



**HAL**  
open science

## Boreal forest sensitivity to increased temperatures at multiple successional stages

David Lutz, Herman Shugart, Dmitry Ershov, Jacquelyn Shuman, Alexander Isaev

► **To cite this version:**

David Lutz, Herman Shugart, Dmitry Ershov, Jacquelyn Shuman, Alexander Isaev. Boreal forest sensitivity to increased temperatures at multiple successional stages. *Annals of Forest Science*, 2013, 70 (3), pp.299-308. 10.1007/s13595-012-0258-4 . hal-01201474

**HAL Id: hal-01201474**

**<https://hal.science/hal-01201474>**

Submitted on 17 Sep 2015

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Boreal forest sensitivity to increased temperatures at multiple successional stages

David A. Lutz · Herman H. Shugart · Dmitry V. Ershov ·  
Jacquelyn K. Shuman · Alexander S. Isaev

Received: 7 May 2012 / Accepted: 3 December 2012 / Published online: 8 January 2013  
© INRA and Springer-Verlag France 2012

## Abstract

• **Introduction** Rising temperatures may force boreal forests in central Siberia to transition to alternative ecological states, affecting species composition and carbon storage dynamics. A full understanding of how forests of different ages respond to warming remains elusive, despite being fundamental for proper forest management in the region.  
• **Aims** To document the sensitivity of Siberian forests of different successional stages to rising temperatures.  
• **Methods** We use the FAREAST forest gap model to investigate the variation in biophysical response of boreal forests of different stand ages as temperatures rise and question whether there is varying sensitivity at different successional states.  
• **Results** Our model predicts that mid-successional forests are more resistant to warming temperatures in low-level warming scenarios and resist biophysical changes more so

than forests over 200 years old. This response diminished in more intense warming scenarios. Specifically, forest biomass increased with temperature; however, dieback of Siberian larch and replacement by Siberian Silver birch and by Siberian pine in early-successional stands yielded a net decrease in carbon storage. Mid-succession and old growth forests did not transition to pine forests, however, and may serve as a location for refugia of northern boreal species.

**Keywords** Gap model · Forest ecology · Climate change · Stand age · Boreal forest

**Handling Editor:** Gilbert Aussenac

D.A.L. designed the research, collected data, analyzed data, and wrote the manuscript. H.H.S. advised the direction of research. J.K.S., D.V.E., and A.S.I provided assistance with model functioning.

D. A. Lutz (✉)  
Department of Sustainability, Office of Sustainability, Wake Forest University, P.O. Box 7191, Winston-Salem, NC 27109, USA  
e-mail: lutzda@wfu.edu

D. A. Lutz · H. H. Shugart · J. K. Shuman  
Center for Regional and Environmental Studies, Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA

D. V. Ershov · A. S. Isaev  
Center for Problems of Ecology and Productivity of Forests, Russian Academy of Sciences, Moscow, Russia

## 1 Introduction

Russian boreal forests form the largest contiguous terrestrial biome on the planet and are important components of the global carbon budget. In addition to storing large quantities of carbon (Houghton et al. 2007), these forests have influence on global and regional climate (Bonan 2008). Changes in their composition may alter regional climate appreciably (Chapin et al. 2008; Bonan 2008) and create a positive feedback between land cover change and climate change (Shuman et al. 2011). Economically, Russian forests contribute over \$6 billion to the national economy and Russia is the largest exporter of industrial round wood in the world (Solberg et al. 2010). Additionally, these forests are crucial for conservation efforts of boreal species (Bradshaw et al. 2009).

However, Siberian boreal forests are threatened by the effects of climatic change, particularly higher temperatures (Soja et al. 2007). Regional analyses of climate trends have shown extensive temperature increases within central

Siberia in the past several decades (e.g., Hansen et al. 2006). Comparing the decades from 1990–2010 to a baseline period of 1961–1990, Tchebakova et al. (2011) found that temperatures in central Siberia have generally increased between 1–3 °C. Precipitation, although decidedly variable, has increased throughout much of the area by 10 %, with decreases of 10–20 % in southern Siberia (Tchebakova et al. 2011). Future climate projections for the region also suggest substantial change for Siberian forests in the next century. Global circulation models routinely predict increases in temperature throughout the region on the range of 4–6 °C by the end of the century (Meleshko et al. 2008). These projections suggest that northern Eurasia and much of Siberia are among the regions expected to experience the largest climatic change effects on the planet. This level of warming will approach the upper limit of the climatic tolerance of many tree species within the ecosystem (Shugart et al. 2005), particularly at the southern edge of species ranges.

In order for forest management approaches in Siberia to adequately address future temperature increases and climate change, it is essential to improve estimates of forest sensitivity to fluctuations in temperature and precipitation (Allen et al. 2010; Noss 2001; Ogden and Innes 2007). Since timber production is linked to the successional trajectory of forests (Kellomäki et al. 2008), knowledge of forest sensitivity to increased temperature at different successional stages may provide vital information to boreal forest managers. Conservationists, interested in providing effective reserve zones at various successional states, may also benefit from such sensitivity studies. Understanding regional vulnerability will help overall adaptation strategies for forest management in a time of climate change (Füssel and Klein 2006).

Ecological models have long been used to reveal patterns and processes in boreal forests, particularly those applicable to forest management (Kellomäki and Väisänen 1997; Kolström 1998). Modeling studies that investigate species and stand specific responses to changes in climate will be helpful to identify vulnerable areas most likely to change (Bolte et al. 2009). Mechanistic process models, such as those that simulate the growth, death, and reproduction for individual trees within stands, may be particularly useful in elucidating relationships between forest properties and climate change (Bodin and Wiman 2007). Individual-based dynamic gap models typically simulate individual trees, their growth, mortality, and decomposition into litter in a relatively small area, typically the size of a forest gap (Urban and Shugart 1992). Generally, these models can be classified as non-spatial, in that they do not include spatial interactions between each area that they simulate. However, these models typically contain ecosystem processes such as nutrient cycling and interactions with the local abiotic

environment (Scheller and Mladenoff 2007), can simulate detailed species assemblages with high accuracy (Xiaodong and Shugart 2005), have been successfully used in climate reconstruction efforts, and provide the simulation of multiple forest properties of interest.

In this study, we test whether forests of different successional stages show varying sensitivity to higher temperatures using an individual gap model, FAREAST (Xiaodong and Shugart 2005). Although the FAREAST model was originally designed to simulate forests in Northern China and the far-eastern forests of Russia, it has subsequently been used to replicate stand structure and species dynamics in many locations successfully throughout Russia (Shuman and Shugart 2009) as well as to investigate forest response to climate change (Zhang et al. 2011; Shuman et al. 2011). We utilize FAREAST to explore boreal forest sensitivity to higher temperatures by analyzing properties of simulated forests such as the leaf area index (LAI), stand height, stand biomass, and the ratio of evergreen to deciduous elements in a stand. Using multivariate statistics, we determine which forest properties in the study area are most sensitive to increased temperature, and interpret the results in the context of future forest management strategy.

## 2 Materials and methods

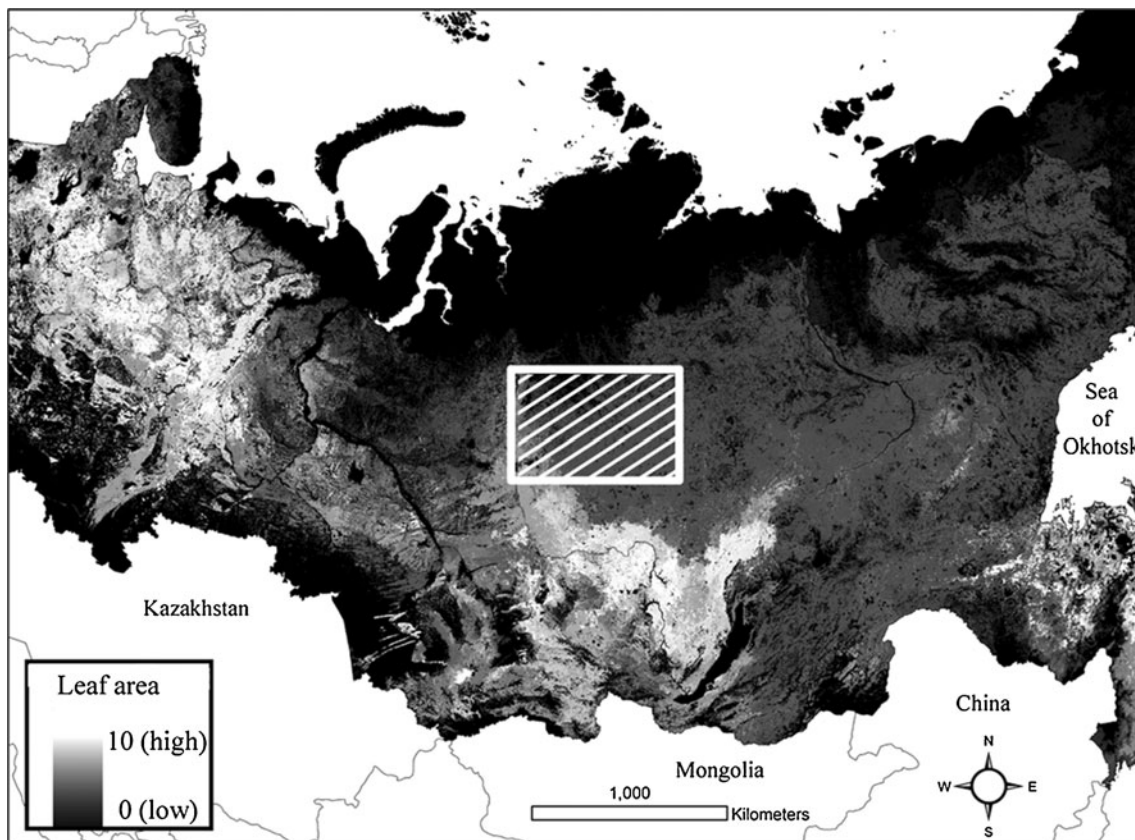
The FAREAST model simulates forest stands the size of a large canopy tree gap, an area large enough to consider the size and structural dynamics of a forest with sufficient replicates (Shugart 1984). Three different sub-modules operate within FAREAST to simulate the growth and dynamics of a forest stand. A growth module annually and incrementally adjusts tree structure using equations related to tree diameter growth, height growth, leaf area dynamics, light transmission through the forest canopy, light-productivity relationships, nutrient limitation, and wood volume (Xiaodong and Shugart 2005). Life history and successional dynamics are governed by both a regeneration sub-module, which simulates seed bank dynamics, and a mortality sub-module, which simulates leaf and fine root, branch, and tree death using species-specific parameters (Xiaodong and Shugart 2005). These three sub-modules are governed and interact with an environmental module which addresses climatic and nutrient dynamics. Species parameters were derived from the NEWCOP model (Yan and Zhao 1996), stand data of Russian forests (Nikolov and Helmisaari 1992), and a suite of collections of Siberian forest stand data (see Xiaodong and Shugart 2005 for a full list). FAREAST thus represents one of the most comprehensive efforts to date to simulate Russian boreal forest dynamics.

The FAREAST gap model was used to simulate 609 forest plots within the International Geosphere-Biosphere Program Global Change and Terrestrial Ecosystems (IGBP-GCTE) Central Siberian Transect (CST) (Steffen and Shvidenko 1996) distributed equally along the central one third of the transect (Fig. 1). In order to simulate forest response at each location, environmental conditions in the area encompassing each plot were used to drive the FAREAST model. Soil values for these sites were derived from the Land Resources of Russia IIASA database (Stolbovoi and McCallum 2002). A list of soil variables used in FAREAST can be found in Xiaodong and Shugart (2005). Climate information for each site was derived from a 60-year record of conditions at weather stations across Russia (Razuvayev et al. 1993).

Each of the 609 sites was simulated using climate inputs derived from the historical weather station data; these simulations were used to represent the control scenario. For the temperature change scenario simulations the 609 sites were modeled again and monthly mean temperatures were incrementally increased for a period of 100 years. Three different temperature increase scenarios were simulated: a 2, 4, and 6 °C overall increase by the end of the 100-year period.

Temperature ramp studies have been used to serve as initial guides in understanding climate and forest dynamics (Urban et al. 1993) and these three scenarios represent gradations of expected temperature increases throughout Siberia based on the HadCM3 A2 and B1 scenarios for the region, highlighting both minimal (2 °C increase) and more severe (6 °C increase) results. While precipitation has been assessed in other simulation experiments in Siberia using FAREAST (Shuman and Shugart 2009), projections for definitive precipitation change within the study area are mixed, with slight increases in the middle latitudes and decreases at the southern margins (Tchebakova et al. 2011). Analysis was thus limited to changes in temperature for this sensitivity experiment. Each site run involved the simulation of 200 replicate plots; the average output of all 200 plots was calculated in order to account for variability among individual stands. This procedure is commonly used in gap model simulations (e.g., Xiaodong and Shugart 2005; Shuman and Shugart 2009).

To determine the sensitivity of stands of different successional states to temperature increase each of the 609 sites was simulated initially under historic climate, and then, upon reaching a set stand age, temperature increase was triggered and the simulation continued for 100 years until the maximum



**Fig. 1** The study area within the Central Siberian Transect. A total of 609 sites at equally spaced 20-km intervals were simulated by the FAREAST model and the general area is represented by the hashed

box. These sites were generally composed of a mix of Siberian larch (*Larix sibirica*), Siberian Silver birch (*Betula platyphylla*), and Siberian pine (*Pinus sibirica*)

temperature was reached. Figure 2 displays three of the five stand age simulation designs (stand ages of 25 and 100 years are not shown). A total of five stand ages were examined for the 4° scenario (0, 25, 50, 100, and 200 years) and three stand ages were examined for the 2° and 6° scenarios.

The total stem count, maximum DBH, LAI, total above-ground biomass, and the ratio of evergreen to deciduous biomass for each site under all scenarios were compared to the current climate run of the same age. Multivariate statistical analysis using canonical discriminant analysis was performed in order to investigate the sensitivity of different stand ages and to indicate which forest output variables were most sensitive to temperature increase. Comparisons of individual variables comparison between simulations of historical climate and a temperature increase scenario were performed using repeated measures MANOVA in order to investigate those variables highlighted by the canonical discriminant analysis.

Canonical discriminant analysis derives a linear combination of the output variables and identifies the combination with the largest multiple correlation among groups. In this case, the groups were the baseline climate runs and climate change runs. Computationally, this procedure is equivalent to a canonical correlation analysis between the plot variables and “dummy” variables which are derived from the class variable (SAS Institute Inc 2008). If the sample covariance matrix for the dummy ( $y$ ) and the quantitative ( $x$ ) variables is:

$$S = \begin{pmatrix} S_{xx} & S_{xy} \\ S_{yx} & S_{yy} \end{pmatrix} \tag{7}$$

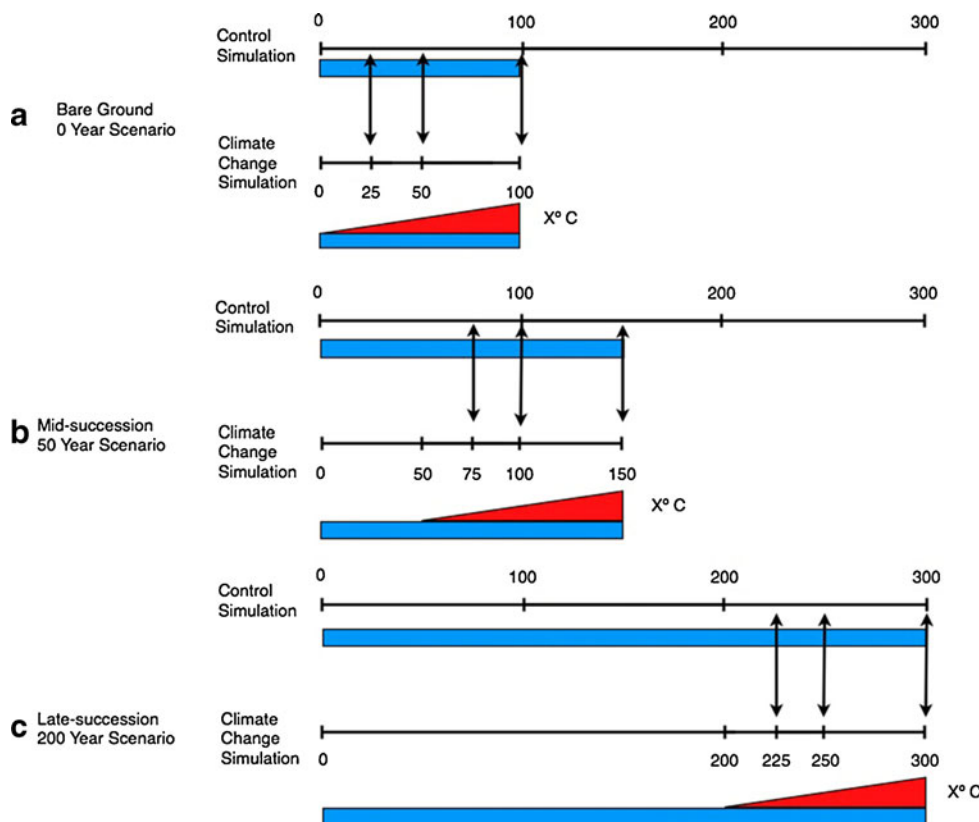
then the within-class pooled covariance matrix for the quantitative variables, if  $c$  is the number of groups,  $n_t$  is the number of observations in group  $t$ , and  $S_t$  is the sample covariance matrix for the quantitative  $x$  variables in the group (SAS Institute Inc 2008), is:

$$S_p = \frac{1}{\sum (n_t - 1)} \sum (n_t - 1) S_t \tag{8}$$

The canonical correlations, which describe the ability of the discriminant function to differentiate the two groups, are then the square roots of the eigenvalues of the resulting matrix. In this situation, a higher canonical correlation indicates a larger deviation between simulated forests with historical climate and simulated forests with temperature increase.

Discriminant function analysis requires several assumptions and actions, all of which were satisfied. Firstly, all sample sizes were equal. Secondly, all data represented a multivariate normal distribution. Thirdly, nine outliers showing a complete lack of forest growth, which resulted from the lack of a correct field capacity input from the collected spatial data, were eliminated from the analysis using a visual interpretation of the distributions. As the number of outliers was small compared to the total number of sites, the removal of these outliers was assumed to have a minimal statistical effect

**Fig. 2** Methodological timeline of FAREAST simulations. Forests were simulated under historical climate for 0 (a), 50 (b), and 200 (c) years before temperature was incrementally increased over the following 100 years. Canonical discriminant analysis was performed using model output at 25, 50, and 100 years into the temperature change scenarios as indicated by the arrows



on the results and these sites were not re-run. Finally, all independent variables had low collinearity with each other; only one set of variables, stand LAI and total biomass, contained a collinearity  $r$  of  $x > 0.65$ . Raw canonical coefficients for the first discriminant function were calculated as:

$$R = S_p^{-\frac{1}{2}}V$$

where  $V$  is the matrix of eigenvectors corresponding to non-zero eigenvalues (SAS Institute Inc 2008). These raw values were standardized and express the relative strength and importance of each stand variable in the discriminant procedure.

### 3 Results

Table 1 displays the canonical correlations of discriminant procedures comparing forests modeled with historical climate and increased temperatures. All results have  $p$  values of  $< 0.001$ . Three different temperature increase scenarios are represented: a  $2^\circ$  increase (A), a  $4^\circ$  increase (B), and a  $6^\circ$  increase (C). For each temperature scenario, the canonical correlation for different stand ages (the rows) and different time points within the simulation (the columns) are given. In this way, one can compare the relative degree of change as indicated by all the modeled forest variables for a multitude of temperature increase scenarios and stand ages. Large values indicate a greater success of the discriminant procedure and indicate a greater quantitative difference between the control and the increased temperature scenario.

At 25 years into the climate increase simulation (column 1), canonical correlations for the bare ground (0 years) and late-succession (200 years) are 0.57 and 0.55 for the  $4^\circ$

scenario. Forests at a stand age of 100 years, however, did not change as severely and the analysis resulted in a canonical correlation of 0.24. A similar trend is evident in the  $2^\circ$  scenario, in which the canonical correlation drops for stands in mid-succession (in this case, at 50 years). However, at years 50 and 100 of the simulations, this trend does not stay consistent. Increasing forest change with increasing temperatures is exacerbated in the  $6^\circ$  warming scenario (C). Here, forests change very quickly by simulation year 25 and by simulation year 100, mid-successional forests are no more resistant to change than stands of other ages.

In addition to describing the magnitude of change that occurs in forests with warming temperatures, the discriminant function analysis provides us with information on which biophysical variables changed the most. This information is represented by the standardized coefficients in Table 2 for the  $4^\circ$  scenario. Total biomass is the variable with the largest standardized coefficient across all stand ages. Total stand leaf area index, another measure of productivity, was also frequently greater in magnitude than other variables, particularly in late-successional forests (200 years) which experienced warmer.

A more detailed analysis of model simulations revealed how two particular forest properties changed throughout the experiment. Stand biomass, a measure of productivity, and a property highly related to temperature, was noticeably affected. Stands which encounter a warming climate at year 0, when compared to simulated forests with no temperature increase, experience stand turnover beginning at year 70 (Fig. 3b) whereas under historic conditions, no turnover is evident through 100 years of simulation (Fig. 3a). Mid-successional stands which encounter temperature increases at an age of 50 years (Fig. 3d) also noticeably decline and

**Table 1** Canonical correlations for  $2^\circ$ (A),  $4^\circ$ (B), and  $6^\circ$ (C) increases in temperature for the study area when compared to the base case

In all cases Year 100 of the simulation had larger canonical correlations indicating a greater degree of change compared to the base case. Notice the difference between mid-successional (stand age of 50 years) and late-successional (stand age of 200 years) values, indicating resistance of mid-successional stands and vulnerability for old-growth stands. This trend decreases with a larger magnitude of temperature increase

Canonical correlations				
Beginning stand age	Simulation year 25	Simulation year 50	Simulation year 100	
(A) 2 degree increase				
0 years	0.345	0.535	0.711	
50 years	0.188	0.366	0.636	
200 years	0.334	0.524	0.73	
(B) 4 degree increase				
0 years	0.57	0.771	0.904	
25 years	0.467	0.797	0.893	
50 years	0.381	0.621	0.822	
100 years	0.244	0.782	0.853	
200 years	0.546	0.746	0.896	
(C) 6 degree increase				
0 years	0.715	0.874	0.93	
50 years	0.518	0.771	0.886	
200 years	0.664	0.852	0.9	

**Table 2** Standardized coefficients for the 4 °C increase scenario

0 Years of spinup			
Variable	Year25	Year50	Year100
Sum stem	-0.441	0.372	0.703
Max DBH	-0.343	0.240	-0.054
SUM LAI	-0.806	1.517	0.250
SUM BIO	2.087	1.558	1.700
E/D Bio	0.214	-0.259	0.343
25 Years of spinup			
Sum stem	0.186	0.837	0.824
Max DBH	0.124	-0.308	0.027
SUM LAI	1.217	0.481	0.059
SUM BIO	1.174	1.019	1.604
E/D Bio	-0.123	0.257	0.299
50 Years of spinup			
Sum stem	0.593	0.420	0.088
Max DBH	-0.524	0.027	0.147
SUM LAI	0.517	0.334	-0.174
SUM BIO	1.072	1.138	1.801
E/D bio	0.013	0.035	0.342
100 Years of spinup			
Sum stem	0.616	1.311	0.150
Max DBH	-0.315	0.023	-0.011
SUM LAI	-0.123	-0.044	2.944
SUM BIO	1.414	0.654	-1.134
E/D bio	0.291	0.102	-0.603
200 Years of spinup			
Sum stem	0.603	-0.534	-0.290
Max DBH	0.472	-0.705	-0.448
SUM LAI	-3.321	2.744	0.978
SUM BIO	2.544	-1.122	1.618
E/D Bio	0.964	-0.607	0.003

The five variables listed are those used in the discriminant analysis procedure and are: the sum of all stems within the plot, the maximum diameter at breast height of any tree within the plot, the sum of the leaf area index of the stand, the sum of the biomass in tons of carbon per hectare for the stand, and a ratio of the Evergreen to deciduous biomass for these species within the stand

turnover 70 years into temperature increase with some stands losing over two third of their total biomass, in contrast to when simulated under historic conditions (Fig. 3c). Stands that encounter increased temperatures from year 200 to year 300 in their life cycle (Fig. 3f) also decline at 70 years into the warming trend. Older forests ( $x > 200$  years) that do not encounter increased temperatures (Fig. 3e) do not show this partial collapse. A repeated measures MANOVA was performed to compare biomass between control and temperature increase simulation runs. For all temperature increase scenarios, biomass increased significantly ( $p < 0.001$ ). Analysis of the evergreen to deciduous ratio of biomass

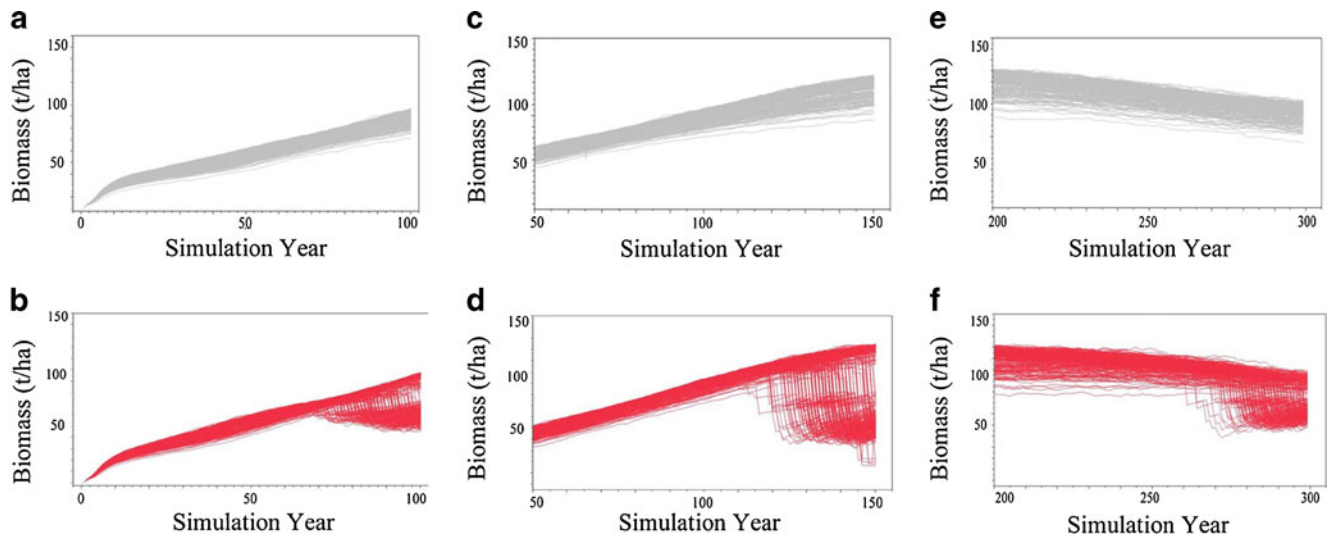
for each scenario (Fig. 4) and the biomass of larch, pine, and birch (Fig. 5) reveals the influence of climate upon forest species composition.

#### 4 Discussion

Results of this sensitivity study suggest that boreal forests in this region may respond differently depending on the stand age at which they encounter increased temperatures. At low levels of temperature increase (the 2° scenario), mid-succession stands represented by forests at an age of 50 years, changed more slowly and less significantly than forests which encountered higher temperatures at a stand age of 200 years. These results mimic previous observations of mature and old-growth forests changing with slow warming trends by Allen et al. (2010) which reviewed documented old-growth forest mortality due to temperature stress.

Temperature increases frequently result in greater vapor pressure deficits within trees and cause plant water loss through transpiration (Allen et al. 2010). This mechanism is captured within FAREAST through the calculation of evapotranspiration wherein monthly temperature values are incorporated and a bucket soil–water model is used, following Hargreaves and Allen (2003). This simulation of increased water loss lowers annual tree diameter growth through a drought parameter in the growth sub-module. Field studies have concluded that decreased individual growth can increase the likelihood of individual mortality (Monserud 1976), particularly when growth is below a threshold of 10 % of the optimal growth per year (Hawkes 2000; Dai et al. 2012). Since this entire mechanism is contained within FAREAST, temperature-related mortality and decreases in biomass shown in these simulations is likely a result of this same process, wherein increased water stress decreases stem growth and increases the likelihood of mortality of branches and individuals.

Decreases in annual growth and increased mortality of old-growth forests in Asian boreal forests have been documented within the literature. Dai et al. studied forests on Changbaishan Mountain, an area used to test and validate FAREAST (2012). Analyzing 30 years of radial growth increments from forests within the reserve, they observed decreased radial growth, high tree mortality, and a decrease in biomass storage of old-growth spruce-fir forests. While the main species collapsing as a result of temperature increase in our simulations were Siberian larch, these results are similar in that both species faced temperature increases beyond their realized niche. Similarly, both spruce within Dai et al.'s study and larch in our simulation study, have maximum age ranges of under 300 years (2012). Further testing on forests in Northwestern Russia with longer



**Fig. 3** Stand biomass in tons/hectare (y-axis) for control (a, c, e) and 4° temperature increase (b, d, f) scenarios at different time periods (x-axis) within a stand life cycle. Stands from 0–100 years (a, b), 50–

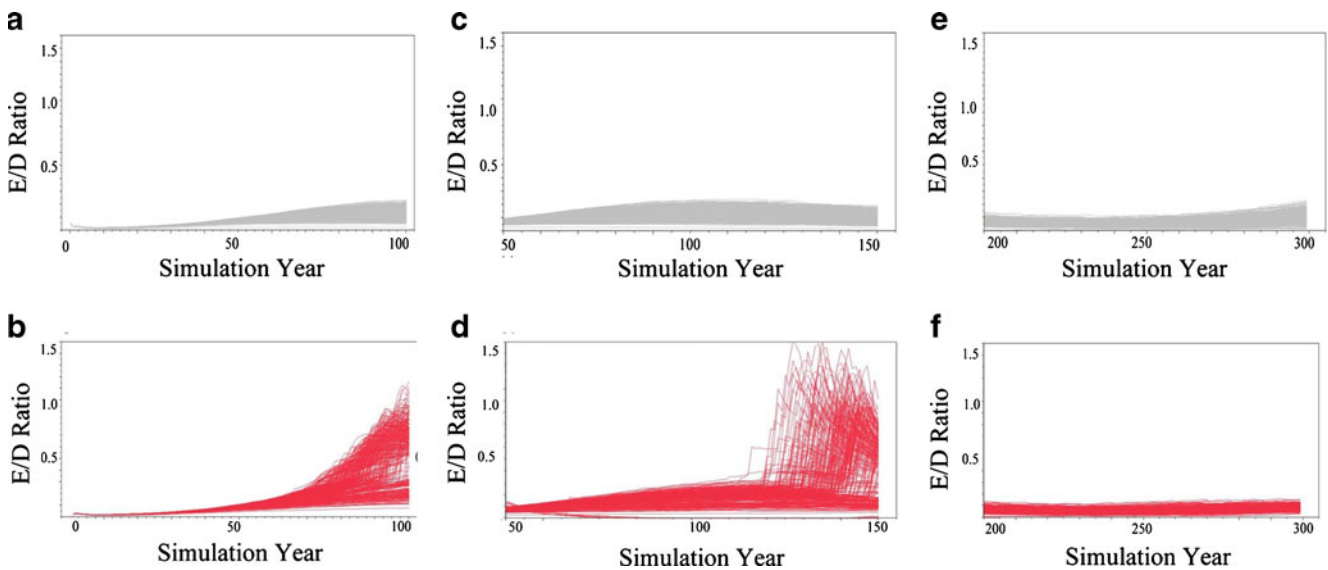
150 years (c, d), and 200–300 years (e, f) are shown for comparison. Biomass significantly decreases 60–70 years after temperatures amplify for all scenarios (b, d, f)

expected life spans are necessary to fully understand how these two factors interact and refine our estimates.

In more rapid warming scenarios, mid-successional stands (aged 50 and 100 years) show no noticeable increased resistance to warmer temperatures than old-growth stands (Table 1 (B and C)). As the magnitude of temperature increase became more drastic, forests of all ages changed at rates similar to one another. These results are surprising, as traditional models of disturbance and forest succession generally indicate vulnerability in older forests to change. For example, Holling, in his adaptive cycle framework, suggests several phases of forest

growth which differ in their proclivity to release and stand reorganization (Holling 1986). In particular, old-growth forests are considered within a conservation phase and close to the event of an ecological release. Modeling results from this study suggest that at rapid warming rates, these traditional phases may be blurred.

The sequestration of carbon by managed forests has been suggested as a key methodology to reduce greenhouse gases in the atmosphere, particularly in the context of avoided deforestation strategy. Enhanced productivity in boreal forests in response to projected temperature increase has been

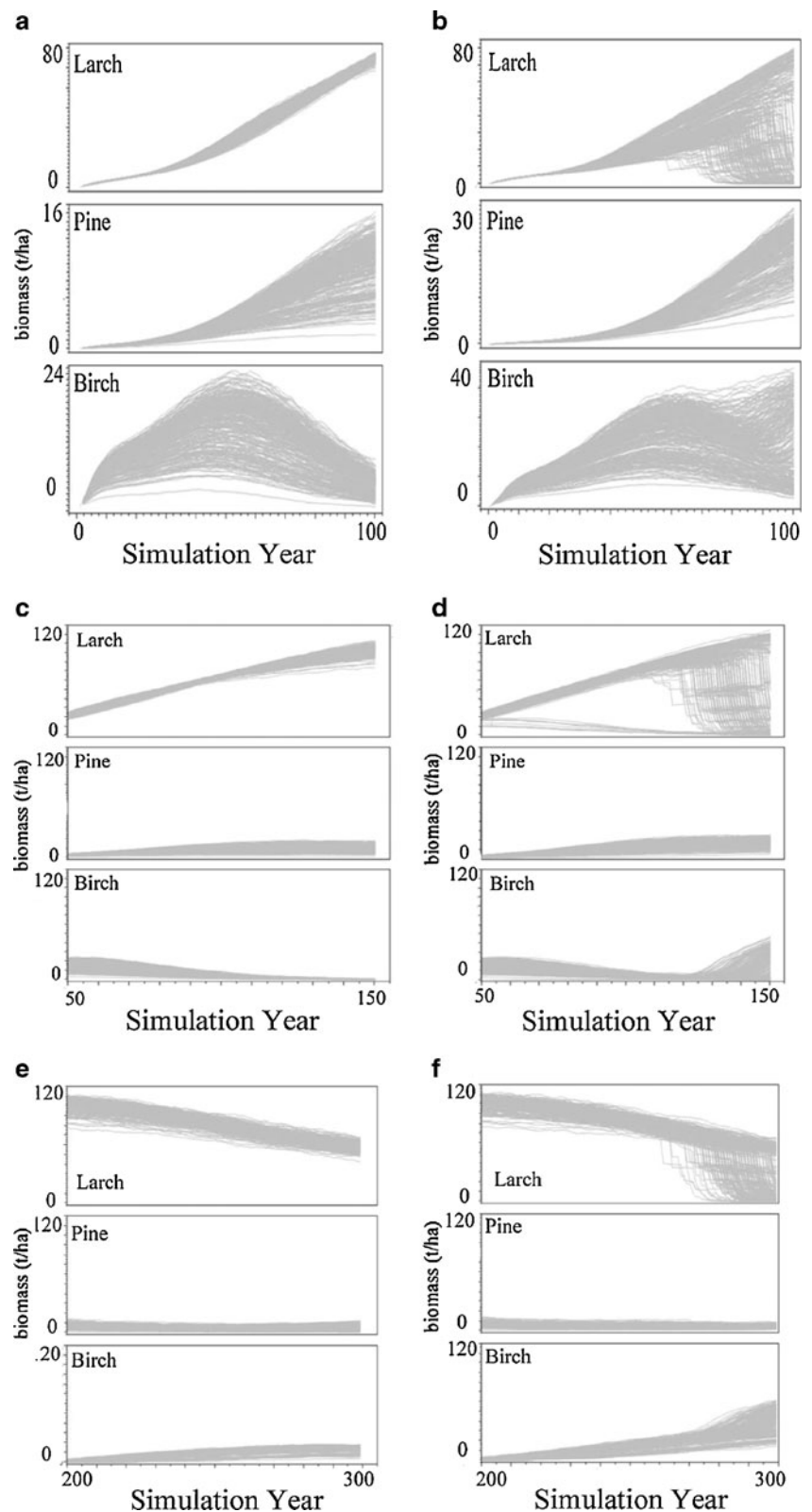


**Fig. 4** The ratio of evergreen species biomass to deciduous species biomass (t/ha, y-axis) for control (a, c, e) and 4° temperature increase (b, d, f) scenarios at different time periods (years, x-axis) within a stand life cycle. Stands from 0–100 years (a, b), 50–150 years (c, d), and 200–

300 years (e, f) are shown for comparison. With increased temperatures, evergreen species (*P. sibirica*) increase while the deciduous Siberian larch collapses. In the 200–300-year time period, Siberian birch increase balances Siberian larch collapse and maintains the E/D ratio



**Fig. 5** Larch, pine, and birch biomass for control (a, c, e) and 4° temperature increase (b, d, f) scenarios at different time periods within a stand life cycle. Stands from 0–100 years (a, b), 50–150 years (c, d), and 200–300 years (e, f) are shown for comparison. In early-successional stands (b), pine and birch increase their abundance at the expense of larch. However, forests which encounter temperature increases further into succession do not see a replacement of larch by pine; only birch manages to increase in biomass (d, e)



thought to increase forest yield and carbon sequestration in tree biomass (Kellomäki and Väisänen 1997), although increased drought stress, particularly in the southern boreal zone, has been thought to balance out productivity gains

through tree mortality (Briceño-Elizondo et al. 2006). In these simulations, stand biomass values declined in the 4° scenario once larch populations collapsed and were replaced by Siberian pine and Siberian Silver birch throughout the

simulation. Other modeling studies have projected similar losses in overall carbon sequestration when forest composition is altered in boreal forests (Kellomäki et al. 2008). While in the first 50 years of the simulation stands show increased productivity, stand transition into an alternative state of birch/pine ultimately results in a forest with lower carbon storage capacity. The transition from a larch-dominated forest to one of birch aligns with other previous predictions of boreal forest response (Bonan 2008; Thuiller et al. 2006, Kellomäki et al. 2008).

Forest management strategies which consider the effects of warmer temperatures consistently call for rapid and definitive prioritization of vulnerable areas requiring substantive action (Spittlehouse and Stewart 2003; Millar et al. 2007). This research suggests that late-successional forests are more likely to experience biophysical changes due to warm temperatures even at low-level warming scenarios, however, forests at all successional stages will change in their community composition. Research in Finland has described decreasing northern boreal bird species abundance due to climate shift and decreasing habitat area (Virkkala and Rajasärkkä 2011) and these projects suggest similar declines in larch-dependent bird populations will also occur in central Siberia due to a loss of larch habitat. Forests that are already in mid- to late-succession may not encounter such rapid change because Siberian pine does not appear from these simulations to encroach over the 100-year simulation period; therefore, these areas may serve as refuges for northern boreal bird species.

The ability of old-growth forests to act as permanent sinks for carbon in a warmer landscape has been a subject of recent discussion in the scientific community (Luyssaert et al. 2008) and is of interest for adaptive forest management. Forests of all stand ages increase in short-term carbon storage with warming, but decline when warming induces larch collapse. This result indicates that although old-growth forests in boreal Russia may serve as a potential carbon sink in the short-term and under low levels of temperature increase, they are likely also to be the harbingers of boreal response to climate and store less carbon than previously thought. The age-dependent response of forests to warmer temperatures in our simulations disappears in situations with rapid temperature increase, as all stands appear to be equally affected. In summary, large temperature increases may render forests in central Siberia of all ages equally susceptible to biophysical changes and may not provide the carbon sink that could be useful for carbon sequestration projects.

**Acknowledgments** The authors would like to thank Karen Vandecar, Miles Silman, Howard Epstein, David McGuire, and two anonymous

reviewers. Funding for this project comes from NASA CARBON NNG-05-GN69G, the Civilian Research and Development Foundation Joint Climate Change Grant, and the University of Virginia Presidential Fellowship.

## References

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 4:660–684
- Bodin P, Wiman BLB (2007) The usefulness of stability concepts in forest management when coping with increasing climate uncertainties. *For Ecol Manag* 242:541–552
- Bolte A, Ammer C, Löff AC, Naburs G-J, Schall P, Spathelf P (2009) Adaptive forest management: a prerequisite for sustainable forestry in the face of climate change. *Manag For Ecosyst* 19:115–139
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449
- Bradshaw CJA, Warkentin IG, Sodhi NS (2009) Urgent preservation of boreal carbon stocks and biodiversity. *Trends Ecol Evol* 24:541–548
- Briceño-Elizondo E, Garcia-Gonzalo J, Peltola H, Matala J, Kellomäki S (2006) Sensitivity of growth of Scots Pine, Norway Spruce, and silver birch to climate change and forest management in boreal conditions. *For Ecol Manag* 232:152–167
- Chapin FS, Randerson JT, McGuire AD, Foley JA, Field CB (2008) Changing feedbacks in the climate-biosphere system. *Front Eco Environ* 6:313–320
- Dai L, Jia J, Yu D, Lewis BJ, Zhou L, Zhou W, Zhao W, Jiang L (2012) Effects of climate change on biomass carbon sequestration in old-growth forest ecosystems on Changbai Mountain in Northeast China. *For Ecol Manag*. doi:10.1016/j.foreco.2012.06.046
- Füssel H-M, Klein RJT (2006) Climate change vulnerability assessments: an evolution of conceptual thinking. *Clim Change* 75:301–329
- Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. *Proc Nat Acad Sci* 103:14288–14293
- Hargreaves GH, Allen RG (2003) History and evaluation of Hargreaves' evapotranspiration equation. *J Irrig Drain E* 129:53–63
- Hawkes C (2000) Woody plant mortality algorithms: descriptions, problems and progress. *Ecol Model* 126:225–248
- Holling CS (1986) The resilience of terrestrial ecosystems: local surprise and global change. In: Clark WC, Munn RE (eds) Sustainable development of the biosphere. Cambridge University Press, Cambridge, pp 292–317
- Houghton RA, Butman D, Bunn AG, Krankina ON, Schlesinger P, Stone TA (2007) Mapping Russian forest biomass with data from satellites and forest inventories. *Environ Res Lett* 2:045032
- Kellomäki S, Peltola H, Nuutinen T, Korhonen KT, Strandman H (2008) Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. *Phil Trans R Soc B* 363:2339–2349
- Kellomäki S, Väisänen H (1997) Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecol Model* 97:121–140
- Kolström M (1998) Ecological simulation model for studying diversity of stand structure in boreal forests. *Ecol Model* 111:17–36
- Luyssaert S, Schulze ED, Börner A, Knohl A, Hessenmöller D, Law BE, Ciais P, Grace J (2008) Old-growth forests as global carbon sinks. *Nature* 455:213–215

- Meleshko VP, Kattsov VM, Mirvis VM, Govorkova VA, Pavlova TV (2008) Climate of Russia in the 21st Century. Part 1. New evidence of antropogenic climate change and the state of the art of its simulation. *Russ Meteor Hydro* 33:341–350
- Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecol Appl* 17:2145–2151
- Monserud RA (1976) Simulation of forest tree mortality. *For Sci* 22:438–444
- Nikolov N, Helmisaari (1992) Silvics of the circumpolar boreal forest tree species. In: Shugart HH, Leemans R, Bonan GB (eds) *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge, pp 9–84
- Noss RF (2001) Beyond kyoto: forest management in a time of rapid climate change. *Conserv Biol* 15:578–590
- Ogden AE, Innes J (2007) Incorporating climate change adaptation considerations into forest management planning in the boreal forest. *Int Forest Rev* 9:713–733
- Razuvayev VN et al (1993) Daily temperature and precipitation data for 223 U.S.S.R. Stations. ORNL/CDIAC, numerical data package 040. Oak Ridge National Laboratory, Oak Ridge
- Institute Inc SAS (2008) SAS/STAT 9.2 User's Guide. SAS Institute Inc, Cary
- Scheller RM, Mladenoff DJ (2007) An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecol* 22:491–505
- Shugart HH (1984) *A theory of forest dynamics: the ecological implications of forest succession models*. Springer, New York, p 278
- Shugart HH, Leemans R, Bonan GB (2005) *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge, 580 p
- Shuman JK, Shugart HH (2009) Evaluating the sensitivity of Eurasian forest biomass to climate change using a dynamic vegetation model. *Environ Res Lett* 4:1–7
- Shuman JK, Shugart HH, O'Halloran TL (2011) Sensitivity of Siberian larch forests to climate change. *Glob Change Bio* 17:2370–2384
- Soja A, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS III, Stackhouse PW Jr (2007) Climate-induced boreal forest change: predictions versus current observations. *Glob Planet Change* 56:274–296
- Solberg B, Moiseyev A, Maarit A, Kallio I, Toppinen A (2010) Forest sector market impacts of changed roundwood export tariffs and investment climate in Russia. *For Pol Econ* 12:17–23
- Spittlehouse DL, Stewart RB (2003) Adaptation to climate change in forest management. *BC J Ecos Manag* 4:1–11
- Steffen WL, Shvidenko AZ (1996) IGBP Northern Eurasia study: prospectus for an integrated global change research project. IGBP Global Change Report 37:1–95
- Stolbovoi V, McCallum I (2002) *Land Resources of Russia*, CD-ROM, IASA and Russian Academy of Sciences. Laxenburg, Austria
- Tchebakova NM, Parfenova EI, Soja AJ (2011) Climate change and climate-induced hot spots in forest shifts in central Siberia from observed data. *Reg Environ Change* 11:817–827
- Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Divers Distrib* 12:49–60
- Urban DL, Harmon ME, Halpern CB (1993) Potential response of Pacific northwestern forests to climatic change, effects of stand age and initial composition. *Clim Chang* 23:247–266
- Urban DL, Shugart HH (1992) Individual-based models of forest succession. In: Glenn-Lewin DC, Peet RK, Veblen TT (eds) *Plant succession: theory and prediction*. Chapman and Hall, London, pp 249–293
- Virkkala R, Rajasärkkä A (2011) Climate change affects populations of northern birds in boreal protected areas. *Biol Letters* 7:395–398
- Xiaodong Y, Shugart HH (2005) FAREAST: a forest gap model to simulate dynamics and patterns of eastern Eurasian forests. *Jour Biogeogr* 32:1641–1658
- Yan X, Zhao S (1996) Simulating the response of Changbai Mountain forests to potential climate change. *J Environ Sci* 8:354–366
- Zhang N, Yasunari T, Ohta T (2011) Dynamics of the larch taiga-permafrost coupled system in Siberia under climate change. *Environ Res Lett* 6:024003