Forest Sciences Project Y09-2200:

Assessing ecosystem vulnerability to climate change from the tree- to stand- to landscape-level

The influence of disturbance type, competition and resource availability on species response to climate change in northwest British Columbia, Canada

Technical Report and Draft Manuscript

Prepared in partial fulfilment of Year 2 Project deliverables for the:

British Columbia Forest Sciences Program
The Province of British Columbia

By:

Dr. Craig Nitschke and Dr. Rasmus Astrup

Bulkley Valley Research Centre
Smithers, British Columbia

April 2009

Abstract

The incorporation of dynamics and disturbance is important for understanding the impacts of climate change on species response. In this study we investigated the biotic interactions (competition) between species, the influence of disturbance type, and changes in resource availability (moisture, substrate, and light) on the response of four tree species to climate change in the northwest region of the sub-boreal forest in central British Columbia, Canada. Two ecological models were parameterised using field data and linked together to explore the interactions between the response of species in their fundamental regeneration niche to climate change and the role of disturbance, resource availability and competition on determining a species realised niche under climate change. Climate change was found to reduce soil moisture availability which resulted in a decline in regeneration potential for all species on dry sites and negative to neutral responses on mesic to moist sites. Stand dynamics and composition where predicted to undergo significant changes under the 2080s climate compared to current climate conditions. Species response was exacerbated following fire particularly on dry to mesic sites with lower intensity bark beetle disturbances mediating the response of the ecosystems *Picea* and *Abies* species. Site type also had an influence in interaction with disturbance type with the site with the highest moisture availability maintaining the same stand dynamics and composition following bark beetle disturbances under climate change. This study highlights the need to consider species response to climate change in interaction with existing stand conditions, disturbance type, competition, resource availability, not just climate.

Keywords: competition; climate change; disturbance; SORTIE; modelling; resource availability; stand dynamics

Introduction

In Western Canada, climate change is predicted to increase both winter and summer temperatures while precipitation is predicted to increase in the winter and either increase or decrease in the summer (Christensen at al., 2007). Theses predicted changes in climate are expected to have significant impact on forest ecosystems through increases in disturbance events such as drought, fire, insect and disease outbreaks which in turn will facilitate the migration of species to new ranges, where possible, and extirpation or extinction where not, which may lead to changes in ecosystem compositions (Gitay et al. 2002; IPCC 2007). The shift in species distributions is expected to occur along environmental gradients if their environmental tolerances are exceeded (Miller and Urban 1999). These shifts will be complex since species have different physiological and climatic requirements which may make it difficult to determine whether shifts will be due to direct responses to climate change or indirectly through interactions with other species (Brzeziecki et al. 1995). It is typically assumed that species distributions are in equilibrium with climate however this assumption cannot be applied globally and must be considered on a species by species basis (Pearson and Dawson 2003; Araújo and Pearson 2005). At the macro scale, climate is the principal driver of species distributions (Huntley et al. 1995); however, autogenic, allogenic, and biogenic effects interact with species ecophysiology and resource availability to affect species distributions at finer scales (Pearson et al. 2004; Guisan and Thuiller 2005). Autogenic interactions are driven by competition between individuals and species which can have a significant influence on species distributions (Araújo and Luoto 2007). Araújo and Luoto (2007) argue for the need to consider these interactions, particularly competition, at both the site and landscape-level to improve our ability to assess the impact of climate change on species distributions.

Allogenic factors such as fire, drought, frost, etc as well as biogenic factors such as insect epidemics and diseases all interact with resource availability to affect species distributions, presence and abundance (Pulliam 2000; Kimmins 2004). These interactions can be both spatially and temporally complex with biotic interactions occurring in one time period or at one scale that may not hold true in another due to changes in climate (Araújo and Luoto 2007). The type, severity and timing of disturbance events (allogenic or biogenic) also influences species distributions which can lead to declines in abundance and range of one species and the expansion of others at the site and landscape-scale (see Allen and Breshears 1998). The magnitude and/or frequency of a disturbance interacting with each species' unique physiology, demographics and life-cycle characteristics can cause divergent responses (Walker 1989). Species are also known vary in their tolerance to environmental stresses in different parts of their life cycle with their highest sensitivity occurring during their regeneration phase (Bell 1999). This creates a potential interaction between species regeneration potential under both climate and the resources made available by the disturbance type. Astrup et al. (in press) found that disturbance type can have a significant impact on the ability of sub-boreal tree species to regenerate which is leading towards shifts in stand composition due to resource availability (substrate and light). The inclusion of both competitive and biotic and abiotic agents was identified by Guisan and Zimmerman (2000) as important attributes for being able to differentiate between the fundamental and realised niches of species allowing for improved predictions of species response to changing environmental conditions.

To understand the responses of vegetation to changes in climate modelling is typically used predict individual species, ecosystem or biome responses (Zolbrod and Peterson 1999). Biome modelling generally focuses on broad life-forms or plant functional types versus individual species (Neilson 1995; Eeley et al. 1999; Gavin and Brubaker 1999). This generally results in species-specific responses being masked by the broad scale of the analysis (Bakkenes et al. 2002; McKenzie et al. 2003a). Individual species modelling is typically done using one of two techniques: statistical modelling (e.g. Iverson and Prasad 2001; Schwartz et al. 2001; Thuiller et al. 2005) or mechanistic modelling (e.g. Prentice et al. 1992; Sykes and Prentice 1995; Cumming and Burton 1996; He et al. 1999; Miller and Urban 1999; Zolbrod and Peterson 1999). Statistical models generally take the form of bioclimatic envelope models and typically assume that species are at equilibrium with climate and do not consider biotic and abiotic factors directly (Fischlin and Gyalistras 1997; Guisan and Zimmerman 2000; Thuiller et al. 2005; Araújo and Luoto 2007). These types of models generally reflect the realised (i.e. ecological niche) of species but provide no explanation of the physiological mechanisms that may drive change and are poor predictors species dynamics under changing environmental conditions (Guisan and Zimmerman 2000; Kimmins 2004). These models are also sensitive to the spatial extent and resolution of data used for their development, which limits the ability to extrapolate over space and time (McKenzie and Halpern 1999). Despite these limitations these models can be useful for modelling species responses at multiple scales if both direct climatic and resource factors are used but where abiotic (disturbance) and biotic (competition) factors are not considered (Guisan and Zimmerman 2000). The incorporation of dynamics and disturbance is important for understanding the impacts of climate change on species response and requires the use of mechanistic modelling to provide more accurate predictions of species response to climate change (see Guisan and Zimmerman 2000).

In this study we investigate the biotic interactions (competition) between species, the influence of disturbance type, and changes in resource availability on the response of four tree species to climate change in the northwest region of the sub-boreal forest in central British Columbia, Canada. Two ecological models were parameterised using field data and linked together to explore the interactions between the response of species in their fundamental regeneration niche to climate change and the role of disturbance, resource availability and competition on determining a species realised (ecological) niche under climate change.

The following research questions are:

- What impact do changes in climatic and resource availability have on the regeneration potential of species?
- Does the interaction between changes in climatic and resource availability and competition increase the sensitivity of species to climate change?
- What is the role of disturbance type on increasing the sensitivity of species to climate change?

- Will the interaction between biotic, abiotic, and climatic factors result in changes in stand dynamics and species composition?

Study Area

Sub-Boreal Spruce Zone

The province of British Columbia it classified into 14 broad ecosystems referred to as biogeoclimatic (BEC) zones (Meidinger and Pojar 1991). The Sub-Boreal Spruce (SBS) Zone is located between 52° and 57° North latitude and 122° and 128° West longitude, between 500 and 1400 m in elevation, within the central interior plateau of British Columbia (BC) (Pojar et al. 1982) (see Fig 1). The SBS zone has a continental climate with warm and moist summers and cold winters with extended periods of snow (Ministry of Forests 1998). The SBS zone is considered a transitional zone between the montane forests of Douglas-fir (*Pseudotsuga menziesii*) in southern BC, the boreal forests of northern BC and the subalpine forests that occur at higher elevations within the central interior (Pojar et al. 1982). The following description of species in the SBS is based on Pojar et al. (1982). The climax forests in the SBS zone are dominated by interior spruce (*Picea engelmanni X glauca*) and subalpine fir (*Abies lasiocarpa*). Lodgepole pine (*Pinus contorta var. latifolia*) is the dominant fire climax species. Early seral stands are dominated by lodgepole pine and trembling aspen (*Populus tremuloides*).

Bulkley Valley Study Area

The study area is located within the Bulkley Valley region of northwest BC (see Fig 1). The study area is approximately 600,000 ha in area and has an elevation range from 356 m to 2736 m. The Sub-boreal Spruce (SBS) ecosystem is found from 500 m to 1100 m.

Figure 1 shows the location of two weather stations within the study area which represent the SBS ecosystem in the Bulkley Valley. The average climate conditions for each station are presented in Table 1, the average climate conditions for the entire SBS zone within the study area are presented in Fig. 2. Sampling plots established within the study area have identified that the dominant tree species within the study area are interior spruce, subalpine fir, lodgepole pine and trembling aspen.

<Fig 1>

<Table 1>

<Fig 2>

Methods

Ecological Models

SORTIE-ND is a spatially-explicit simulation model that is used to study stand-level forest dynamics and has been parameterised for use in the sub-boreal forests of British Columbia (Kobe and Coates 1997; Coates et al. 2003). SORTIE-ND is a descendent of SORTIE, developed by Pacala et al. (1993; 1996). The model predicts individual tree growth, survival, dispersal and recruitment as a function of light availability throughout the growing season in relation to its neighbourhood (Pacala et al. 1993). SORTIE-ND also allows for the simulation of disturbance events that affect resource availability (Pacala et al. 1993; Coates et al. 2004).

The ecological model, TACA (Tree And Climate Assessment) (Nitschke and Innes 2008), was modified and parameterised for use in the Sub-Boreal Spruce (SBS) ecosystems of the province. TACA is a mechanistic model that analyses the response of trees in their fundamental regeneration niche to climate-driven phenological and biophysical variables. It conducts a sensitivity analysis to determine the probability of species presence under a range of climatic and edaphic conditions. The modelling of species presence reflects the fundamental regeneration niche of a species, because presence is directly related to establishment (McKenzie et al. 2003). The original TACA model developed by Nitschke and Innes (2008) was modified to incorporate a frost free period mechanism. Hamann and Wang (2006) found that the annual number of frost days had a significant interaction with observed species ranges in BC. The phenology component of TACA was also improved to increase the interaction between chilling, heat sum accumulation, frost, and budburst based on Bailey and Harrington (2006). Previous interaction in the model was limited to the accumulation of a heat sum without considering chilling period length and frost effects during this stage and then frost damage occurring after bud burst. The new phenology component integrates the obtainment of a species chilling requirement with the accumulation of it heat sum which then interacts with frost events that delay bud burst and/ or causes frost damage after bud burst occurs. The soil moisture function was upgraded to the full Penman-Monteith equation (McNaughton and Jarvis 1983; Waring and Running 1998) which is driven by estimates of daily solar radiation based on calculations from Bristow and Campbell (1984) and Ferro Duarte et al. (2006). In addition the soil component of TACA was expanded to allow for three different soil types (texture and depth) to be run simultaneously allowing for the representation of multiple edaphic conditions across the resource gradient used in this study.

Model Parameterisation

Growth, Recruitment, Survival

Seventy one sample plots were established across the SBS zone around Smithers, BC. The sites occur across a resource gradient composed of dry poor sites to wet rich sites. Within each sampling plot the following variables were measured: species composition, stand structure (seedlings, saplings, mature trees), density, basal area, crown openness, growth rates, and growth light indices. The stand structure and growth data were used to calibrate the SORTIE-ND model to represent species growth and stand conditions found across the identified resource gradient.

Soils

At each sample site, soil depth to parent material, rooting zone depth, soil texture was measured. The soil moisture and nutrient class of each site were classified based on the presence and absence of tree, shrub, herb and moss species that are used as indicators for delineating distinct site series (combinations of soil moisture and nutrient classes). Soils were categorised into three soil types based on these soil moisture and nutrient regimes. The first soil type represents crest and upper slope positions and has a loamy sand texture with an average soil depth of 0.75 m and rooting depth of 0.27 m. This soil type represents xeric to sub-xeric (dry and poor) edaphic conditions found across the zone. The second soil type classified represents mid-slope positions and has a sandy loam texture with an average soil depth of 2 m and rooting depth of 0.34 m. This soil type represents sub-mesic to mesic (mesic and medium) edaphic conditions found across the zone. The final soil type classified represents lower slope and level positions and has a loam to silt loam texture with an average soil depth of 2 m and rooting depth of 0.33 m. This soil type represents sub-hygric (moist and rich) edaphic conditions found across the zone.

Climate Parameters

Multiple scenarios of current and future climates are being used to test the sensitivity of species' responses. In modelling climate, we are utilising local climate data and global climate change model (GCM) predictions. A direct adjustment approach is being used to integrate climate change scenarios into the historical climate records for the 2 climate stations that represent the SBS zone in the study area (Table 1). A direct adjustment approach was used by Hamann and Wang (2006) and Nitschke and Innes (2008) to model species response to predicted climate change. Three different GCM's are being used, the Canadian GCM2 (Flato et al. 2000), Hadley CM3 models (Johns et al. 2003) and the CSIROmk2b. The regional climate change predictions for the SBS zone were obtained from the Pacific Climate Impacts Consortium (2009). Multiple climate scenarios were generated following Nakicenovic et al. (2000), who argued that due to the large amount of uncertainty regarding future climate change, multiple scenarios that span a range of possible future climates should be adopted. The Intergovernmental Panels SRES emission scenarios are being used to represent a range of potential future climate conditions (Nakicenovic et al. 2000). The ensemble values of these projections are presented in Table 2.

<Table 2>

Climate transects and microclimatic conditions

To model the response of tree species across the elevation gradient of the SBS zone within the Bulkley Valley, synthetic climate transects were used. This approach has previously been used by Zolbrod and Peterson (1999) to model the response of tree species in the Pacific Northwest of the USA. Using environmental lapse rates for temperature and precipitation (Parker 1994) the climate scenarios were modified to represent climatic conditions at 100 m intervals from 500m to 1100 m in elevation. To represent differences in climate by open and closed canopy conditions the open climatic conditions representative of the weather stations were modified to represent cooler temperatures represented by sheltered conditions (Ashton 1976; Hewlett and Fortson 1982).

Modelling Scenarios

The modelling analysis involved the assessment of stand dynamics following disturbance with the empirically derived SORIE-ND parameters for three site types: Dry and Poor, Mesic and Medium, Moist and Rich. For each site type, three disturbance simulations were applied: fire; mountain pine beetle (*Dendroctonus ponderosae*) attack, and spruce bark beetle attack (*D. rufipennis*). The model was run for the four dominant SBS species in the region for which we have empirical parameters over a time horizon of 200 years. For trembling aspen the ability to regenerate vegetative was enabled while for lodgepole pine the vegetative regeneration parameter was modified to represent its aerial seed bank that is released following disturbance. For each lodgepole pine individual it was assumed that 144 seeds could be released following a disturbance. This was calculated based on the average number of serotinous cones and seeds/ cone found on mature lodgepole pine (Lotan and Critchfield 1990). Interior spruce and subalpine fir lack the ability to re-sprout and have do not form aerial seed banks but they due form large seedling banks in the understory (Alexander et al. 1990; Nienstaedt and Zasada 1990); particularly in the sub-boreal spruce forests of the study area (Astrup et al. in press).

Model Linkage

To incorporate climate change in SORTIE-ND the results from the TACA model were incorporate in two ways. First, the change in regeneration probability between current and predicted climate change was used to modify the establishment parameters for each species. The species response in the current scenarios was as a baseline and the establishment parameters modified by the proportion of change that species exhibit under the climate change scenarios. Secondly, the TACA model tracks changes in moisture availability on a site as a function of actual to potential evapotranspiration. The change in this ratio between climate scenarios was used to determine if the moisture availability at each modelled site type will shift along the resource gradient under climate change. Shifts in moisture availability were used to adjust the growth rates of each species based on the current relationships between moisture regime and growth that exist in other ecosystems in the province.

Statistical Analysis

Statistical analysis of modelling results will be used to determine if differences exist between the response of measured variables under current scenarios and future climate change scenarios. Two-sample Student's t-test and Analysis of Variance (ANOVA) will be performed to test for differences in variable responses (Sokal and Rohlf 1995; Tabachnick and Fidell 2001).

Results

Trees and Climate

The results of the TACA modelling analysis identified that all species may suffer declines in their regeneration potential on xeric sites due to climate change (Fig 3) while lodgepole pine and trembling aspen are likely to exhibit neutral responses on mesic sites (Fig 4) and positive responses on sub-hygric sites (Fig 5). Interior spruce and subalpine fir both exhibited negative responses to climate change on both mesic and sub-hygric sites. These latter two species exhibited the highest sensitivity to climate change on xeric sites followed by mesic then sub-hygric sites which highlights the impact of soil moisture availability on exacerbating and mediating species response to climate change.

<Fig. 3>

<Fig. 4>

<Fig. 5>

Moisture Availability and Productivity

Predicted climate change resulted in a change in soil moisture availability (Fig 6). By the 2080s the soil moisture index for all sites shifts significantly (T-test: $P < 0.001$ in all cases) towards a drier relative moisture gradient with the mesic sites having a moisture index similar to the moisture index of the current xeric sites. The new relative moisture gradient is similar to the relative moisture gradients identified in the north Okanagan by

Nitschke (2006). Nitschke (2006) modelled the moisture index for dry sites in the Interior Douglas Fir (IDF) very dry and hot ecosystem to be 0.54, the IDF moist and warm ecosystem to be 0.57 and in the Montane Spruce dry and mild ecosystem to be 0.64. By the 2080s, the moisture index n the SBS zone of the Bulkley Valley on dry sites was modelled to shift to 0.59. Within the north Okanagan, the IDF dry and mild is an intermediary ecosystem between these ecosystems and was therefore chosen as the proxy ecosystem for determining changes in productivity under climate change. To ensure species response reflected the changes in moisture indices the TACA model was used to explore the response of species that are currently found in the IDF to climate change in the SBS and it was found that the climatic suitability for all species associated with the current IDF dry and mild may be mirrored in the SBS zone within the Bulkley Valley by the 2080s (see Nitschke and Astrup 2008). The congruency between modelled species presence and change in soil moisture indices towards conditions that currently exist in the IDF dry and mild were the two driving factors that support our use of species productivity from this ecosystem to reflect changes in productivity within the SBS zone by the 2080s (see Table 3).

The use of species productivity in this ecosystem assumes that the species in the study area have the adaptive capacity and plasticity to shift productivity in response to changes in temperature and soil moisture availability. Strong clinal variation does exist between populations of these species which will likely result in adaptation lags that may prevent species from capitalising on changes in climate (Aitken et al. 2008). For the purpose of this study we assume that species productivity will shift due to changes in soil moisture and temperature and that using species productivity from a warmer region with soil moisture indices that are similar to those predicted in the future is a sufficient proxy to parameterise the growth rates of species in the future SBS.

<Fig. 6>

<Table 3>

Climate, Competition and Disturbance Interactions

Xeric Sites

On xeric sites a decline in stand basal area was modelled to occur under 2080s climate conditions compared to the current in all disturbance treatments (Figs 7 – 9). For the fire treatment, the decline was not significant (P: 0.095; n = 201) but for the mountain pine beetle (MPB) and spruce bark beetle (SBB) treatments significant declines in basal area were modelled under the 2080s climate (P: < 0.001; n = 201) (Figs 7 – 9). At the species-level, lodgepole pine was modelled to increase in basal area following fire and MPB attack, though these increases were not significant over current climate conditions (P: 0.98 & P: 0.12; n = 201); following SBB attack, lodgepole pine was modelled to increase significantly (P: < 0.001; n = 201). After fire, the remaining three species were all modelled to suffer a significant decline in basal area under the 2080s climate (P: < 0.001; n = 201). Following MPB attack, interior spruce and trembling aspen responded with significant increases in basal area (P: <0.001, n =201), while following SBB attack only interior spruce responded with a significant decline in basal area (P: < 0.001; n = 201). Subalpine fir responded with significant declines in basal area following MPB and SBB attack (P: < 0.001; n = 201) under the 2080s climate. See Figures 7 to 9 for a summary of species responses.

<Fig. 7>

<Fig. 8>

<Fig. 9>

Mesic Sites

On mesic sites an increase in stand basal area was modelled to occur under 2080s climate conditions compared to the current in the MPB and SBB treatments, while basal area remained unchanged following fire (Figs 10 – 12). For the SBB treatment, the increase was significant (P: < 0.001; n = 201). For the MPB treatment a non significant increase in basal area was detected using ANOVA over the 201 year model simulation but a significant decrease in basal area was modelled from 0 to 100 years (P: < 0.015; n = 101) and a significant increase from 100 to 201 years (P: < 0.001; n = 101) (Fig. 11). An F-test two sample for variances analysis was used to determine if the population variances of two distributions were different and it was found that a significant difference exists (P: 0.002; n = 201) between the variances of the distributions which suggests that the trajectory of stand-development under the current and 2080s climate may be different. At the species-level, lodgepole pine was modelled to increase significantly in basal area following fire and SBB attack (P: 0.012 & P: < 0.001; n = 201), but remain unchanged following MPB attack. After fire, the interior spruce and subalpine fir were modelled to suffer a significant decline in basal area under the 2080s climate (P: < 0.001; n = 201), while trembling aspen was modelled to remain unchanged. Following MPB attack, interior spruce and trembling aspen responded with significant increases in basal area (P: <0.001 & P: 0.028; n =201), while following SBB attack only interior spruce responded with a significant increase in basal area (P: < 0.005; n = 201). Subalpine fir responded again with significant declines in basal area following MPB and SBB attack (P: < 0.001; n = 201) under the 2080s climate. See Figures 10 to 12 for a summary of species responses.

<Fig. 10>

<Fig. 11>

<Fig. 12>

Sub-Hygric Sites

On sub-hygric sites a significant increase in stand basal area was modelled to occur under 2080s climate conditions compared to the current in the fire treatment only (P < 0.006; n= 201), basal area did not change significantly following MPB and SBB attack (Figs 13 – 15). At the species-level, lodgepole pine was modelled to increase significantly in basal area following fire (P: 0.004; n = 201), but remain unchanged following MPB and SBB attack. After fire and SBB attack in the 2080s climate, trembling aspen was modelled to increase but these changes were not significant (P: 0.063 & P: 0.15; n = 201), while after MPB attack a significant declined in basal area (P; < 0.001; n = 201) was modelled. For both interior spruce and subalpine fir significant declines in basal area were modelled to occur following fire under the 2080s climate (P: < 0.001; n = 201), Following MPB attack, interior spruce was modelled to incur a decrease in basal area and subalpine fir an increase under the 2080s climate but these changes were not significant (P: 0.19 & P: 0.20; n =201). Following SBB attack, both species spruce responded with an increase in basal area but these changes did not differ significantly compared to the current climate treatment (P: 0.92 for interior spruce and P: 0.31 for subalpine fir; n = 201). See Figures 13 to 15 for a summary of species responses.

<Fig. 13>

<Fig. 14>

<Fig. 15>

Discussion

In British Columbia (BC), as in many parts of the world, species response to climate change has been largely evaluated using bioclimatic envelope modelling. In the Bulkley Valley region of northwest BC it was predicted by Hamann and Wang (2006) that the region would transition from a spruce dominated ecosystem to ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) dominated ecosystems by the 2080s. Hamann and Wang (2006) used a bioclimatic envelope modelling approach to determine individual species responses and assumed that species would maintain similar realised niches and associations under a changing climate. These approaches generally provide no explanation of the mechanisms of change and are considered poor predictors of forest growth and succession under different environmental conditions (Kimmins 2004). The static nature of these statistical models can be overcome by using mechanistic models that are driven by empirically-derived parameters. Mechanistic models, typically based on JABOWA (Botkin et al. 1972) and FORET (Shugart and West 1977), are the most commonly used models for predicting species response and forest succession under climatic change (Zolbrod and Peterson 1999). Competition between species is based primarily on light with nutrient, moisture and temperature constraints used to modify the growth of different species (Botkin 1993). The omission of growth processes in favour of growth modifiers for nutrients, moisture, shade tolerance, and growing degree days is regarded as a crude and generalised representation of ecological processes (Pacala et al. 1996; Kimmins 2004). In this study, we used a mechanistic model, TACA, driven by empirically derived climatic and soil parameters to determine species response to climate and then linked the outcomes to SORTIE-ND, a spatially explicit individual tree model (Kimmins 2004). In SORTIE, growth is based on empirical relationships between light and radial growth with growth parameters in our study empirically derived from three site types that represent the typical moisture gradient found within the study area. The empirical foundation of SORTIE allowed us to improve on the generalised representation of ecological processes typically used in mechanistic models

The response of species in their fundamental regeneration niche within the study region was variable. All four species were predicted to decline on xeric sites in response to climate change with lodgepole pine and trembling aspen showing only slight declines in regeneration potential on mesic sites but slight increases on sub-hygric sites. Leonelli et al. (2008) predicted that trembling aspen in northeast BC will likely be negatively effected by climate change on sites were moisture resources are limiting but should also be able to maintain growth or increase productivity on sites where moisture is not consistently limiting. The response of trembling aspen in this study, as modelled by the TACA model, supports the hypothesis of Leonelli et al. (2008). Interior spruce and subalpine fir were both modelled to incur declines in regeneration potential on all sites with species response mediated by edaphic conditions that promoted increased moisture availability. Ettl and Peterson (1995a; 1995b) found that subalpine fir is sensitive to variation in soil moisture with species response to climate also being mediated on sites which maintain suitable soil moisture and exacerbated on sites where moisture is limiting.

Within the study region it is likely that climate change will have an impact on the regeneration potential of the studied species but these responses will not be uniform. Divergent responses should be expected, both between species and between site types. The species-specific changes in regeneration potential and potential productivity suggest that species will respond individualistically to climate change. Individualistic responses to climate change are expected to result in changes in ecosystem composition and structure (Bartlein et al. 1997; Bush 2002).

To differentiate between the fundamental response and realised response of species to climate change both competitive and biotic and abiotic agents need to be considered (Guisan and Zimmerman 2000). Being able to differentiate between the fundamental and realised niches of species is considered to be important for improving predictions of species response to changing environmental conditions (Guisan and Zimmerman 2000). The linkage of the TACA model to SORTIE-ND allowed for the investigation of both the role of disturbance and competition on species response to climate change. On xeric sites, a shift to lodgepole pine dominated forests occurred following fire and SBB attack. The dominance of pine following fire in the 2080s climate did not differ significantly from the current climate but the composition shifted towards more lodgepole pine and less trembling aspen, very few spruce and no subalpine fir. Following a SBB attack, a change in composition was modelled in the 2080s versus the current climate with the stands shifting from becoming dominated by subalpine fir over time to being dominated by lodgepole pine instead with both spruce and subalpine fir declining in abundance. Following a MPB attack, xeric stands were modelled to shift from being dominated by subalpine fir, under the current climate conditions, to becoming co-dominated with interior spruce under the 2080s climate. Following all disturbances, productivity decreases but the largest decline occurs after the MPB attack due to the inability of lodgepole pine to regenerate under the low light conditions that persist within the stand. The ability of interior spruce to regenerate on organic substrates, which are maintained following SBB and MPB attacks, along with declines in climatic suitability results in the recruitment of interior spruce being severely restricted which in turn limits productivity under the 2080s climate. Astrup et al. (in press) identified that low light and substrate availability are important factors that are currently limiting recruitment of pine and spruce, respectively, in stands following MPB attack within the study region. For subalpine fir, the decline in regeneration potential results in the absence of recruitment due to increased soil moisture stress particularly after fire and the and reliance on advanced regeneration following MPB and SBB attack. Cui and Smith (1991) found that subalpine fir is sensitive to soil moisture stress which can prevent establishment on exposed sites. In this study, the exposed sites created by fire exacerbated the response of both subalpine fire and interior spruce compared to sheltered conditions found within MPB and SBB attacked stands.

On both mesic and sub-hygric sites an increase in lodgepole pine was modelled following fire with decreases in both interior spruce and subalpine fir. Trembling aspen did not exhibit any significant changes in basal area between the current and 2080s climate. The most striking shifts in stand structure and composition occur on the mesic sites following MPB and SBB attack. Under the 2080s climate, stands were modelled to become dominated by interior spruce following MPB attack versus subalpine fir. After a SBB attack, the stands transitioned from being co-dominated by interior spruce and subalpine fir to being dominated by interior spruce followed by lodgepole pine and then subalpine fir. On sub-hygric sites, following MPB and SBB attack, species exhibited the highest inertia to climate change. On these sites, following MPB and SBB disturbance events, stands were modelled to maintain their current composition and structure of species and productivity. The cooler climatic conditions offered by sheltered sites and the higher soil moisture conditions provide by the finer textured soils found on sub-hygric sites mediated the response of species. Subalpine fir and white spruce (*Picea glauca*) (interior spruce is a hybrid of white spruce) have both been documented establishing under sheltered conditions while failing to establish under exposed conditions due to moisture stress (Cui and Smith 1991; Man and Lieffers 1999). The findings of this study support this mechanism and highlight the importance that microclimatic and edaphic conditions may have in mediating species response, even under competition. Stand conditions that provide higher humidity, cooler temperatures and wetter edaphic conditions are regarded as being important for maintaining species that cannot tolerate climatic change (Meave et al. 1991; Aide and Rivera 1998; Burke 2002). For subalpine fir and interior spruce, the combination of a disturbance that maintains a forest canopy and soil properties that provide higher soil moisture availability are likely to be important for preventing a shift towards pine-dominated ecosystems in the future.

The findings also highlight that climate climax plant communities (mesic sites) and edaphic climax communities (xeric and sub-hygric sites) are likely to behave differently under climate change. The interaction of physiological and edaphic factors that were modelled to occur on sub-hygric sites are likely will play an important role in allowing the current sub-boreal spruce ecosystem species to persist under future climates as extrazonal, edaphic climax communities within a landscape of newly developing climatic climax communities (Theurillat and Guisan 2001). The responses of species on xeric and mesic sites point towards shifts towards an alteration in species composition and stand structure that is more representative of the Sub-Boreal Pine and Spruce and Montane Spruce ecosystems found in the warmer and drier regions south of the study area.

The findings of this study suggest the role of disturbance type under climate change will have an impact of species response. The interaction between biotic, abiotic, and climatic factors may result in changes in stand dynamics and species composition within the sub-boreal spruce ecosystems of the Bulkley Valley. If an increase in the frequency of fire occurs within the study region under climate change an increase in the frequency of lodgepole pine species may occur at the expense of the interior spruce and subalpine fir dominated forests (Bartlein et al. 1997). Across all edaphic sites, fire resulted in an increase in lodgepole pine which on mesic and sub-hygric sites resulted in the maintenance and increase in stand-level productivity, respectively. Interestingly, subalpine fir is currently benefitting from a MPB epidemic within the study region which if it were to happen under the predicted 2080s climate would result in a shift in dominance towards interior spruce on mesic and xeric sites with positive and negative effects on productivity, respectively.

The potential change in productivity under climate change is a large unknown for all of the study species; however, for lodgepole pine, productivity across BC under climate change has been predicted by Wang et al. (2006) and O’Neill et al. (2008). O’Neill et al. (2008) predicted that lodgepole pine productivity is expected to decline by 45 to 74 % with lodgepole pine disappearing completely from portions of the study region. Wang et al. (2006) predicted that productivity could increase in the region by 20 to 30 % if seed source is optimised but would only increase by 6.9 % under a 2 °C increase in temperature and may decrease by 9.1 % with a 4 °C increase in temperature if seed source is not optimised. In this study, lodgepole pine productivity was predicted to decline by 24 % on xeric sites which resulted, however, in a 6 % increase in basal area following fire as pine benefited from the decline in site suitability of the other species due to climate change. On mesic sites, a 1 % increase in productivity was assumed to occur which resulted in a 21 % increase in basal area following a fire even though other species were predicted to incur losses in productivity due to increases in soil moisture stress. On sub-hygric sites a 16 % increase in productivity was predicted which, following fire, resulted in only a 12 % gain in basal area. For trembling aspen a 14 % decline was predicted which resulted, however, in a 15 % increase in basal area, while for interior spruce and subalpine fir, three and 11 % increases were predicted but -28 % and -78 % changes in basal area were modelled, respectively. These divergent responses highlight the need for considering both resource availability and competition when investigating changes in species productivity in response to changes in climate.

In this study, soil moisture, light, and substrate availability all had impacts on species response to climate change. Disturbance type and severity, along with climate, interacted to maintain and create potential shifts in stand composition within the study area. Climate change will interact with disturbances to create opportunities for species to migrate in to new habitats but also it is likely to allow for some species to persist. In this study, we only considered the four dominant species found within the SBS ecosystem of the Bulkley Valley; though the region is also expected to increase in suitability for species from warmer and drier regions of the province. Nitschke and Astrup (2008) modelled that the study area could increase in climatic suitability for both Douglas-fir and ponderosa pine by 71 % and 91 %, respectively, under the 2080s climate. Unfortunately, no empirical data exists on these species for the study area since they do not occur naturally in the region so they were not included in this paper but are the focus of follow-up research to parameterise these species in order to incorporate the influence these species, and others, will have on the future composition and structure of the SBS ecosystem. The increase in climatic suitability of these species supports our hypothesis that the SBS ecosystem in the study area will shift towards favouring the development of new climatic climax communities that may resemble the stand compositions and structures that exist in the warmer and drier regions of the southern interior of BC. This will particularly be the case for these species in stands that occupy xeric and mesic site types.

Conclusion

A synergistic relationship exists between climate, disturbance and species which will influence the response of species to climate change (Dale et al. 2001; Hansen et al. 2001). Competition between species for resources under changing environmental conditions will have an impact the future niche space that a species will occupy (Guisan and Zimmerman 2000). The local response of forests and species is also mediated by edaphic and microclimate variation due to topography and soil types (Peters 1992; Urban et al. 1993). In this study, we considered the impacts that climate, disturbance, resource availability and competition will have on the response of four dominant tree species in the SBS ecosystem on the Bulkley Valley region of BC across different edaphic sites. All species were modelled to incur changes in climatic suitability with differential responses identified between species and between sites. The results highlight the need to consider local responses of species, not just regional or landscape responses that are commonly investigated by bioclimatic envelope models. Species were modelled to undergo the largest changes on dry sites with a shift to an increase in lodgepole pine abundance and the loss of subalpine fir and interior spruce. On mesic sites, a shift in dominance to pine following fire and interior spruce following SBB and MPB attack were modelled. The response of species following different disturbance types on xeric and mesic sites is an important finding of this study. These finding highlight the influence of climate, resource availability and disturbance type can have on shifting ecosystem dynamics. Changes in any biotic or abiotic component are able to alter the dynamic equilibrium that exists between species leading to creation of new equilibrated systems (Tansley 1935). In this study, fire and/ or changes in soil moisture were important components that may result in shifts towards new ecosystem dynamics. The results of this study also highlight the role that edaphic variation may have in mediated species response. On sub-hygric sites ecosystem dynamics and composition were modelled to be maintained following MPB and SBB disturbance events. Fire did, however, result in an increase in lodgepole pine abundance and a decline in other species even on these sites. Fire is regarded as the disturbance type that typically causes the most adverse affects on ecosystems (Dale et al. 2001). In this study, fire had significant influence on species response across all sites with less intense disturbance types having a more mediating affect as soil moisture availability increased along the modelled resource gradient.

The individualistic responses of species to climate, disturbance and resource availability in this study highlights the complex interactions that may occur under future climate change. As a result, model outcomes of species response to climate at larger spatial scales may not be representative of species response at smaller spatial and vice versa (Bugmann et al. 2000; Barrio et al. 2006). The local differentiations in environmental conditions may allow some species to cope with change at the local-scale where suitable resources are maintained (Theurillat and Guisan 2001). The findings highlight the potential inertia that species may exhibit to climate change when biotic and abiotic factors are considered. Inertia is considered a significant mechanism of ecological resistance which causes vegetation change to lag behind climate change (Noss 2001). Structural and compositional adjustments of ecosystems to environmental change are often delayed by community inertia which in turn can accelerated by large- or small-scale disturbances (Hofgaard 1997; Shriner and Street 1998). In this study, disturbance drove change which removed inertia on all sites following fire and on xeric and mesic sites following smaller-scale SBB and MPB disturbances. On sub-hygric sites inertia was maintained following smaller-scale SBB and MPB disturbances which suggests that change in these forest communities may be a slow process that will allow for species to persist in this composition and structure under climate change until a fire occurs. These findings also highlight the need to consider management actions that reduce disturbance risk and promote healthy ecosystem functions in order to exploit the biological inertia that seemingly exists in these systems (Noss 2001). Maintenance of this inertia will assist the ability of these ecosystems to cope with rapid environmental change (Brereton et al. 1995) whilst the migration or selection of suitable phenotypes or genotypes occurs which will allow for the maintenance of the SBS ecosystem or new species migrate into the region facilitating a transition to a new ecosystem. Based on the results of this study, fire will be a large driver of change and change will be greatest on xeric and mesic sites which may create the best opportunities for new ecosystems to form while moist to wet sites may provide the best opportunities for conserving the biodiversity and ecosystem composition and structure that currently exists within the SBS zone under predicted climate change.

Acknowledgments

We would like to thank Dave Coates and Alex Woods of the British Columbian Ministry of Forests and Range and John Innes of the University of British Columbia for their active support and input into this project. Finally we would like to thank British Columbia’s Forest Sciences Program for funding this project.

References

Aide, T.M. and E. Rivera. 1998. Geographic patterns of genetic diversity in *Poulsenia armata* (Moraceae): implications for the theory of Pleistocene refugia and the importance of riparian forest. Journal of Biogeography 25: 695–705.

Aitken, S.N., S. Yeaman, J. A. Holliday, T. Wang and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1: 95–111.

Alexander, R.R., R.C. Shearer, and W.D. Sheppard. 1990. Subalpine Fir. Pp. 60-70, In: R. M. Burns and B. H. Honkala (Eds); Silvics of North America, Volume 1: Conifers. Agriculture Handbook 654. United States Department of Agriculture and Forest Service, Washington, D.C., USA.

Allen, C.D. and D.D. Breshears. 1998. Drought-induced shift of a forest-woodland landscape in response to climate variation. Proceedings of the National Academy of Science. USA 95: 14839–14842.

Araújo, M.B. and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16: 743–753.

Araújo, M.B. and R.G. Pearson. 2005. Equilibrium of species' distributions with climate. Ecography 28: 693–695.

Ashton, D.H. 1976. The vegetation of Mount Piper, Central Victoria: a study of a continuum. The Journal of Ecology 64 (2): 463–483.

Astrup, R., K.D. Coates and E. Hall. In press. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology and Management: doi:10.1016/j.foreco.2008.07.025

Bailey, J.D., and C.A. Harrington. 2006. Temperature regulation of bud-burst phenology within and among years in a young Douglas-fir (Pseudotsuga menziesii) plantation in western Washington, USA. Tree Physiology 26: 421–430.

Bakkenes, M., J.R.M. Alkemade, F. Ihle, R. Leemans and J.B. Latour. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology 8: 390–407.

Barrio, G. del, P.A. Harrison, P.M. Berry, N. Butt, M.E. Sanjuan, R.G. Pearson and T. Dawson. 2006. Integrating multiple modelling approaches to predict the potential impacts of climate change on species' distributions in contrasting regions: comparison and implications for policy. Environmental Science and Policy 9: 129–147.

Bartlein, P.J., C. Whitlock and S.L. Shafer. 1997. Future Climate in the Yellowstone National Park Region and Its Potential Impact on Vegetation. Conservation Biology 11 (3): 782–792.

Bell, D.T. 1999. Turner Review No. 1: The process of germination in Australian species. - Australian Journal of Botany 47: 475–517.

Botkin, J.B., J.F. Janak and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60: 849–873.

Brereton, R., S. Bennett and I. Mansergh. 1995. Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis. Biological Conservation 72: 339–354.

Bristow K.L., and G.S. Campbell. 1984. On the relationship between solar radiation and daily maximum and minimum temperature. Agricultural and Forest Meteorology 31: 159–166.

Brzeziecki, B., F. Kienast and O. Wildi. 1995. Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. Journal of Vegetation Science 6: 257–268.

Bugmann, H., M. Lindner, P. Lasch, M. Flechsig, B. Ebert and W. Cramer. 2000. Scaling issues in forest succession modelling. Climatic Change 44: 265–289.

Burke, A. 2002. Island-matrix relationships in Nama Karoo inselberg landscapes. Part I: Do inselbergs provide refuge for matric species? Plant Ecology 160: 79–90.

Bush, M.B. 2002. Distributional change and conservation on the Andean flank: a palaeoecological perspective. Global Ecology & Biogeography 11: 463–473.

Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli,W.T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr and P. Whetton. 2007. Regional climate projections. Pp. 847–940, In: Solomon, S. Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor M., Miller, H.L. (eds.); Climate Change 2007: The Physical Science Basis, Contribution of: Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Coates, K. D., C. D. Canham, M. Beaudet, D. L. Sachs and C. Messier. 2003. Use of a spatially-explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. Forest Ecology and Management 186: 297–310.

Cui, M. and W.K. Smith. 1991. Photosynthesis, water relations and mortality in *Abies lasiocarpa* seedlings during natural establishment. Tree Physiology 8: 31–46.

Cumming, S.G. and P.J. Burton. 1996. Phenology-mediated effects of climate change on some simulated British Columbia forests. Climatic Change 34 (2): 213–222.

Dale, V.H., L.A. Joyce, S. McNulty, R.P. Neilson, M.P. Ayres, M.D. Flannigan, P.J. Hanson, L.C. Irland, A.E. Lugo, C.J. Peterson, D. Simberloff, F.J. Swanson, B.J. Stocks and B.M. Wotton. 2001. Climate change and forest disturbances. Bioscience 51 (9): 723–734.

Eeley, H.A.C, M.J. Lawes and S.E. Piper. 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. Journal of Biogeography 26: 595–617.

Ettl, G.J. and D.L. Peterson. 1995a. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. Global Change Biology 1: 213–230.

Ettl, G.J. and D.L. Peterson. 1995b. Extreme climate and variation in tree growth: individualistic response in subalpine fir (*Abies lasiocarpa*). Global Change Biology 1: 231–241.

Ferro Duarte, H., L.D. Nelson and S.R. Maggiotto. 2006. Assessing daytime downward longwave radiation estimates for clear and cloudy skies in Southern Brazil. Agricultural and Forest Meteorology 139: 171–181.

Fischlin, A. and D. Gyalistras. 1997. Assessing impacts of climate change on forests in the Alps. Global Ecology and Biogeography Letters 6 (1): 19–37.

Flato, G.M., G.J. Boer, W.G. Lee, N.A. McFarlane, D. Ramsden, M.C. Reader and A.J. Reader. 2000. The Canadian centre for climate modelling and analysis global coupled model and its climate. Climate Dynamics 16: 451–467.

Gavin, D.G. and L.B. Brubaker. 1999. A 6000-year pollen record of subalpine meadow vegetation in the Olympic Mountains, Washington, USA. Journal of Ecology 87: 106–122.

Gitay H., A. Suárez and R. Wilson. 2002. Climate Change and Biodiversity. Technical Paper V. Intergovernmental Panel on Climate Change. Geneva.

Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993–1009.

Guisan, A. and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.

Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87: 2773–2786.

Hansen, A.J., R.P. Neilson, V.H. Dale, C.H. Flather, L.R. Iverson, D.J. Currie, S. Shafer, R. Cook and P.J. Bartlein. 2001. Global change in forests: responses of species, communities and biomes. Bioscience 51 (9): 765–779.

He, H.S., D.J. Mladenoff and T.R. Crow. 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecological Modelling 114: 213–233.

Hewlett, J.D. and J.C. Fortson. 1982. Stream temperature under an inadequate buffer strip in the southeast Piedmont. Water Resource Bulletin 18: 983–988.

Hofgaard, A. 1997. Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. Global Ecology and Biogeography Letters 6 (6): 419-429.

Huntley, B., P.M. Berry, W. Cramer and A.P. McDonald. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography 22: 967–1001.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Iverson, L.R. and A.M. Prasad. 2001. Potential changes in tree species richness and forest community types following climate change. Ecosystems 4: 186–199.

Johns, T.C., J.M. Gregory, W.J. Ingram, C.E. Johnson, A. Jones, J.A. Lowe, J.F.B. Mitchell, D.L. Roberts, D.M.H. Sexton, D.S. Stevenson, S.F.B. Tett and M.J. Woodage. 2003. Anthropogenic climate change for 1860 to 2100 simulated with the HadCM3 model under updated emission scenarios. Climate Dynamics 20: 583–612.

Kimmins, J.P. 2004. Forest Ecology: A Foundation for Sustainable Forest Management and Environmental Ethics in Forestry, 3rd ed. Prentice Hall.

Kobe, R.K. and K.D. Coates. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Canadian Journal of Forest Research 27: 227–236.

Leonelli, G., B. Denneler and Y. Bergeron. 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. Canadian Journal of Forest Research 38: 1211–1222.

Lotan, J.E. and W.B. Critchfield. 1990. Lodgepole Pine. Pp. 302–315, In: R. M. Burns and B. H. Honkala (eds); Silvics of North America, Volume 1: Conifers. Agriculture Handbook 654. United States Department of Agriculture and Forest Service, Washington, D.C., USA.

Man, R.Z. and V.J. Lieffers. 1999. Effects of shelterwood and site preparation on microclimate and establishment of white spruce seedlings in a boreal mixedwood forest. The Forestry Chronicle 75 (5): 837–844.

McKenzie, D., D.W. Peterson and D.L. Peterson. 2003a. Modelling conifer species distributions in mountain forests of Washington State, USA. The Forestry Chronicle 79 (2): 253–258.

McKenzie, D., D.W. Peterson, D.L. Peterson and P.E. Thornton. 2003b. Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. Journal of Biogeography 30: 1093–1108.

McNaughton, K.G. and P.G. Jarvis. 1983. Predicting effects of vegetation changes on transpiration and evaporation. Pp. 1–47, In: T.T. Kozlowski (ed.); Water Deficits and Plant Growth Vol. 7. Academic Press, London.

Miller, C. and D.L. Urban. 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. Ecosystems 2: 76–87.

Meave, J., M. Kellman, A. MacDougall and J. Rosales. 1991. Riparian habitats as tropical forest refugia. Global Ecology and Biogeography Letters 1 (3): 69–76.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Victoria, B.C.

Nakicenovic, N., J. Alcamo, G. Davis, B. de Vries, J. Fenhann, S. Gaffin, K. Gregory, A. Grübler, T. Yong Jung, T. Kram, E. Lebre La Rovere, L. Michaelis, S. Mori, T. Morita, W. Pepper, H. Pitcher, L. Price, K. Riahi, A. Roehrl, H.H. Rogner, A. Sankovski, M. Schlesinger, P. Shukla, S. Smith, R. Swart, S. van Rooijen, N. Victor and Z. Dadi. 2000. Emission Scenarios. A Special Report of Working Group II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Nienstaedt, H. and J. C. Zasada. 1990. White Spruce. Pp. 204–226, In: R. M. Burns and B. H. Honkala (eds); Silvics of North America, Volume 1: Conifers. Agriculture Handbook 654. United States Department of Agriculture and Forest Service, Washington, D.C., USA.

Nitschke, C.R. 2006. Integrating Climate Change into Forest Planning: A Spatial and Temporal Analysis of Landscape Vulnerability. PhD dissertation, The University of British Columbia. Vancouver, Canada. 532 pp.

Nitschke, C.R. and R. Astrup. 2008. The vulnerability of the dominant tree species in the Sub-Boreal Spruce Ecosystem of Northwest British Columbia to predicted climate change. Government of British Columbia Forest Sciences Program Technical Report Y081200.

Nitschke, C.R. and J.L. Innes. 2008. A Tree and Climate Assessment Tool for Modelling Ecosystem Response to Climate Change. Ecological Modelling 210 (3): 263–277.

Noss, R.F. 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conservation Biology 15 (3): 578–590.

O'Neill, G.A., A. Hamann and T. Wang. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. Journal of Applied Ecology 45: 1040–1049.

Pacala, S.W., C.D. Canham, J. Saponara, J.A. Silander Jr., R.K. Kobe and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66 (1): 1–43.

Pacala, S. W., C. D. Canham, and J. A. Silander, Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23: 1980–1988.

Pacific Climate Impacts Consortium. 2009. Pacific Climate Impact Scenarios. Available from: http://www.pacificclimate.org/tools/ [Accessed on Feb 7, 2009).

Pearson, R. G. and T.E. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361–371.

Pearson, R.G., T.E. Dawson and C. Liu. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27: 285–298.

Peters, R.L. 1992. Conservation of biotic diversity in the face of climate change. Pp 15–26, In: R.L. Peters, J.E. Lovejoy (eds.); Global Warming and Biological Diversity. Yale University Press, New Haven, Connecticut.

Pojar, J., R. Love, D.V. Meidinger and R.K. Scagel. 1982. Some Common Plants of the Sub-Boreal Spruce Zone. B.C. Ministry of Forests; Land Management Handbook 06.

Prentice I.C., W. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud and M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19 (2): 117–134.

Pulliam, H.R. 2000. On the relationship between niche and distribution. Ecology Letters 3: 349–361.

Schwartz, M.W., L.R. Iverson and A.M. Prasad. 2001. Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing. Ecosystems 4: 568–581.

Shriner, D.S. and R.B. Street. 1998. North America: Ecosystems: Forested. Pp 273–278, In: R.T Watson, M.C. Zinyowera, R.H. Moss (eds.); The Regional Impacts of Climate Change. A Special Report of IPCC Working Group II. Cambridge University Press, UK.

Shugart, H.H. and D.C. West. 1977. Development of an Appalchian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. Journal of Environmental Management 5: 161–170.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. 2nd ed. W. H. Freeman, New York.

Sykes, M.T. and I.C. Prentice. 1995. Boreal forest futures: modelling the controls on tree species range limits and transient responses to climate change. Water, Air and Soil Pollution 82: 415–428.

Tabachnick, B.G. and L.S. Fidell. 2001. Using Multivariate Statistics: 4th Edition. Allyn and Bacon, Boston, Massachusetts, USA. 966 pp.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16 (3): 284–307.

Theurillat, J.P. and A. Guisan. 2001. Potential impact of climate change on vegetation in the European Alps: a review. Climatic Change 50: 77–109.

Thuiller W., S. Lavorel, M.B. Araujo, M.T. Sykes, I.C. Prentice and H.A. Mooney. 2005. Climate change threats to plant diversity. Proceedings of the National Academy of Sciences of the Unites States of America 102 (23): 8245–8250.

Urban, D.L., M.E. Harmon and C.B. Halpern. 1993. Potential response of Pacific Northwestern forests to climate change, effects of stand age and initial composition. Climatic Change 23 (3): 247–266.

Walker, D. 1989. Diversity and stability. Pp 115–146, In: J.M. Cherrett (ed.); Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World. Blackwell Scientific Publications, Oxford, UK. 385 pp.

Wang, T., A. Hamann, A. Yanchuck, G.A., O'Neill and S. N. Aitken. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12: 2404–2416.

Waring, R.H. and S.W. Running. 1998. Forest Ecosystems: Analysis at Multiple Scales. 2nd Ed. Academic Press, London.

Zolbrod, A.N. and D.L. Peterson. 1999. Response of high-elevation forests in the Olympic Mountains to climatic change. Canadian Journal of Forest Research 29: 1966–1978.

List of Tables and Figures

Table 1: Study area weather station characteristics and average climate conditions

Table 2: Average annual predicted climate change in the Bulkley Valley based on ensemble of global circulation model scenarios

Table 3: Change in species productivity by the 2080s on three site types with the Sub-Boreal Spruce ecosystem of the Bulkley Valley

Fig. 1: Sub-Boreal Spruce zone research area in the Bulkley Valley of Northwest British Columbia. Smithers Airport and Topley Landing weather stations are demarcated with triangles.

Fig. 2: Average annual climate in the Bulkley Valley based on Smithers Airport and Topley Landing weather stations

Fig. 3: Species response to climate and moisture availability on xeric sites with the SBS zone in the Bulkley Valley.

Fig. 4: Species response to climate and moisture availability on mesic sites with the SBS zone in the Bulkley Valley.

Fig. 5: Species response to climate and moisture availability on sub-hygric sites with the SBS zone in the Bulkley Valley.

Fig. 6: Change in moisture availability between current conditions and 2080s. Site Type 1 = xeric sites; 2 = mesic sites; and, 3 = sub-hygric sites. Error bars represent the 95 % confidence intervals for modelled results.

Fig. 7: Species response on a xeric site following a fire under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 8: Species response on a xeric site following a mountain pine beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 9: Species response on a xeric site following a spruce bark beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 10: Species response on a mesic site following a fire under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 11: Species response on a mesic site following a mountain pine beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 12: Species response on a mesic site following a spruce bark beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 13: Species response on a sub-hygric site following a fire under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 14: Species response on a sub-hygric site following a mountain pine beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Fig. 15: Species response on a sub-hygric site following a spruce bark beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

Table 1: Study area weather station characteristics and average climate conditions

Station	**Smithers Airport**	**Topley Landing**
Latitude	54° 49'	54° 49'
Longitude	127° 11'	126° 10'
Elevation	522 m	722 m
Manager	Environment Canada	Environment Canada
Mean maximum Temperature	9 °C	8 °C
Mean minimum Temperature	- 1.6 °C	- 2.1 °C
Mean Annual Precipitation	514 mm	535 mm
Record Range	1943-2000	1966-2000

Table 2: Average annual predicted climate change in the Bulkley Valley based on ensemble of global circulation model scenarios

Climate Period	Min Temp. (°C)	Mean Temp. (°C)	Max Temp. (°C)	Precipitation (%)
2020s (2010-2039)	1.1	1.2	1.2	1.1
2050s (2040-2069)	2.0	2.2	2.3	2.3
2080s (2070-2100)	3.6	3.8	4.0	5.0

Table 3: Change in species productivity by the 2080s on three site types with the Sub-Boreal Spruce ecosystem of the Bulkley Valley

Site	Interior Spruce	Lodgepole Pine	Subalpine Fir	Trembling Aspen
Xeric	-70%	-24%	-70%	0%
Mesic	-19%	1%	-70%	-12%
Sub-Hygric	3%	16%	11%	-14%

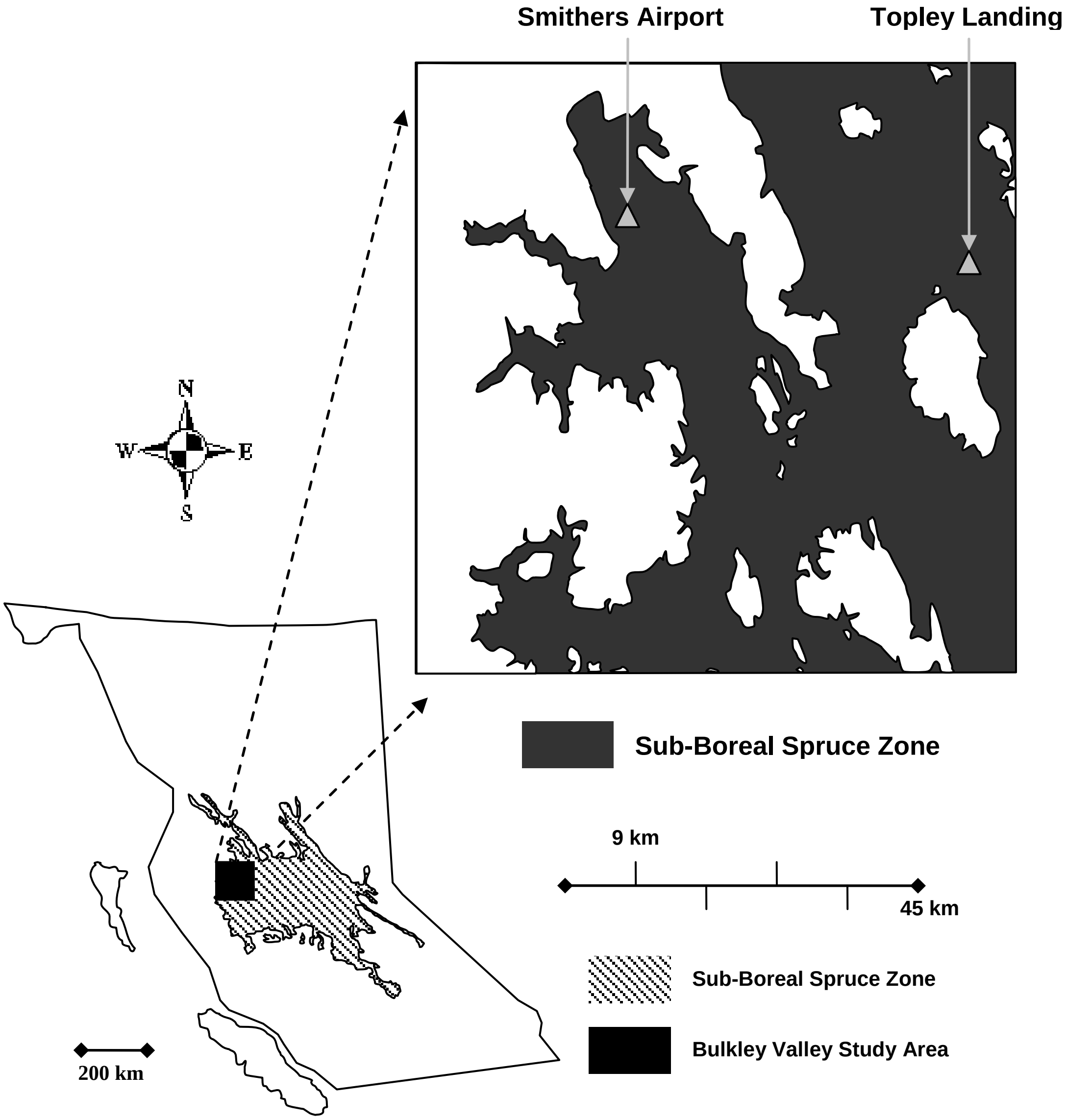

Fig. 1: Sub-Boreal Spruce zone research area in the Bulkley Valley of Northwest British Columbia. Smithers Airport and Topley Landing weather stations are demarcated with triangles.

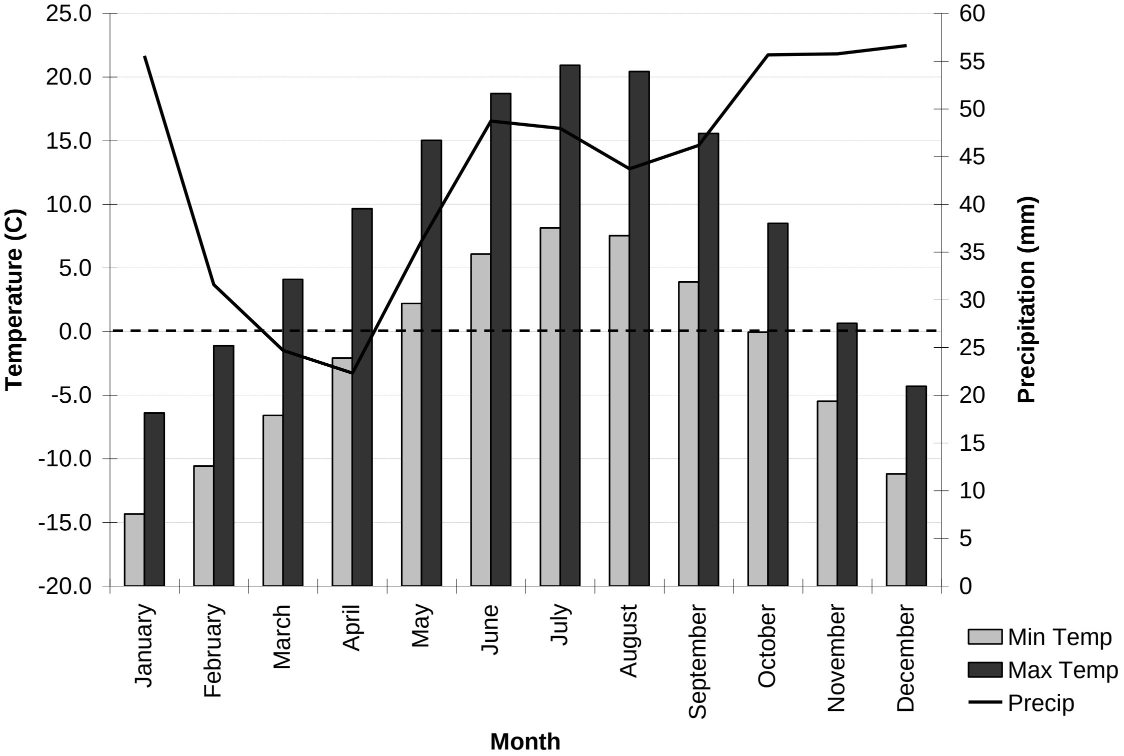

Fig. 2: Average annual climate in the Bulkley Valley based on Smithers Airport and Topley Landing weather stations

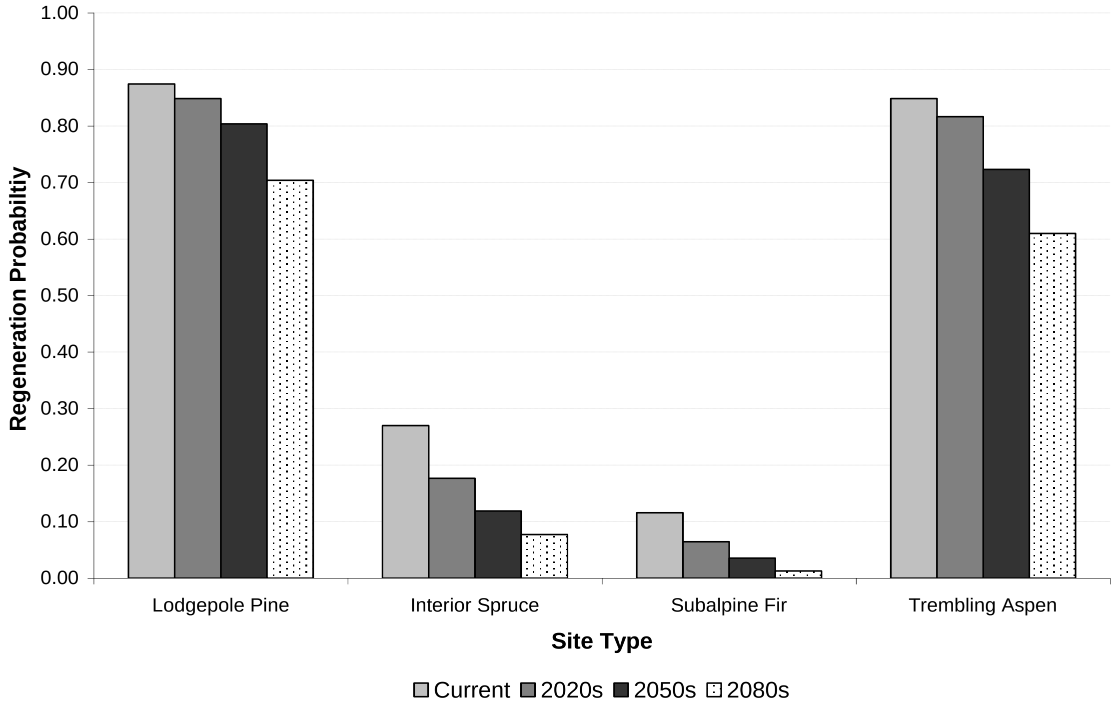

Fig. 3: Species response to climate and moisture availability on xeric sites with the SBS zone in the Bulkley Valley.

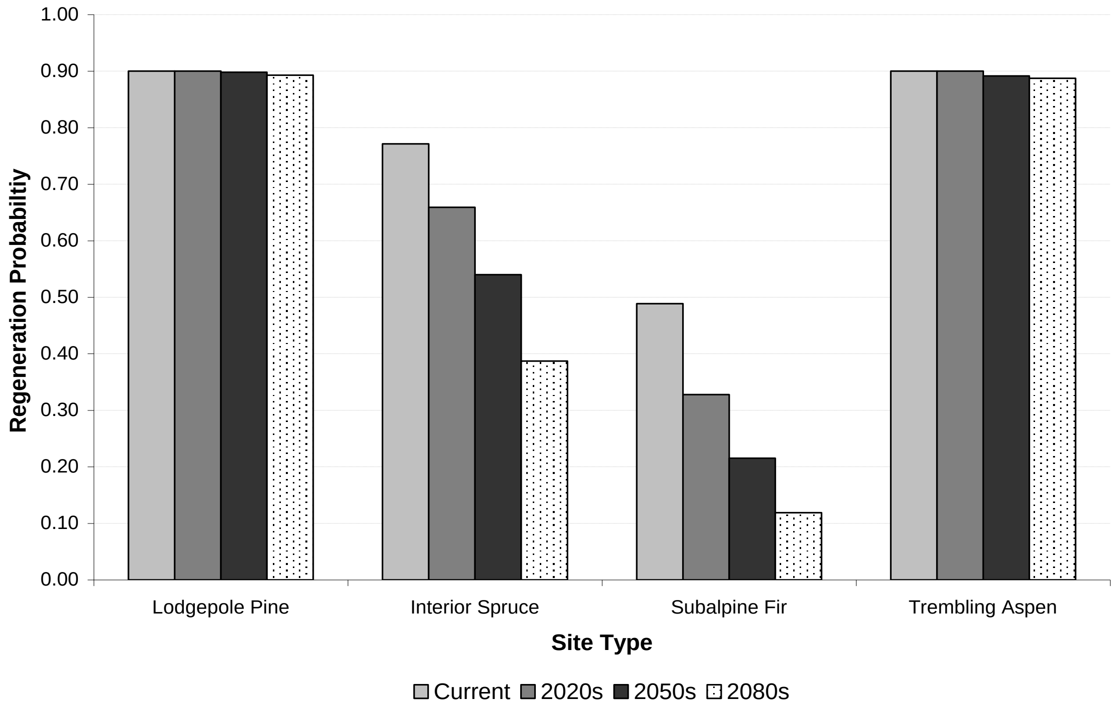

Fig. 4: Species response to climate and moisture availability on mesic sites with the SBS zone in the Bulkley Valley.

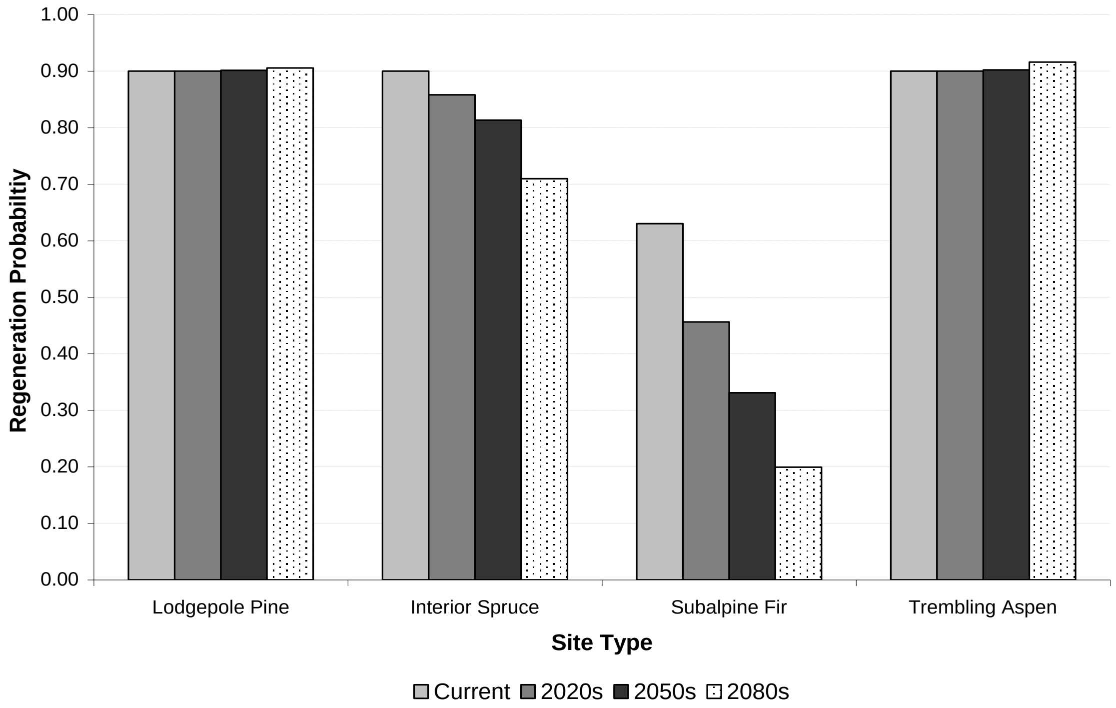

Fig. 5: Species response to climate and moisture availability on sub-hygric sites with the SBS zone in the Bulkley Valley.

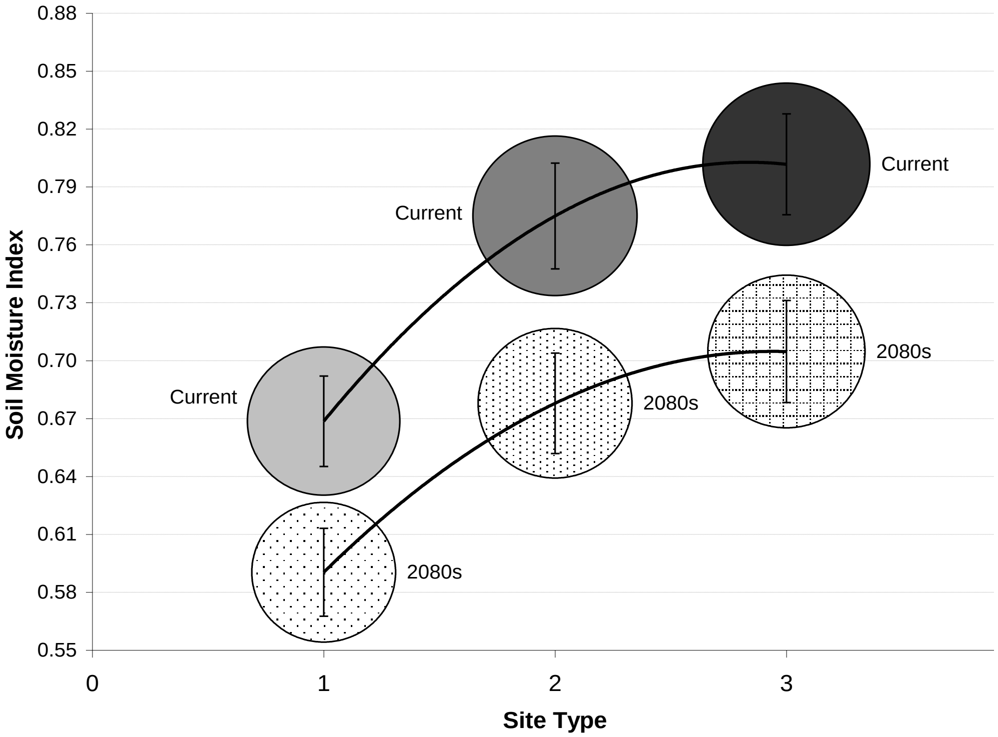

Fig. 6: Change in moisture availability between current conditions and 2080s. Site Type 1 = xeric sites; 2 = mesic sites; and, 3 = sub-hygric sites. Error bars represent the 95 % confidence intervals for modelled results.

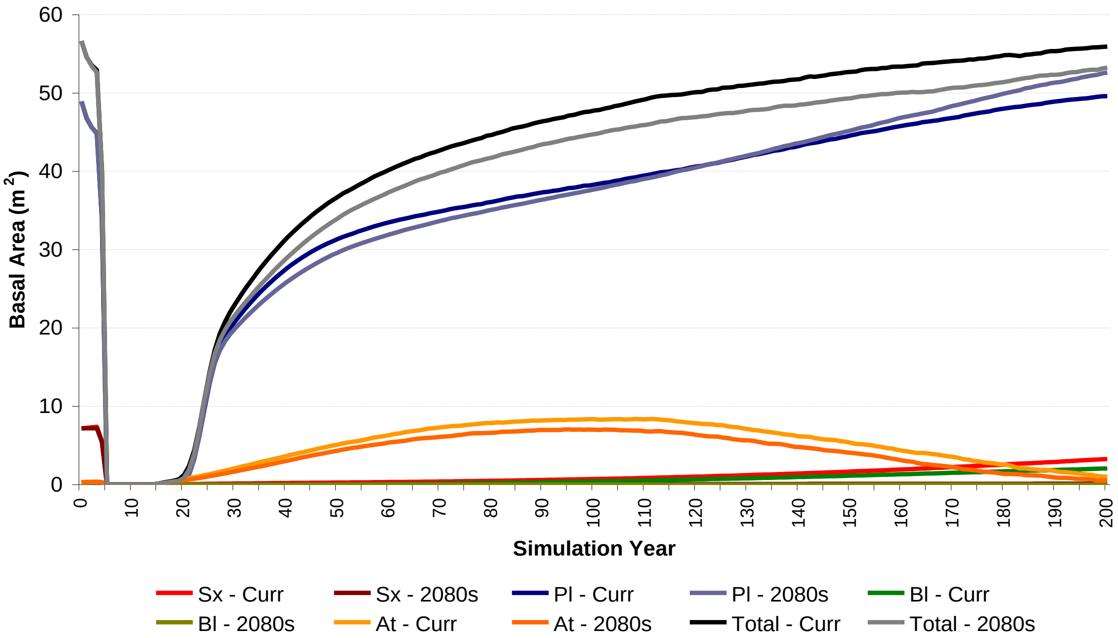

Fig. 7: Species response on a xeric site following a fire under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

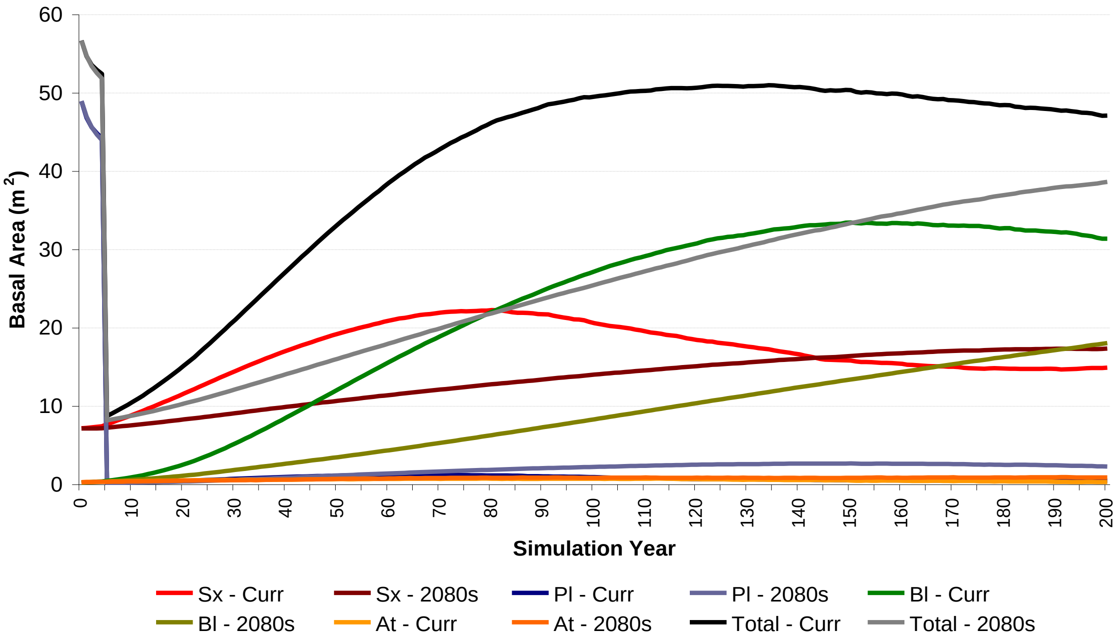

Fig. 8: Species response on a xeric site following a mountain pine beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

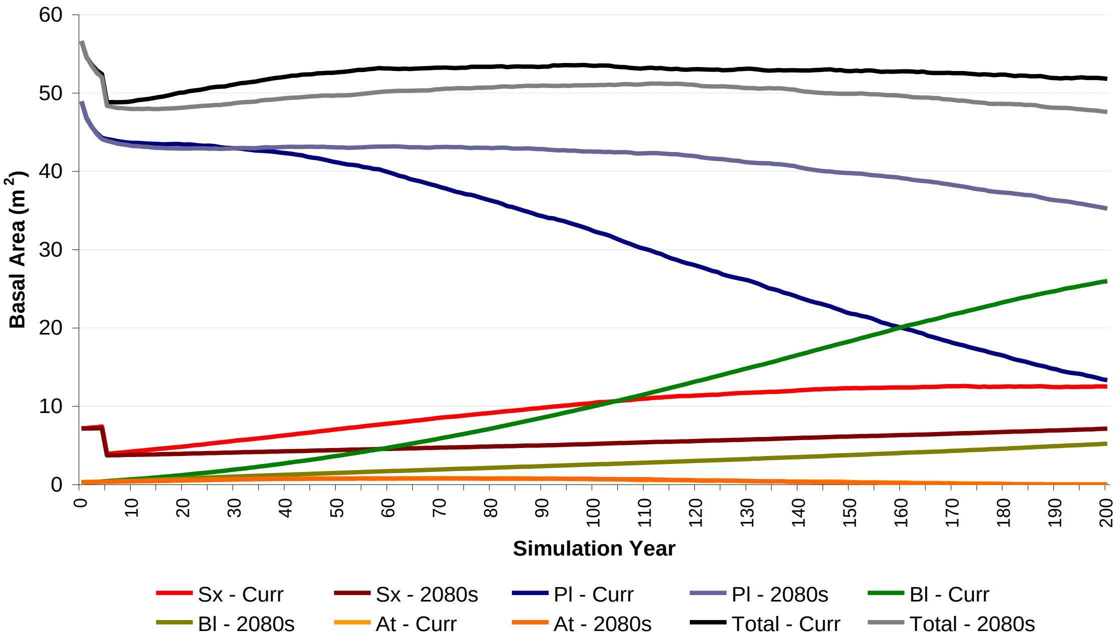

Fig. 9: Species response on a xeric site following a spruce bark beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

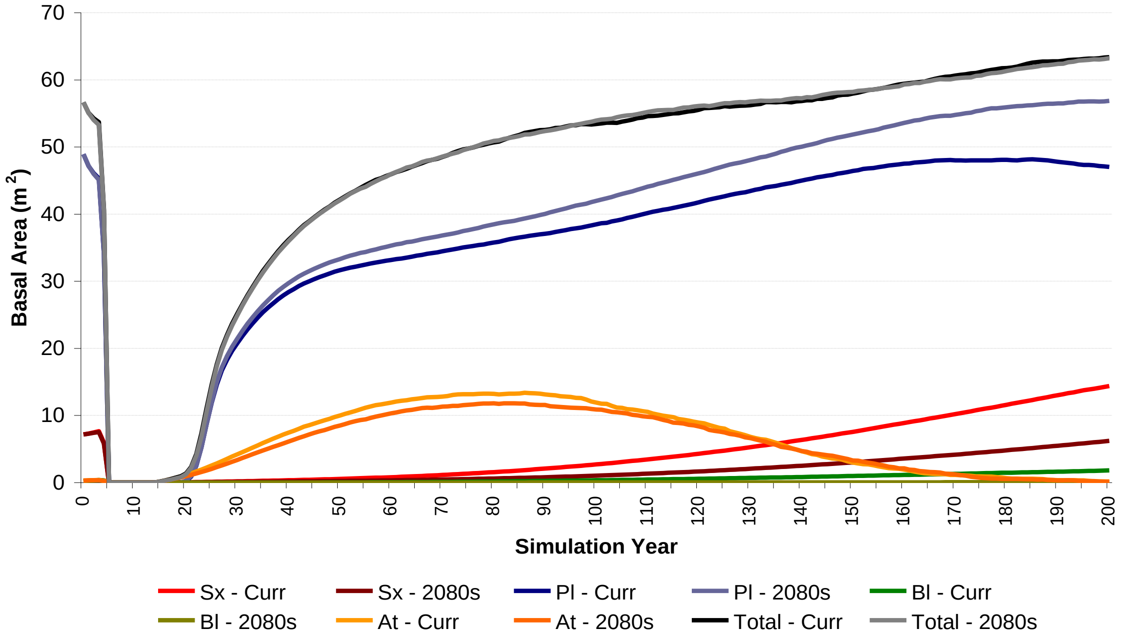

Fig. 10: Species response on a mesic site following a fire under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

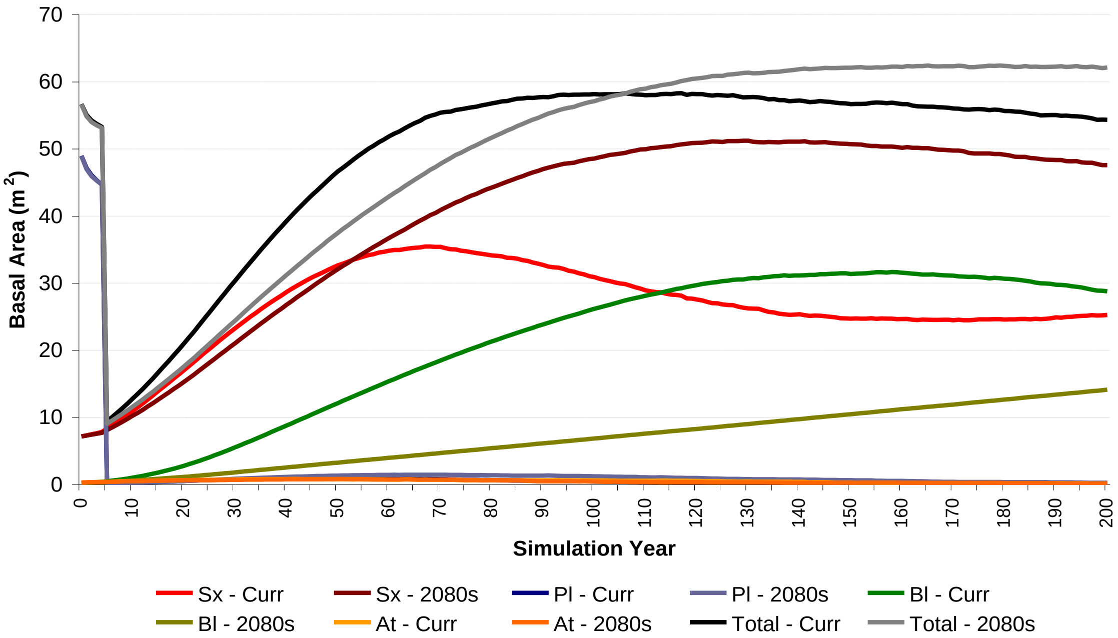

Fig. 11: Species response on a mesic site following a mountain pine beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

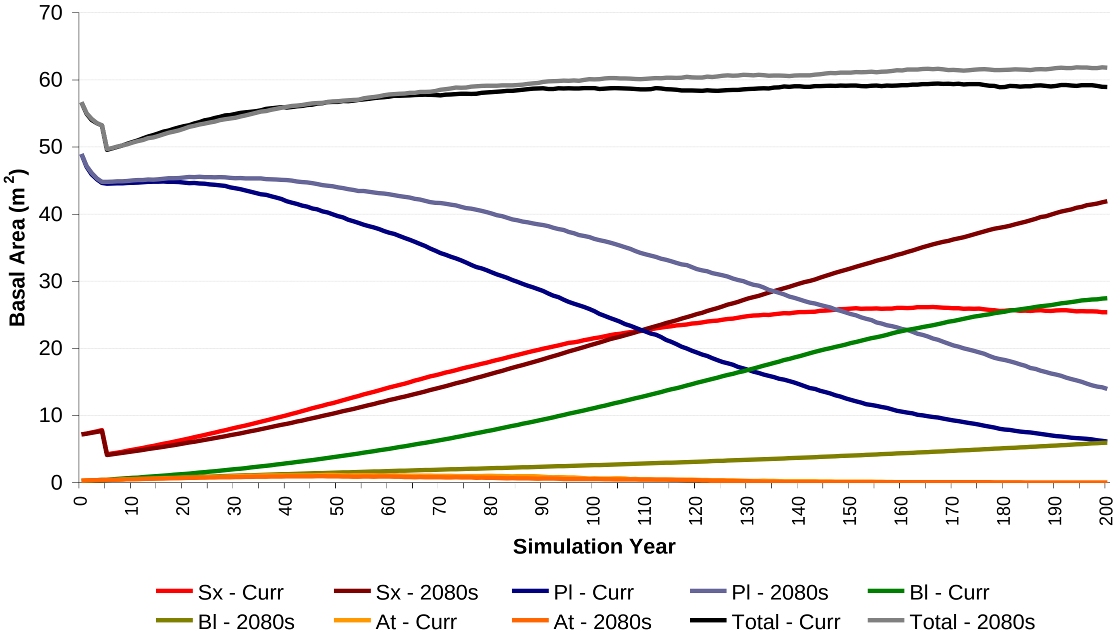

Fig. 12: Species response on a mesic site following a spruce bark beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

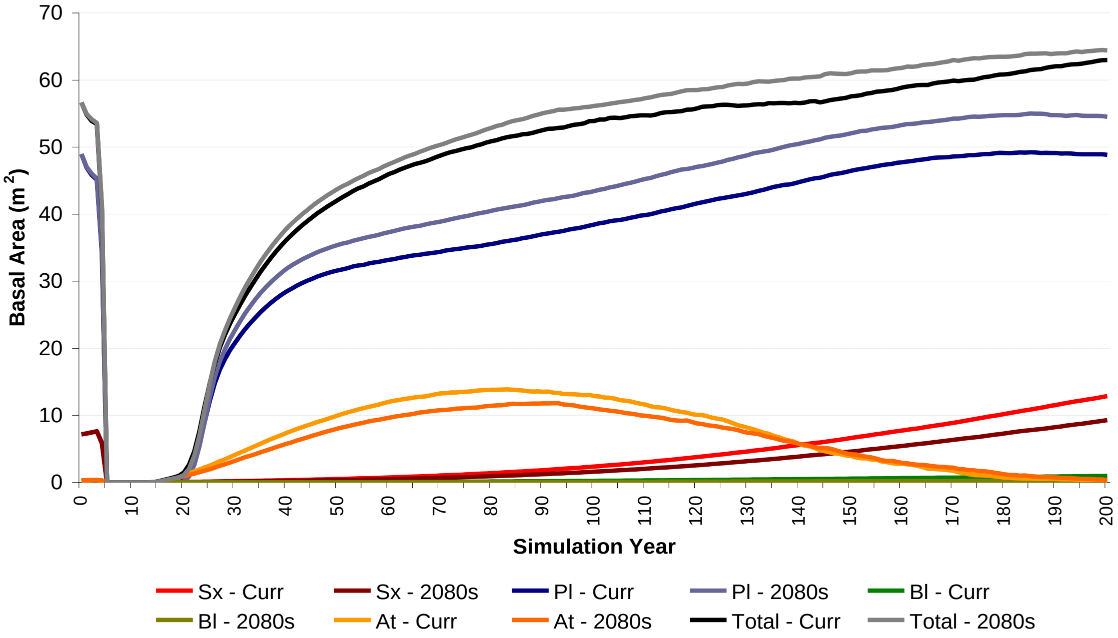

Fig. 13: Species response on a sub-hygric site following a fire under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

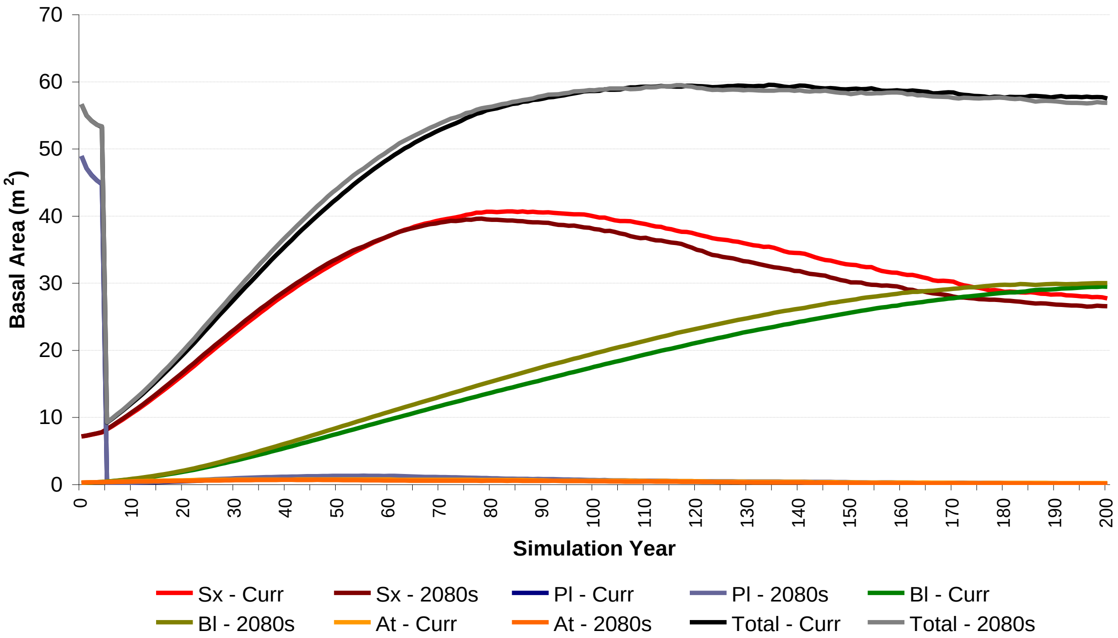

Fig. 14: Species response on a sub-hygric site following a mountain pine beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).

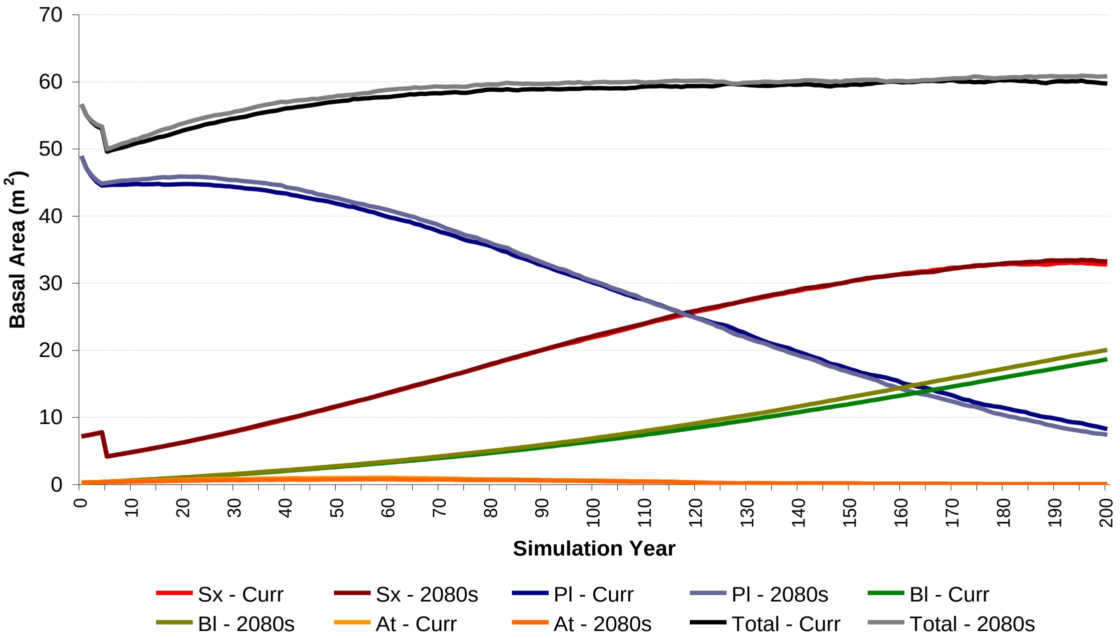

Fig. 15: Species response on a sub-hygric site following a spruce bark beetle attack under current climate conditions and predicted climate in the 2080s: Current (Curr); interior spruce (Sx), lodgepole pine (Pl), subalpine fir (Bl), and trembling aspen (At).