and black spruce forest (mixed)

2 chronosequence (chrono); Cooperative Alaska Forest Inventory (CAFI); eddy covariance (EC)
Table C-5: Model experiments

<table>
<thead>
<tr>
<th>Simulation name</th>
<th>Duration (years)</th>
<th>Experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td>burn-mild</td>
<td>500</td>
<td>Initial organic layer depth 60 cm</td>
</tr>
<tr>
<td>burn-severe</td>
<td>500</td>
<td>Initial organic layer depth 3 cm</td>
</tr>
<tr>
<td>OLon-SMon</td>
<td>300</td>
<td>Initial organic layer depth 60 cm, organic layer dependent seedling mortality module on, dynamic soil organic layer on</td>
</tr>
<tr>
<td>OLon-SMoff</td>
<td>300</td>
<td>Initial organic layer depth 60 cm, organic layer dependent seedling mortality module off, dynamic soil organic layer on</td>
</tr>
<tr>
<td>OOff-SMoff</td>
<td>300</td>
<td>Initial organic layer depth 60 cm, organic layer dependent seedling mortality module off, dynamic soil organic layer off</td>
</tr>
<tr>
<td>OLon-\text{SMoff-warm}</td>
<td>300</td>
<td>Initial organic layer depth 60 cm, organic layer dependent seedling mortality module on, dynamic soil organic layer on, 4°C mean annual temperature increase, conserve relative humidity</td>
</tr>
<tr>
<td>OOff-SMoff-warm</td>
<td>300</td>
<td>Initial organic layer depth 60 cm, organic layer dependent seedling mortality module off, dynamic soil organic layer on, 4°C mean annual temperature increase, conserve relative humidity</td>
</tr>
<tr>
<td>T-0Cwarm</td>
<td>300</td>
<td>Initial organic layer depth 3 cm (60 cm in QC), current meteorological forcing</td>
</tr>
<tr>
<td>T-2Cwarm</td>
<td>300</td>
<td>Initial organic layer depth 3 cm (60 cm in QC), 2°C mean annual temperature increase, conserve relative humidity</td>
</tr>
<tr>
<td>T-4Cwarm</td>
<td>300</td>
<td>Initial organic layer depth 3 cm (60 cm in QC), 4°C mean annual temperature increase, conserve relative humidity</td>
</tr>
<tr>
<td>Ndep-0.1</td>
<td>300</td>
<td>Initial organic layer depth 3 cm, nitrogen deposition 0.1 gN m$^{-2}$ yr$^{-1}$</td>
</tr>
<tr>
<td>Ndep-0.5</td>
<td>300</td>
<td>Initial organic layer depth 3 cm, nitrogen deposition 0.5 gN m$^{-2}$ yr$^{-1}$</td>
</tr>
<tr>
<td></td>
<td>300</td>
<td></td>
</tr>
<tr>
<td>-------</td>
<td>-----</td>
<td>-------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Ndep-2</td>
<td>300</td>
<td>Initial organic layer depth 3 cm, nitrogen deposition 2 gN m^-2 yr^-1</td>
</tr>
<tr>
<td>Ndep-20</td>
<td>300</td>
<td>Initial organic layer depth 3 cm, nitrogen deposition 20 gN m^-2 yr^-1</td>
</tr>
<tr>
<td>CO2-370</td>
<td>300</td>
<td>Atmospheric CO2 370 ppm, initial organic layer depth 3 cm (60 cm in QC),</td>
</tr>
<tr>
<td>CO2-1000</td>
<td>300</td>
<td>Atmospheric CO2 1000 ppm, initial organic layer depth 3 cm (60 cm in QC),</td>
</tr>
</tbody>
</table>
### Table C-6: Error statistics for model runs

<table>
<thead>
<tr>
<th>Observational dataset</th>
<th>Mean percent error</th>
<th>Ensemble Range</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>BOREAS NSA dry black spruce basal area chronosequence</td>
<td>26.2</td>
<td>16.1/36.7</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>BOREAS NSA dry black spruce LAI chronosequence</td>
<td>4.5</td>
<td>2.5/4.7</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>BOREAS NSA old aspen forest basal area</td>
<td>0.4</td>
<td>4.9/35.1</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>BOREAS NSA old aspen forest LAI</td>
<td>21.3</td>
<td>0.5/3.7</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>BOREAS SSA old black spruce forest basal area</td>
<td>4.2</td>
<td>18.0/37.8</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>BOREAS SSA old aspen forest basal area</td>
<td>0.7</td>
<td>27.8/36.7</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>BOREAS SSA old aspen forest LAI</td>
<td>1.5</td>
<td>2.6/3.5</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>Quebec moderately burned black spruce basal area chronosequence</td>
<td>40.4</td>
<td>6.0/45.4</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>Quebec moderately burned organic layer depth chronosequence</td>
<td>17.6</td>
<td>40.2/53.0</td>
<td>cm</td>
</tr>
<tr>
<td>Quebec mildly burned black spruce basal area chronosequence</td>
<td>31.9</td>
<td>4.1/39.0</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>Quebec mildly burned organic layer depth chronosequence</td>
<td>9.7</td>
<td>46.7/53.6</td>
<td>cm</td>
</tr>
<tr>
<td>CAFI northern black spruce forest basal area inventory</td>
<td>4.5</td>
<td>4.0/26.9</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>Basal Area Inventory</td>
<td>Mean Basal Area (m²/ha)</td>
<td>Range (m²/ha)</td>
<td>Unit</td>
</tr>
<tr>
<td>----------------------</td>
<td>-------------------------</td>
<td>--------------</td>
<td>------</td>
</tr>
<tr>
<td>CAFI southern black spruce forest basal area inventory</td>
<td>5.4</td>
<td>11.0/19.8</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>CAFI northern aspen forest basal area inventory</td>
<td>0.3</td>
<td>16.8/28.4</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>CAFI southern aspen forest basal area inventory</td>
<td>9.1</td>
<td>13.5/24.5</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>CAFI; mixed stand black spruce basal area inventory</td>
<td>45.3</td>
<td>3.9/26.9</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>CAFI; mixed stand aspen basal area inventory</td>
<td>3.1</td>
<td>9.5/24.5</td>
<td>m² ha⁻¹</td>
</tr>
<tr>
<td>Aspen forest eddy flux measurements near Delta Junction, AK</td>
<td>57.4</td>
<td>(72.4/17.3/12.1/127.8)*</td>
<td>-8.2/-1.8</td>
</tr>
<tr>
<td>Black spruce forest eddy flux measurements near Delta Junction, AK</td>
<td>29.2</td>
<td>(7.7/17.8/22.8/68.7)*</td>
<td>40/71</td>
</tr>
</tbody>
</table>

¹For the chronosequences, the point-wise mean percent error was calculated using ensemble mean and observational mean at all chronosequence points. The mean percent error was calculated as the average of the point-wise mean percent errors. For the forest inventory, the mean percent error was calculated using combined group and ensemble means and the group observational mean at a given return inventory. We then averaged the percent error over all return inventories at a given site. For the eddy covariance data, the mean percent error was calculated using ensemble mean averaged over 2002-2004 for each month in the growing season (May/June/July/August) and the observational mean averaged over 2002-2004 for each month in the growing season. We also computed mean percent error for the entire growing season.

²Ensemble range indicates the simulated minimum/maximum ensemble members at the latest chronosequence point or forest inventory. For the eddy covariance data we computed the average maximum and average minimum over each growing season month (May-August) for 2002-2004.

*The first number represents the mean present error for the entire growing season. We separated out mean percent error by month (May/June/July/August) in the parentheses. 181
Table C-7: RMSE for relative importance analysis of Alberta (AB) and Alaska (AK) Inventories. Instances where the mechanistic hydraulic scheme (M) outperformed the empirical hydraulic scheme (E) are shaded.

<table>
<thead>
<tr>
<th>Location</th>
<th>Driver</th>
<th>Gymo</th>
<th>Angio</th>
<th>Black Spruce</th>
<th>White Spruce</th>
<th>Jack Pine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Empirical (E) or Mechanistic (M) hydraulic scheme</td>
<td>E</td>
<td>M</td>
<td>E</td>
<td>M</td>
<td>E</td>
<td>M</td>
</tr>
<tr>
<td>AB</td>
<td>BA</td>
<td>41.6</td>
<td>29.3</td>
<td>39.0</td>
<td>20.2</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>pcp</td>
<td>3.6</td>
<td>1.5</td>
<td>16.6</td>
<td>2.5</td>
<td>44.1</td>
</tr>
<tr>
<td></td>
<td>vpd</td>
<td>3.2</td>
<td>0.4</td>
<td>25.7</td>
<td>5.7</td>
<td>20.1</td>
</tr>
<tr>
<td></td>
<td>tmp</td>
<td>34.9</td>
<td>28.3</td>
<td>3.3</td>
<td>11.9</td>
<td>9.8</td>
</tr>
<tr>
<td>AK</td>
<td>BA</td>
<td>9.6</td>
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Appendix D

Supplement to Chapter 5

Figure D-1: Observed and model-simulated annual diameter growth increment for (a) twelve species of the savanna guild compared to the savanna plant functional type (PFT) in the model with bark fully included ($BT + \text{tradeoff}$) and (b) twelve species of the forest guild compared to the tropical forest PFT. Variation in the observed growth rates is due to interspecies variation in growth rates (Rossatto et al., 2009). Variation in the simulated growth rates is due to interannual variability in growth as a result of climate. The red line denotes the median diameter the blue box denotes the interquartile range, and the dotted error bars denote ± 2.7σ.
Figure D-2: Model-simulated fraction of above ground biomass (AGB) present in different tree diameter at breast height (dbh in cm) size classes at low (a), intermediate (b), and high (c) MAP for an intermediate frequency (FR) fire regime. Simulations were initialized with tropical tree and C4 grass plant functional types and included a 100-year model spin up from seedlings. The subsequent 20-year average AGB fraction by tree size class is shown for the following models: bark fully included ($BT + trad$), no bark benefit or tradeoff ($nBT$), only the fire survivorship benefit of bark ($BT$), only the growth tradeoff associated with bark ($tradeoff$).
References


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