

LIMITED REPORT

Tree Species Vulnerability and Adaptation to Climate Change: Final Technical Report

Submitted to the Climate Change Task Force

Lead Author:

Mark Johnston, Saskatchewan Research Council

Contributing Authors:

David Price, Canadian Forest Service, Northern Forestry Centre
Sylvia L'Hirondelle, BC Ministry of Forests and Range, Research Branch
Rich Fleming, Canadian Forest Service, Great Lakes Forestry Centre
Aynslie Ogden, Yukon Department of Energy, Mines and Resources

“Human interference will be essential for the maintenance of ecosystem stability.”

(C. Mátyás: Migratory, genetic and phenetic response patterns of forest tree populations facing climate change, *Acta Silv. Lign. Hung.* 2: 33-46, 2006)

SRC Publication No. 12416-1E10

June 2010



LIMITED REPORT

Tree Species Vulnerability and Adaptation to Climate Change: Final Technical Report

Submitted to the Climate Change Task Force

Lead Author:

Mark Johnston, Saskatchewan Research Council

Contributing Authors:

David Price, Canadian Forest Service, Northern Forestry Centre
Sylvia L'Hirondelle, BC Ministry of Forests and Range, Research Branch
Rich Fleming, Canadian Forest Service, Great Lakes Forestry Centre
Aynslie Ogden, Yukon Department of Energy, Mines and Resources

SRC Publication No. 12416-1E10

June 2010

Saskatchewan Research Council
125 – 15 Innovation Blvd.
Saskatoon, SK S7N 2X8
Tel: 306.933.5400
Fax: 306.933.7817

Tree Species Vulnerability and Adaptation to Climate Change

Chapter Outline

1.0	INTRODUCTION	1
1.1	Vulnerability	1
2.0	IMPACTS OF CLIMATE VARIABILITY AND CHANGE	4
2.1	Climate Trends and Projections	4
2.1.1	Observed Changes in Temperature and Precipitation	4
2.1.2	Other Observed Changes	5
2.1.3	Projected Temperature and Precipitation	5
2.2	Maladaptation: Interaction Between Trees, Site Factors and Climate	6
2.2.1	Physiological Basis for Maladaptation (Including Regeneration and Phenology)	9
2.2.1.1	Why We Need to Understand Tree Physiology and Adaptation in the Face of Climate Change	9
2.2.1.2	Paleohistory and History	9
2.2.1.3	Responses of Trees to Temperature, CO ₂ , Nutrients, Water, Light, and Ozone	10
2.2.1.4	Phenological and Developmental Processes	14
2.2.1.5	Reproductive Physiology	16
2.2.1.6	Population Differences	16
2.2.1.7	Epigenetics, After-effects, Nursery and Cultural Effects	17
2.2.1.8	Summary of CO ₂ and Temperature Effects	19
2.2.1.9	Summary of Climate Change Effects on Species with Current Range in Canada	19
2.2.2	Response to Maladaptation: Migration	23
2.2.2.1	Modelling Species and Ecosystem Range Shifts	25
2.2.2.1.1	Introduction	25
2.2.2.1.2	Climate Envelope Models (CEM)	26
2.2.2.1.3	Forest Gap Models	29
2.2.2.1.4	The Importance of Genetics in Vegetation Models	32
2.2.2.1.5	Review of Modelling Studies	33
2.2.2.1.6	Regional Syntheses	35
2.2.2.1.6.1	Northern Boreal Treeline	35
2.2.2.1.6.2	British Columbia	36

2.2.2.1.6.3	Western Boreal	37
2.2.2.1.6.4	Eastern Boreal	39
2.2.2.1.6.5	Southern Ontario, Québec and Maritimes	39
2.2.2.1.7	Concluding Remarks	41
2.2.3	Response to Maladaptation: Species Adaptation	41
2.2.4	Index of Vulnerability	43
2.2.4.1	Results	45
2.3	Disturbance	46
2.3.1	Fire	46
2.3.1.1	Invaders	47
2.3.1.2	Evaders	47
2.3.1.3	Avoiders	48
2.3.1.4	Resisters	48
2.3.1.5	Endurers	48
2.3.2	Insects	49
2.3.2.1	Introduction	49
2.3.2.1.1	Why Are Insect Disturbances in Canada’s Forests Important?	50
2.3.2.1.1.1	Disturbances Drive Ecosystem Change in Canada’s Forest	50
2.3.2.1.2	Insect Outbreaks are Dominant Disturbances in Canada’s Forests	51
2.3.2.2	How Will Insects Respond to Climate Change?	52
2.3.2.2.1	Physiological Responses to Climate Change	53
2.3.2.2.2	Seasonal Responses to Climate Change	53
2.3.2.2.3	Changes in Distribution in Response to Climate Change	54
2.3.2.3	Complicating Factors	54
2.3.2.3.1	Complicating Factor: Changes in Multiple Variables	54
2.3.2.3.2	Complicating Factor: Separation in Time and Space	55
2.3.2.3.3	Complicating Factor: Differential Adaptability	56
2.3.2.4	Which Insect Species are the Prime Suspects for Future Damage to Canada’s Forests as a Result of Climate Change?	56
2.3.2.4.1	Mountain Pine Beetle	56
2.3.2.4.2	Spruce Budworm and Jack Pine Budworm	58
2.3.2.4.3	Forest Tent Caterpillar	60
2.3.2.4.4	Invasives	61
2.3.2.4.4.1	Asian Longhorned Beetle	61
2.3.2.4.4.2	Emerald Ash Borer	61

2.3.2.4.4.3	European Wood Wasp.....	62
2.3.2.4.4.4	North American Gypsy Moth.....	62
2.3.2.4.4.5	Brown Spruce Longhorned Beetle	62
2.3.2.4.4.6	Pine Shoot Beetle	63
2.3.2.4.4.7	Hemlock Woolly Adelgid	63
2.3.2.4.5	Surprises	64
2.3.2.5	SO WHAT (Are Key Issues for Management to Consider in this Context)?.....	64
2.3.2.5.1	Insect Management for Sustainable Forest Benefits.....	65
2.3.2.5.2	Interactions with Other Disturbance Types.....	66
2.3.2.5.3	Carbon Storage.....	68
2.3.2.6	Research Directions	69
2.3.3	Tree Diseases	70
3.0	MANAGEMENT OPTIONS FOR ADAPTATION	76
3.1	Adaptation Planning.....	77
3.2	Assisted Migration	79
3.3	Silviculture: Regeneration, Stand Management, Landscape-level Management and Planning	85
3.3.1	Regeneration	86
3.3.2	Stand Management.....	88
3.3.3	Landscape-level Management and Planning	88
3.3.3.1	Adaptive Capacity.....	89
4.0	RESEARCH NEEDS.....	90
4.1	Adapted Genetic Material	90
4.2	Tree Physiology	91
4.3	Insects and Disease	91
4.4	Fire	91
4.5	Silviculture.....	91
4.6	Genetic Diversification.....	92
5.0	CONCLUSIONS.....	92
6.0	ACKNOWLEDGEMENTS.....	93
7.0	REFERENCES	94

LIST OF FIGURES

Figure 1. A general framework for assessing the vulnerability of species to global climate change.	3
Figure 2. Interaction among climate factors and other stressors. I&D refers to insects and disease.	8
Figure 3. Species-level modelling studies of climate change impacts on forest trees in Canada superimposed on the Terrestrial Ecozones map of Wiken 1986.	34
Figure 4. Conceptual linkages among climate change and free-growing standards, stand growth and economic benefits from timber harvest (from Woods 2009).	76
Figure 5. An approach to climate change adaptation planning in the context of Sustainable Forest Management.	78
Figure 6. Decision pathway for implementing species translocation (modified from Hoegh-Guldberg et al. 2008).	84

LIST OF TABLES

Table 1. Summary of the most common effects of increased CO ₂ or temperature on physiological responses of tree species.	19
Table 2. Summary of physiological responses to climate change for Canadian tree species.	20
Table 3. Climate velocity and residence time for three forested biomes in Canada.	24
Table 4. Index and ranking of nine species' vulnerability to climate change.	45
Table 5. Adaptations of species groups to fire cycles (modified from Rowe 1983).	48
Table 6. Tree diseases in Ontario and estimated effect of climate change.	75
Table 7. Summary of main Canadian literature on species and transfer functions.	81

1.0 INTRODUCTION

The forested portions of Canada are expected to experience greater impacts of climate change than many areas of the world (Field et al. 2007). Impacts of particular concern to Canadian forest managers include increased frequency and intensity of fires (Flannigan et al. 2005), increased outbreaks of forest pests, both insects and disease (Volney and Hirsch 2005), increased frequency of drought leading to forest dieback, particularly on the southern fringe of the boreal forest (Hogg and Bernier 2005), and changes to growth and amount of harvestable wood volume (Johnston and Williamson 2005, Girardin et al. 2008). Some of these (and other) biophysical impacts are already being observed, although in many cases we lack the details needed to understand site-specific impacts and identify adaptation options (Williamson et al. 2009).

The objective of this report is to provide scientific background information (the Technical Report) for the report recently published by the Canadian Council of Forest Ministers (CCFM): “Vulnerability Of Canada’s Tree Species To Climate Change And Management Options For Adaptation - An Overview for Policy Makers and Practitioners” (Johnston et al. 2009). These reports arose from a meeting of the Council of the Federation in January 2008 in which the issue of tree species vulnerability to climate change was identified as important to the future of both Canada’s forest environment and the forest industry. The CCFM established the Climate Change Task Force which has overseen the creation of both the Overview and Technical reports. The Technical Report was based on extensive consultation with forest scientists and practitioners across Canada and a literature review targeting the current understanding of the vulnerability of tree species to climate change in Canada’s forested landscapes.

1.1 Vulnerability

The Intergovernmental Panel on Climate Change (IPCC) has adopted a general approach for assessing climate change vulnerability. Details of the IPCC approach are given in Smit and Wandel (2006), and Johnston and Williamson (2007) show how the IPCC approach can be adapted to forest management. Briefly, a system's vulnerability to climate change is a function of the impacts¹ of climate change on the system (e.g., a forest ecosystem or the forest sector in general) and of the system's adaptive capacity. Adaptive capacity is the ability of a natural or human system to adapt to the impacts of climate change. In biological systems, adaptive capacity is based on potential for genetic adaptation, physiological adjustment, migration, etc. For human systems, adaptive capacity is determined by such factors as access to technology, availability of resources, social and human capital and management of information (Moser et al. 2008). Vulnerability can be assessed in the context of either current or future climate scenarios. Adaptation measures can then be proposed that may reduce vulnerability by reducing potential negative impacts and by improving adaptive capacity. In this report we focus on the impacts of climate change at the tree species level, and discuss management options that may provide opportunities for adapting to these impacts. Phase 2 of this project will address ecosystem-level impacts of climate change and the adaptive capacity of the Canadian forest sector.

¹ Climate change impacts are a function of exposure to climatic conditions (e.g., a particular temperature or precipitation regime) and a system's sensitivity or degree of response to the exposure (e.g., a forest's sensitivity to drought).

Williams et al. (2008) provide a general framework for assessing species vulnerability to climate change (Figure 1) based on concepts similar to those used in the IPCC approach. In this report we address the components of vulnerability shown in Figure 1, where data are available. Given the focus on species-level analysis, the majority of the report addresses species sensitivity (yellow boxes in Figure 1) and management adaptive capacity. In Section 2 we focus on the impacts of climate change on Canada's tree species, with a focus on two aspects: maladaptation and the potential species responses of migration and adaptation under a changing climate, and how changing disturbance regimes may affect tree species. Section 3 discusses forest management options that may allow adaptation to climate change at the species level. In Section 4 we identify research needs related to increasing our understanding of tree species vulnerability and what adaptation options may exist. Ecosystem-level impacts, forest sector adaptive capacity and adaptation planning approaches will be addressed in Phase 2 of the CCFM climate change project.

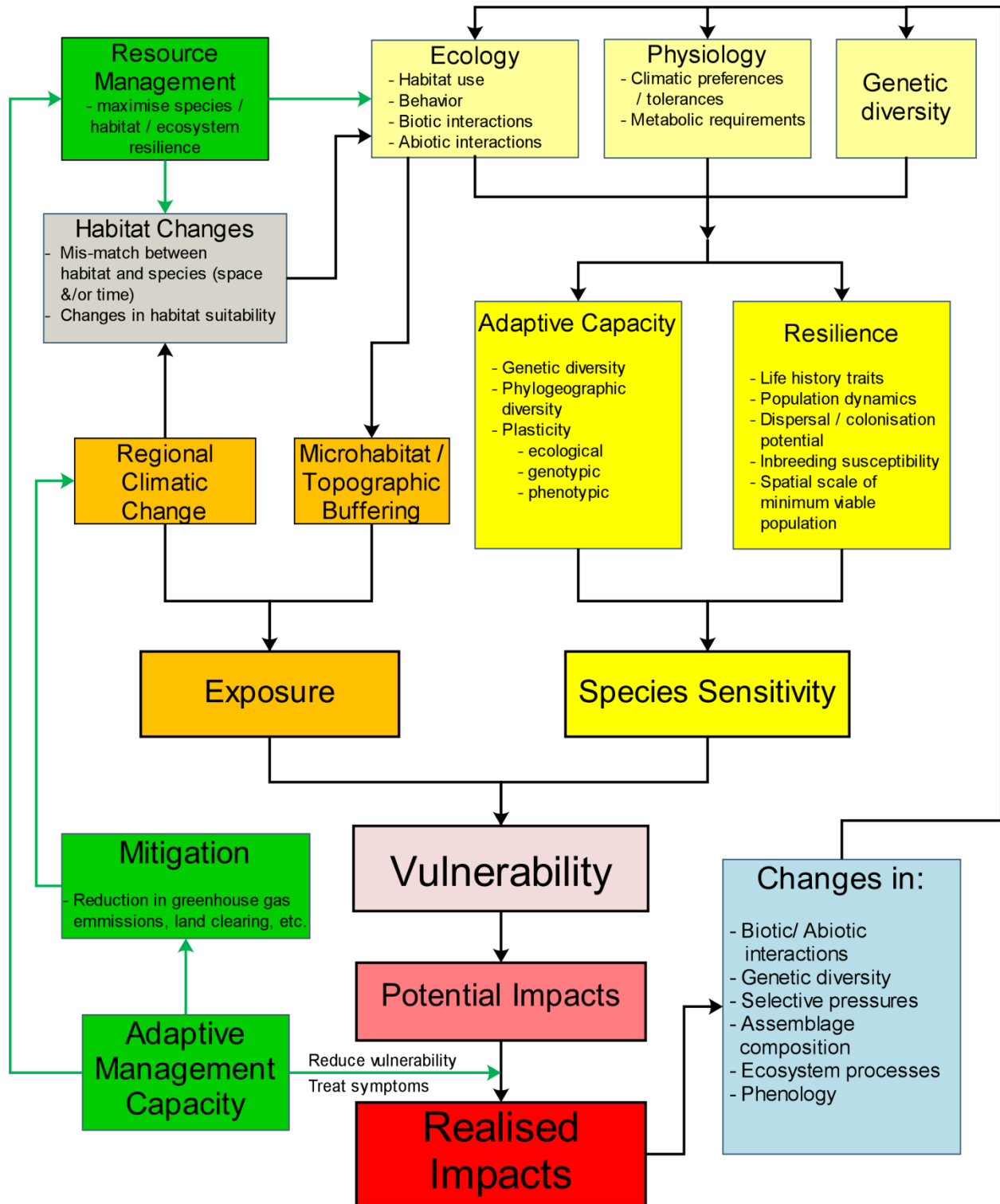


Figure 1. A general framework for assessing the vulnerability of species to global climate change. Reproduced under the Creative Commons Attribution License from Williams, S., L. Shoo, J. Isaac, A. Hoffmann and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. Public Library of Science Biology 6:2621-2626, doi:10.1371/journal.pbio.0060325.

2.0 IMPACTS OF CLIMATE VARIABILITY AND CHANGE

Recent research has demonstrated a significant “fingerprint” of climate change on a wide range of species around the world. In a recent review paper, Parmesan (2006) summarizes these findings:

“These observed changes are heavily biased in the directions predicted from global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research.” (Parmesan (2006), p. 637).

For Canadian species, long-lived tree species with long generation times have shown a few unambiguous signs of being affected by climate change directly. Treelines in the Canadian Rockies (Luckman and Kavanagh 2000) and in northern Québec (Caccianiga and Payette 2006) have migrated upward and northward, respectively. Recent drought events have significantly affected tree populations and may be examples of future effects of climate change, e.g. Hogg et al. (2008), van Mantgem et al. (2009). As climate change unfolds across Canada’s forested landscapes, the expectation is that species will begin to show effects as climate changes, particularly at the margins of their current ranges (Aitken et al. 2008, Lemmen et al. 2008, Mátyás et al. 2009).

At the tree species level, the impacts of climate change can be grouped into two general categories: maladaptation and changing disturbance regimes. We begin this chapter with an overview of the changes in climate expected for the forested regions of Canada. Detailed descriptions of these projections are available in Barrow et al. (2004) and Lemmen et al. (2008). This is followed by a discussion of the impacts of climate change on tree species, divided into two sections: maladaptation and disturbance. The first section begins with a discussion of the physiological basis for maladaptation, followed by a review of the literature regarding two potential species responses to maladaptation, migration and adaptation. This is followed by the section on disturbance which focuses on fire, insects and disease, as these are generally species-specific in their impacts. Ecosystem-level impacts of changes in disturbance regimes and other effects of climate change will be addressed in Phase 2 of the CCFM climate change project.

2.1 Climate Trends and Projections

The following section summarizes observed changes in climate across Canada and provides an overview of projected climate change during the 21st century, taken from Lemmen et al. (2008). For more detailed information, we suggest the reader consult the regional chapters in Lemmen et al. (2008), the North America chapter of the IPCC Fourth Assessment Report (Field et al. 2007), and Williamson et al. (2009).

2.1.1 Observed Changes in Temperature and Precipitation

Climate data have been collected in southern Canada for more than a century and in other parts of Canada since the mid– twentieth century. These data, together with satellite data from the past couple of decades, provide a detailed picture of how Canadian climate has changed in the past 50

years. Canada has warmed by more than 1.3°C since 1948, a rate that is about twice the global average. During this time period, the greatest temperature increases have been observed in the Yukon and Northwest Territories. All regions of the country have experienced warming since the 1960s, including the eastern Arctic, where there has been a reversal from cooling to a warming trend, starting in the early 1990s.

Seasonally, temperature increases have been higher and more spatially variable during the winter and spring months. In northwestern Canada, winter temperatures increased more than 3°C between 1948 and 2003, while winter and spring cooling trends were observed in parts of the eastern Arctic. Summer warming has been both more modest and more uniform across the country.

Canada has become wetter during the past half century, with mean precipitation across the country increasing by about 12 %. The largest percentage increase in annual precipitation has occurred in the high Arctic, while parts of southern Canada (particularly the Prairies) have seen little change or even a decrease. Portions of southern British Columbia and southeastern Canada show significant increases in precipitation in spring and autumn. In contrast, most of southern Canada has experienced a significant decline in winter precipitation.

There are also significant changes at the regional scale in the numbers of intense precipitation events. On average, the fraction of precipitation falling as intense events (the upper 10%) has been decreasing in southern Canada but increasing in northern Canada, particularly in the northeast. Also, more of the precipitation is falling as rain rather than snow.

2.1.2 Other Observed Changes

A general increase in thaw depth was observed through the 1990s across the Canadian permafrost regions. Shallow permafrost temperatures increased during the last 20-30 years by 0.3 to 0.5°C per decade in the Canadian high Arctic, and ranged from no change to almost 1°C per decade in the western Arctic.

Actual evapotranspiration (AET) has increased in most regions of the country during the last 40 years, although the trend is weak or inconsistent in some areas due to limited availability of water to evaporate. For example, evapotranspiration rates have decreased slightly in the dry regions of the Prairies, where available water is already limited throughout much of the year. Although many areas of the country are expected to experience an increase in precipitation, this may not be sufficient to offset the AET increase due to temperature rise.

2.1.3 Projected Temperature and Precipitation

All of Canada, with the possible exception of the Atlantic offshore area, is projected to warm during the next 80 years, although the amount of warming will not be uniform across the country. During the present century, temperature increases will be greatest in the high Arctic, and greater in the central portions of the country than along the east and west coasts.

On a seasonal basis, warming is expected to be greatest during the winter months due in part to the feedback effect that reduced snow and ice cover has on land-surface albedo. Winter warming by the 2050s is expected to be most pronounced in the Hudson Bay and high Arctic areas, and least in southwestern British Columbia and the southern Atlantic region. Rates of warming will be lower in the summer and fall, and summer warming is projected to be more uniform across the country. The frequency of extreme summer temperatures (exceeding 30°C) is expected to increase across Canada, while extreme cold days are projected to decline significantly.

Annual total precipitation is projected to increase across the country during the current century. By the 2080s, projected precipitation increases range from 0 to 10% in the far south up to 40 to 50% in the high Arctic. Due to enhanced evapotranspiration, many regions will experience a moisture deficit despite greater amounts of precipitation. Seasonal changes in precipitation will generally have greater regional-scale impacts than the annual totals. Throughout most of southern Canada, precipitation increases are projected to be low (0–10% by the 2050s) during the summer and fall months. In some regions, especially the south-central Prairies and southwestern British Columbia, precipitation is even expected to decline in the summer. Other important changes in precipitation include an increase in the percentage of precipitation falling as rain rather than snow, and an increase in extreme daily precipitation.

2.2 Maladaptation: Interaction between Trees, Site Factors and Climate

At the tree species level, maladaptation is the most important impact of future climate change. Tree species and populations will experience one of three fates in a rapidly changing environment: migration, adaptation or extinction (Aitken et al. 2008). Each of these is a potential response to the underlying problem of maladaptation. O'Neill and Yanchuk (2005) explain the problem as follows:

“Populations of forest trees become adapted to their native environments through natural selection by synchronizing their seasonal growth patterns with the average timing of local growing season conditions (favourable moisture and temperature). Despite having large distributional ranges, often encompassing large portions of continents, individual populations (i.e. provenances or ‘seed sources’) of most tree species can be adapted to a relatively narrow climate range.” (O'Neill and Yanchuk 2005, p. 1)

When climate becomes significantly different from that in which the species evolved, maladaptation occurs. Maladaptation includes a direct climate component (e.g. the impacts of increasing temperature) and an indirect component (e.g. changes in soil moisture availability resulting from changes in precipitation and evapotranspiration). These climatic-related effects also render trees more susceptible to additional stressors, e.g. insects (Frey et al. 2004), disease (Kliejunas et al. 2009) and fire (Volney and Hirsch 2005). Examples illustrating the potential effects of maladaptation under current climate include wide-spread aspen (*Populus tremuloides*) die-back in the prairie provinces in 2001–2003 due to drought and insect defoliation (Hogg et al. 2008); widespread mortality in piñon pine (*Pinus edulis*) in the southwest US due to extended drought (Adams et al. 2009) and die-back of yellow cedar (*Chamaecyparis nootkatensis*) in southeast Alaska and northwest BC due to shallow snow pack and consequent frost injury to root systems (Hennon et al. 2006). Figure 2 shows the conceptual relationship between climate

variability or change and additional stressors. Not only are trees rendered more susceptible to insects and diseases by a decoupling of the timing of the annual climate cycle from the timing of each population's genetically programmed phenology, but in addition the frequency and severity of pest outbreaks may increase and new pests may be introduced, exacerbating the problem of maladaptation.

As an example of a quantitative analysis of maladaptation under future climates, St. Clair and Howe (2007) studied current populations of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). They expressed maladaptation as the proportion of non-overlap between two normal distributions in which the means and genetic variances of current and future populations are determined from genealogical models. The risk of maladaptation was large for most traits when compared with the risk associated with current transfers within seed zones, particularly for the more drastic climate change scenario (the CSIRO GCM forced with the SRES A2 emissions scenario). For example, the proportion of non-overlap for a composite trait representing bud set, emergence, growth, and root to shoot ratio was as high as 0.90. The authors recommend supplementing within-population variation by mixing local populations with some proportion of populations from lower elevations and further south. They suggest that populations adapted to climates in 2100 would come from locations 450–1130 m lower in elevation and 1.8–4.9 degrees further south in latitude.

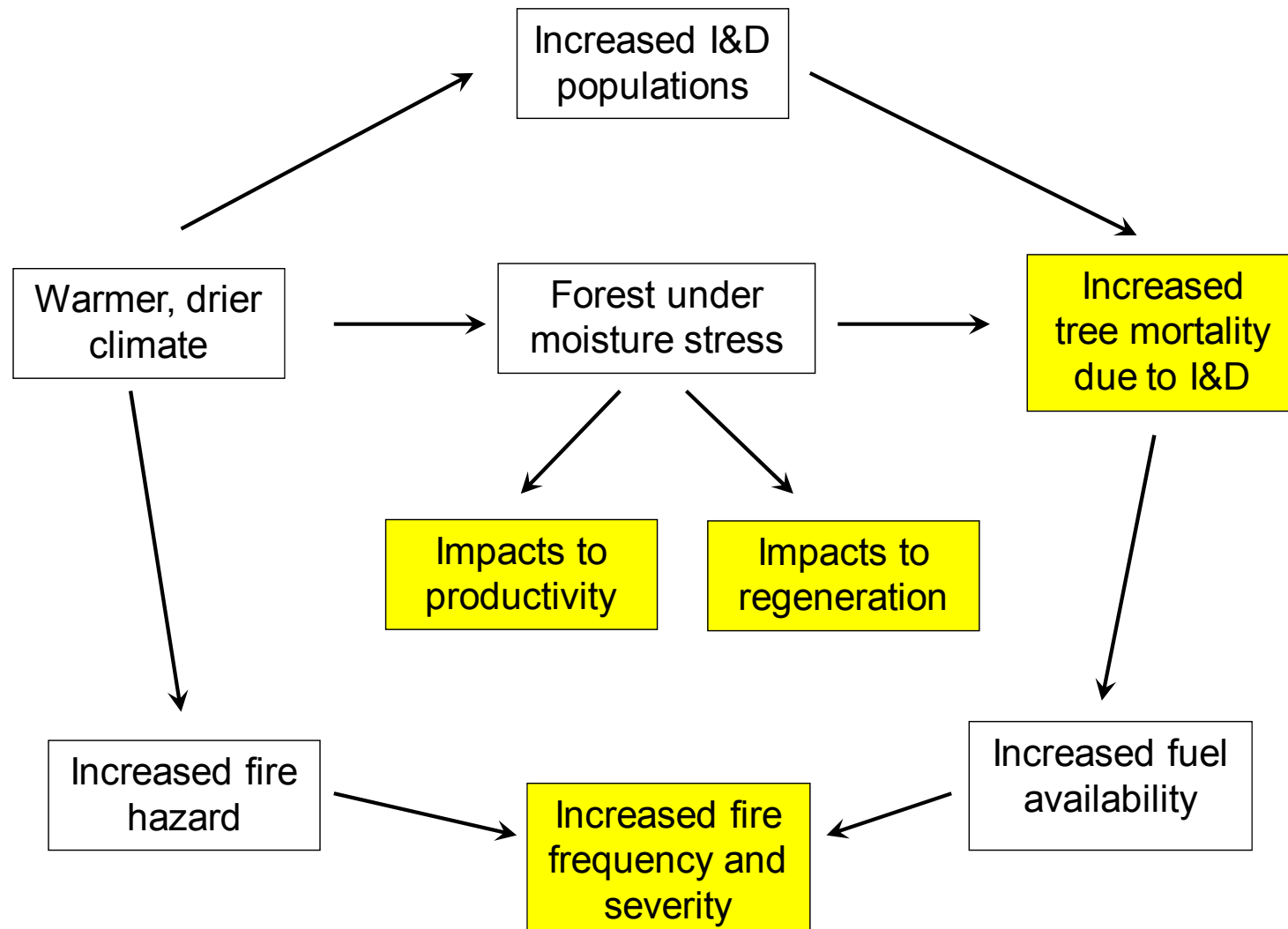


Figure 2. Interaction among climate factors and other stressors. I&D refers to insects and disease. Yellow boxes indicate effects directly related to forest management.

2.2.1 Physiological Basis for Maladaptation (Including Regeneration and Phenology)

Contributed by Dr. Sylvia L'Hirondelle, Research Branch, BC Ministry of Forests and Range, Victoria, BC

2.2.1.1 Why We Need to Understand Tree Physiology and Adaptation in the Face of Climate Change

As Kramer (1986) said, the “physiological processes of trees are the machinery through which genetic potential and environment operate to determine the quantity and quality of growth.” Trees are well-adapted to their environment when they are physiologically suited for high growth, reproduction, and survival to maturity, and have resistance to biotic and abiotic stresses (Zobel and Talbert 1984). Identifying physiological characteristics that improve adaptive fitness gives more useful information than measuring just survival or growth, leading to improved planting guidelines for populations. Finding rare or important traits is also needed for gene conservation. Given the high degree of genetic diversity within tree species, there is a wide range in physiological traits that may allow tree species to adapt relatively quickly to climate change (Hamrick 2004, Aitken et al. 2008). To predict tree responses to environmental changes, we need to understand their adaptive limitations to each factor, as well as interactions and feedbacks (Kirschbaum 2000). And to understand and predict ecosystem functioning, we need to understand physiological processes such as gas exchange, carbon allocation, seasonal growth patterns, development, and aging (Buchmann 2002). With this knowledge we can make sound decisions to ensure the continued growth of forests in their most favourable locations.

2.2.1.2 Paleohistory and History

About 45 million years ago, forests of large deciduous and evergreen trees flourished as far north as Axel Heiberg Island (80°N), when temperatures were considerably warmer than now and precipitation levels were high enough to support genera such as *Metasequoia*, *Larix*, *Picea*, *Chamaecyparis*, and *Tsuga* (Greenwood and Basinger 1994, Kotyk et al. 2003, LePage 2003). These fossil forests show that precursors of modern tree species were physiologically adapted to growth at high latitudes with large annual variations in photoperiod and temperature. Evidence from stomata on fossil leaves suggests that ancient trees also developed under conditions of high CO₂ levels, ranging from 1000 to over 2000 ppm during the Mesozoic era (65 to 250 Mya) and only dropping below 1000 ppm during ice ages in the Neogene (up to 8 Mya) (Retallack 2001). Recent simulations with “living fossil” conifers have shown that these species can maintain productivity in conditions where light levels vary from continuous illumination for 6 wk in summer to continuous darkness for 6 wk in winter (Osborne and Beerling 2003, Llorens et al. 2009a,b).

From more recent paleohistory, evidence shows that the ranges of tree species have fluctuated several times since the last ice age (Hamrick 2004). The effects of environmental changes on trees can be estimated from pollen analysis, dendrochronology, biomass measurements, and stomatal patterns. Pollen records from southern British Columbia during the early Holocene (about 12,000 years BP) indicate that *Abies lasiocarpa* grew at low elevations where it is not present today, and was among the first species to colonize the deglaciated landscapes (Heinrichs

et al. 2002). In Québec, today's scattered stands of *Abies balsamea* are remnants of much larger populations from a warmer period about 7000 years BP, and are no longer in equilibrium with the climate (Ali et al. 2008). Patterns from tree rings show trends of increasing water use efficiency over the past 200 years, corresponding to increased atmospheric CO₂ concentrations (Feng 1999), but direct evidence for wide-scale CO₂ fertilization is somewhat limited (Jacoby and D'Arrigo 1997, Voelker et al. 2006). Studies based on field and satellite measurements of forest productivity have shown mostly positive growth trends in the past 55 years in areas where water was not limiting (Boisvenue and Running 2006). Stomata, which respond to climate change on many time scales, have been used to detect adaptation to changing CO₂ levels (Hetherington and Woodward 2003). Over the past millennium, the record of stomatal frequency from buried *Tsuga heterophylla* needles indicates fluctuations in atmospheric CO₂ on a centennial-scale, with minima about 260 ppm and maxima about 320 ppm CO₂ (Kouwenberg et al. 2005). Comparisons across 60 species in the UK found significant decreases in stomatal density over the past 70 years, consistent with other evidence on the effect of CO₂ on leaf morphology (Beerling and Kelly 1997). These and many other studies show that forest species have adapted to climate change over a wide range of time scales in the past, and continue to adapt under the current changing conditions. What are the physiological traits that make this possible?

2.2.1.3 Responses of Trees to Temperature, CO₂, Nutrients, Water, Light, and Ozone

Physiological changes in response to environmental factors take place in individual trees diurnally, seasonally, or over a period of years (acclimation), and in populations over generations (adaptation). These changes include variations in growth rhythm (the timing of bud burst, elongation, free growth, bud set, leaf senescence, heat and cold acclimation), evergreen leaf retention, gas exchange and biochemical pathways (stomatal conductance, photosynthesis, respiration), water relations (osmotic potential, turgor), nutrient uptake capacity, production of defensive compounds, and synthesis pathways leading to altered morphology and anatomy. The complex interactions among the effects of CO₂, temperature, light, water, and nutrients make it difficult to predict long-term responses of trees when environmental conditions are changing relatively rapidly, but some general observations have emerged from decades of study.

Hundreds of experiments have tested the effects of elevated CO₂ and temperature on growth of seedlings and mature trees, often in combination with different levels of soil moisture and nutrients; these have been reported individually and in syntheses (Curtis and Wang 1998, Saxe et al. 1998, Kirschbaum 2000, Bruhn et al. 2001, Ainsworth and Long 2005, Boisvenue and Running 2006, Seppälä et al. 2009). Increased CO₂ alone or with higher temperatures usually leads to increases in photosynthesis, dark respiration, leaf area, and biomass in woody plants (Curtis and Wang 1998, Saxe et al. 1998, Lewis et al. 2001, Davey et al. 2004). The magnitude of the response varies among species and types of trees, with evergreen conifers often showing a greater increase in biomass than deciduous species (Saxe et al. 1998). Photosynthesis in trees typically increases 25 to 75% when CO₂ doubles, and continues to increase up to an optimal level beyond which effects can be negative (Higginbotham et al. 1985, Farrar et al. 1995, Kirschbaum 2000, Ellsworth et al. 2004). However, after a period of weeks to years when other factors such as nutrients become limiting, photosynthesis often down-regulates at high CO₂ especially in slow-growing evergreens (Curtis and Wang 1998, Ward and Strain 1999,

Kirschbaum 2000, Utriainen 2003, Logan et al. 2009) but also in deciduous conifers (Osborne and Beerling 2003). Unless more nutrients are supplied, foliar nutrient levels decline with photosynthesis and the CO₂ stimulation of biomass falls, leading to a negative feedback of high CO₂ on forest productivity (Curtis and Wang 1998, Kirschbaum 2000, Ellsworth et al. 2004). In some cases, biomass of mature trees (Körner et al. 2005, Asshoff et al. 2006) and seedlings does not increase in response to high CO₂ levels, with the extra assimilated carbon going to soil organisms (Olszyk et al. 2003). Thus, growth stimulation of trees by CO₂ will sometimes be less than expected. For example, Körner et al. (2005) did not find a consistent growth response among several species of large mature deciduous trees at a FACE site in Switzerland. They conclude:

“The Swiss forest FACE study thus points at the crucial role of tree species identity and so far does not support expectations of greater carbon binding in tree biomass in such deciduous trees. ... In summary, we find no evidence that current CO₂ concentrations are limiting tree growth in this tallest forest studied so far.” (Körner et al. 2005, p. 1632).

Increasing temperatures have positive or negative effects on tree growth, depending on other environmental factors (Saxe et al. 2001). Historically, changes in global temperature and CO₂ have been coupled, which benefits plants such as conifers (Cowling 1999). When CO₂ increases but temperature remains low (e.g., 5°C), photosynthetic rates are closer to CO₂ saturation, so there is a much smaller response to high CO₂ levels than at warmer temperatures (Kirschbaum 2000). And when temperature increases without higher CO₂, photorespiration goes up and photosynthesis goes down. In contrast, when both CO₂ and temperature increase, so does photosynthesis, and its temperature optimum becomes higher in some species (Tjoelker et al. 1998a, Kirschbaum 2000). This can lead to increased heat tolerance. Although respiration also increases with increasing temperature, the ratio between photosynthesis and respiration tends to remain constant, suggesting that higher temperatures alone will not lead to greater carbon losses (Kirschbaum 2000, Saxe et al. 2001). However, when both temperature and CO₂ increase, forest respiration may increase (Davey et al. 2004, Boisvenue and Running 2006). In general, a 2°C increase in temperature is likely to benefit trees through increased photosynthesis, albeit with considerable variation in response among species (Saxe et al. 2001).

Overall, tree growth is stimulated more often by increased temperature than by increased CO₂ (Sallas et al. 2003, Utriainen 2003, Beedlow and Tingey 2007), especially under conditions of nutrient limitation, although this is not always the case (Overdieck and Fenselau 2009). Given that nitrogen is often the most limiting factor for tree growth in northern forests, at least in unpolluted areas (Utriainen 2003), the CO₂ fertilization effect will be limited. Without additional nitrogen and other nutrients, trees cannot make use of the additional CO₂ (Saxe et al. 1998, Beedlow and Tingey 2007). However, if increasing temperatures stimulate increased decomposition of soil organic matter, nutrient availability may increase (Kirschbaum 2000, Saxe et al. 2001, Boisvenue and Running 2006).

Light level is another limiting factor that affects species response to increased temperature and CO₂. Growth of some conifer seedlings is more stimulated by warming or CO₂ in low-light conditions, and for shade tolerant species more than others (Kerstiens 1998, Curtis and Wang

1998, Yin et al. 2008, Marfo and Dang 2009). On the other hand, growth of some broadleaved species is stimulated more by CO₂ in full sun than in shade conditions (Kubiske and Pregitzer 1996, Herrick and Thomas 1999). There is not enough information available about CO₂ responses of shaded foliage in mature canopies relative to responses of sun leaves (Saxe et al. 1998). These interacting responses to light, CO₂, and temperature will alter species competitiveness during regeneration.

Increases in water use efficiency (ratio of carbon fixed to water used) at elevated CO₂ are reported, often due to increased photosynthesis in conjunction with decreased stomatal conductance (Ward and Strain 1999, Medlyn et al. 2001, Lewis et al. 2002, Wang et al. 2003, Ainsworth and Long 2005). Some authors report that stomatal conductance is not affected by elevated CO₂ (Lippert et al. 1996, Curtis and Wang 1998, Saxe et al. 1998, Llorens et al. 2009b). These contrasting results may reflect differences between angiosperms and gymnosperms in stomatal response to elevated CO₂, with angiosperms readily reducing stomatal conductance as CO₂ concentration increases above ambient (Brodribb et al. 2009). Different effects on conductance may also be a function of study duration. Exposure to elevated CO₂ for more than one growing season usually leads to decreased stomatal conductance (Medlyn et al. 2001).

High CO₂ may increase or decrease water stress, depending on accompanying temperature increases, changes in biomass, and nutrient supply (Johnsen 1993, Lippert et al. 1996, Saxe et al. 1998, Catovsky and Bazzazz 1999, Soulé and Knapp 2006). High temperature alone can reduce water use efficiency of foliage by more than 30% (Wang et al. 2003). Warmer air in combination with warmer soils will stimulate root growth in some species to partially compensate for increased evapotranspiration, but there will be differences among species in responses (Saxe et al. 2001). Warmer temperatures can accelerate drought stress, which, if severe enough, could lead to regional-scale die-offs for some species (Adams et al. 2009). In areas with warm temperatures and limited water availability, forest productivity may decrease even at elevated CO₂ owing to increases in transpiration rates as vapour pressure deficit increases (Kirschbaum 2000).

Climate change projections for Canada suggest that moisture availability will decline in much of central and western Canada (Hogg and Bernier 2005, Lemmen et al. 2008). The southern interior of BC and the southern edge of the boreal forest in the prairies and north-western Ontario are particularly at risk, and some sites will likely lose forest cover in the next few decades (Lempriere et al. 2008). Areas particularly vulnerable to forest cover loss are the Island Forests of the prairie provinces. These are isolated patches of forest occurring on aeolian sand deposits, often surrounded by agricultural land (Henderson et al. 2002). Forests in these areas are often dominated by jack pine (*Pinus banksiana*) and occur on soils with low water-holding capacity. They are currently vulnerable to fire and dwarf mistletoe (*Arceuthobium americanum*) (Johnston et al. 2008). Under a warmer and drier future climate, an additional source of vulnerability will include attack by mountain pine beetle as it spreads east from Alberta, as well as increased likelihood of fire and drought (Hogg and Bernier 2005).

Recent research has resulted in a new understanding of the mechanisms of drought stress on trees. McDowell et al. (2008) identify three hypotheses accounting for these effects:

- Biotic agent demographic hypothesis: drought causes changes in the demographics of pests and diseases that in turn cause tree mortality. This may occur due to increased number of pest generations per year due to longer growing seasons, or increased overwintering due to shorter, warmer winters.
- Hydraulic failure hypothesis: lack of sufficient soil moisture, together with high evaporative demand, causes water-conducting tissues to become air-filled (cavitation), preventing the flow of water. This causes tissue desiccation and eventually cell death.
- Carbon starvation hypothesis: stomatal closure to prevent hydraulic failure causes photosynthetic uptake of carbon to diminish; the trees suffer carbon starvation resulting from continued metabolic demand for carbohydrates.

They suggest that these mechanisms may work independently or in concert; for example carbon starvation may amplify biotic disturbance due to reduced levels of carbon-based defensive compounds. In a similar illustration of the interaction among these hypotheses, Mattson and Hack (1987) showed that drought increased susceptibility of trees to defoliating insects by increasing the concentration of carbohydrates in foliage.

Adams et al. (2009) exposed piñon pine to artificially increased temperatures (≈ 4 °C) by transplanting mature trees into the Biosphere 2 facility in Arizona. The higher temperatures reduced the time to drought-induced mortality by nearly a third, with temperature-dependent differences in cumulative respiration costs implicating carbon starvation as the primary mechanism of mortality. They extrapolated these results to the historic frequency of water deficits in the southwestern United States and predicted a 5-fold increase in the frequency of regional-scale tree die-off events for this species due to temperature alone. Projected increases in drought frequency due to changes in precipitation and increases in stress from biotic agents (e.g., bark beetles) would further exacerbate mortality under future climate change. They conclude that given projected increases in temperature, these results portend widespread increases in the extent and frequency of vegetation die-off in the southwest US. Portions of Canada expected to be subject to frequent droughts in the future (the southern interior of BC, the forest fringe region in the Prairie Provinces) would also likely see increases in forest die-off due to similar mechanisms.

Several recent studies have documented wide-spread growth declines or increased tree mortality due to changes in temperature and moisture availability. Barber et al. (2000) reported wide-spread growth declines in white spruce (*Picea glauca*) in interior Alaska which were ascribed to the effects of drought. Their data show that temperature-induced drought stress has disproportionately affected the most rapidly growing white spruce, suggesting that, under recent climate warming, drought may have been an important factor limiting carbon uptake in a large portion of the North American boreal forest. Van Mantgem et al. (2009) analyzed old-growth forest data from long-term permanent sample plots across a range of sites from southern British Columbia to Arizona. They found that background (i.e. non-catastrophic) mortality rates have increased rapidly in recent decades, with doubling periods ranging from 17 to 29 years. Because mortality increased in small trees, the overall increase in mortality rates could not be attributed

solely to aging of large trees. They concluded that regional warming and consequent increases in water deficits are likely contributors to the increases in tree mortality rates.

Hogg et al. (2008) identified insects and drought as the main factors causing wide-spread die-back of aspen in the prairie provinces during a regional drought in 2001-2003. Hogg (personal communication May 2009) suggests that this is an example of the carbohydrate starvation hypothesis as proposed by McDowell et al. (2008). Data from an extensive network of aspen health monitoring plots (the CIPHA Network, <http://cfs.nrcan.gc.ca/projects/150/4>) showed that aspen mortality increased during the drought and remained high six years later on drought-affected sites; this seemed more consistent with the carbohydrate starvation hypothesis. If the cause was hydraulic failure alone, there most likely would have been an increase in mortality during the drought, followed by a decrease after the return to moist conditions (2004 on most sites). However, hydraulic failure probably played an important secondary role.

Tropospheric ozone (O_3) is an important greenhouse gas and a ground level pollutant that has been increasing in the northern hemisphere (Utriainen 2003). Increased ozone levels usually lead to decreased photosynthesis, growth, and biomass of trees, with sensitivity varying among species and populations and affected by nutrient status (Utriainen 2003, Kubiske et al. 2006). Elevated CO_2 generally does not offer much protection against O_3 damage to trees, and may increase the negative effects (Constable et al. 1996, Wustman et al. 2001, Utriainen 2003, Karnosky et al. 2005). There may also be interactions between ozone exposure and seasonal variations in temperature that affect growth response to the combination of O_3 and CO_2 (Kubiske et al. 2006). In areas where chronic ozone exposure is a concern, some species will suffer increasing damage with climate change.

2.2.1.4 Phenological and Developmental Processes

An understanding of how the physiological processes of trees change with climate over seasons (phenology) and lifetimes (maturation, aging) is necessary to model and predict stand and ecosystem level changes. Foliage development and senescence have large effects on seasonal patterns of ecosystem gas exchange and water use (Buchmann 2002). Patterns of seasonal acclimation to light, water, and temperature, as well as internally regulated processes, determine which individuals and populations are best adapted (Saxe et al. 2001); these are more likely to survive extreme events and be most productive during the growing season (Rossi et al. 2006). Seasonal development, maturation, and aging are affected by climate change, through an altered relationship between temperature and photoperiod, and elevated CO_2 levels (Ward and Strain 1999).

As global temperatures increase, growing season length is increasing in the northern hemisphere (Schwartz et al. 2006). Most northern tree species flush in the spring in response to air temperature, so spring flush dates are days to weeks earlier with warmer springs (Slaney 2006, Vitasse et al. 2009). However, for species that are cued to daylength for seasonal development, there is little or no increase in carbon gain during warmer spring or fall periods (Oleksyn et al. 1998, Saxe et al. 2001, Busch et al. 2007). Elevated CO_2 can delay bud burst and advance bud set in some conifers, while elevated temperature has the opposite effect (Murray et al. 1994). Increased temperatures during the growing season can accelerate the rate of shoot development

but reduce the length of the growth phase in some species (Post et al. 2008), leading to smaller organs and reduced biomass (Olszyk et al. 1998, Utriainen 2003), while in other species there is no effect of elevated temperature or CO₂ on the duration of shoot growth (Slaney 2006). Elevated temperatures can lead to abnormalities and aborted vegetative buds in conifers (Apple et al. 1998), especially in combination with a higher risk of spring frost damage (Saxe et al. 2001). The work done to date shows that tree species have a wide range of variation in response to spring and growing season temperatures.

There is also variation in response to climate change at the end of the growing season. Some deciduous tree species respond to warmer autumns by delaying leaf senescence, while others do not (Vitasse et al. 2009). Elevated CO₂ also affects autumn senescence independently of temperature, causing prolonged photosynthesis and delayed leaf fall in *Populus* (Taylor et al. 2008). Some ancient genera of conifers capitalize on elevated CO₂ during spring and autumn when days are short, helping to explain their high productivity in polar forests millions of years ago (Osborne and Beerling 2003). In other species, the duration of the growing season does not increase under elevated CO₂ (Saxe et al. 1998). This variety of phenological responses to temperature and CO₂ will affect canopy processes, productivity, and the competitive balance in forest stands, and may also affect susceptibility to spring and fall frosts (Taylor et al. 2008, Vitasse et al. 2009).

Winter temperatures have been increasing more than summer temperatures in the northern hemisphere (Schwartz et al. 2006), which can affect the phenology of cold-climate conifers, e.g. Engelmann spruce (*Picea engelmannii*) (Rehfeldt 2005). Acclimation to winter temperatures occurs in response to a combination of increasing night length and declining temperatures, which varies in synchronization among and within species (Saxe et al. 2001). In some boreal conifers such as balsam fir (*Abies balsamea*), this acclimation follows a rigid timing that makes them susceptible to excess respiratory losses in autumn and winter with increased climate warming (Saxe et al. 2001, Strimbeck et al. 2008). In other species, warming can shift the phases of acclimation. For example, in Douglas-fir (*Pseudotsuga menziesii*) seedlings, elevated temperatures affected all phases of frost hardiness, delaying hardening in the fall, reducing maximum hardiness, and delaying de-hardening in the spring (Guak et al. 1998). Elevated CO₂ can also shift patterns of acclimation; in black spruce (*Picea mariana*) seedlings, high CO₂ reduced frost hardiness in the fall and negatively affected bud development (Margolis and Vezina 1990). Such shifts in timing can increase the risk of frost damage in both fall and spring.

The ability of tree species to meet chilling requirements will be affected by variations in seasonal warming across boreal and temperate zones, sometimes in opposite directions (Schwartz et al. 2006), although there is considerable uncertainty about the relationship between chilling and bud status (Saxe et al. 2001). Some species will meet their chilling requirements earlier, making them susceptible to early de-hardening and frost damage if mild spells in midwinter or spring are followed by colder periods (Hanninen 2006). Although there has been enough work done to model past records of bud phenology and chilling, understanding of the physiological processes is too limited to realistically model future effects under climate warming (Saxe et al. 2001).

As stated above, climate change can accelerate phenological development in trees; it can also accelerate development from juvenile to mature growth and have different effects during

different growth phases. Results of the many studies done with tree seedlings are not directly applicable to predictions for mature trees because of age- and size-dependent changes in physiology (Saxe et al. 1998, Thomas and Winner 2002). As seedlings grow into mature trees, the accelerated growth response from added CO₂ usually declines, especially in fast-growing deciduous species (Boisvenue and Running 2006). A similar effect, consistent with increasing CO₂ levels, has been reported from dendrochronology studies of natural stands of *Quercus* and *Pinus*, in which an exponential decline in growth stimulation was found with increasing cambial age through to age 50 (Voelker et al. 2006).

Although mature trees are less growth-stimulated by elevated CO₂ than seedlings, even a small response can reverse aging-related growth decline in some cases. Renewed growth and physiological activity can occur in trees more than 500 years old, coinciding with increases in global CO₂ and temperature (Phillips et al. 2008). Age-climate interactions are related to tree size, canopy light levels, competition, nutrient availability, and many interacting processes, so it is difficult to predict responses to climate change based on age alone (Kirschbaum 2005). Caution and verification are needed when scaling up in size and age (Thomas and Winner 2002), especially when predicting the effects of climate change on stands of trees.

2.2.1.5 Reproductive Physiology

Given that reforestation for many commercial tree species in Canada depends on propagation from seed orchard or wild seed, it is important to know the effects of climate change on reproduction. For herbaceous species, most studies show that elevated CO₂ increases reproductive output, including flower number, fruit number, and seed production (Ward & Strain 1999). In *Pinus taeda*, trees growing under elevated CO₂ for 8 years matured earlier and produced more seeds and cones than trees growing under ambient CO₂ (Ladeau and Clark 2006). Elevated temperature also affects cone production and embryo maturation, with cold temperatures limiting the northward spread of *Picea glauca*, *P. mariana*, and *Abies balsamea* (Messaoud et al. 2007, Meunier et al. 2007). However, warmer temperatures in seed orchards can negatively affect cone development through increased megagametophyte abnormalities or abortion (Owens et al. 2001). Patterns of temperature and precipitation alter the frequency of cone crops in conifers and affect the relationship between cone production and cone predation (Poncet et al. 2009). In addition, elevated temperatures can alter flowering phenology so that some species or populations flower earlier in the season, while others flower later – this has been reported in grasses and forbs (Sherry et al. 2007) and aspen (Beaubien and Hall-Beyer 2003). The predicted patterns of climate change for northern tree species will likely have beneficial effects on reproduction in some parts of the species' ranges, at least initially, but as temperatures increase the beneficial effects of warming and CO₂ may diminish.

2.2.1.6 Population Differences

Although there are several studies reporting population differences in growth with respect to ambient temperatures, relatively few have compared populations or families for genetic differences in their response to elevated CO₂ with or without elevated temperatures. Genetic variation in physiological responses to environmental stresses is well known in tree species, so more climate change research is needed that includes multiple genotypes (Saxe et al. 1998).

Populations with a narrow range of tolerance to temperature and precipitation will be most affected by climate change, and may be lost as it continues (Kirschbaum 2000), while those with the greatest phenotypic plasticity (ability to change behaviour in response to environment) and flexible gene regulation system may be the least affected initially (Saxe et al. 2001). There is also genetic variation in the rate at which populations and species can adapt to changing environmental conditions, leading to different impacts of climate change on populations throughout the range of a species (Davis et al. 2005, Aitken et al. 2008). Because a large part of the within-species genetic variation in trees is found within rather than among populations, loss of a number of populations probably will not greatly reduce genetic diversity as the climate changes (Hamrick 2004).

As with climate change studies comparing different species, those comparing different genotypes within species have found a range of physiological responses. Some studies have found that populations did not vary much in their relative ranking among CO₂ and temperature treatments, suggesting that sources selected for fast growth under current conditions will continue to perform well (Wang et al. 1994, Johnsen and Seiler 1996, Johnsen and Major 1998). But other studies have found genotype by environment (CO₂ and temperature) interactions, indicating that relative performance of genotypes will change in the future (Centritto and Jarvis 1999, Bigras 2000, Bigras 2005, Wang et al. 2000). Differences in the timing and degree of photosynthetic stimulation by CO₂ and temperature will favour certain genotypes within species, and will also affect their competitiveness for limited resources within plant communities (Wang 2007). Because most genotype studies have used seedlings, it is difficult to predict the persistence of the reported effects through to maturity.

2.2.1.7 Epigenetics, After-effects, Nursery and Cultural Effects

Epigenetics refers to changes in gene expression in an organism without accompanying changes in the DNA sequence; a variety of molecular processes can activate or disable certain genes depending on the environment (Bossdorf et al. 2008). Epigenetic changes induced by the environment can be passed on to future generations, particularly when fluctuating conditions last for more than one generation, and can be reversed (Bossdorf et al. 2008, Jablonka and Raz 2009). Transgenerational effects can provide rapid response to abiotic and biotic stresses, leading to offspring that are physiologically more resistant to changes in climate or increases in pests and pathogens (Bonello et al. 2006, Kvaalen 2008, Lau et al. 2008). Although epigenetic inheritance sounds like the inheritance of acquired characteristics, it is not; the genes for the traits that are switched on or off were already part of the DNA sequence of the organism.

Conifers, like other gymnosperms, have among the most complex and largest genomes of any living organisms (Morse et al. 2009). These long-lived trees show evidence of epigenetic effects that can increase the adaptation of their offspring to changed environmental conditions in one generation. Studies of such effects in conifers were initially done with selected parents moved south from their source environment to new locations in seed orchards, and are often referred to as seed orchard after-effects or memory effects (Greenwood and Hutchinson 1996, Johnsen et al. 2005, Rohde and Junttila 2008). In *Picea abies*, *Pinus sylvestris*, *Larix laricina*, and *Picea glauca*, the temperature during female sexual reproduction affects phenological and physiological processes such as spring de-hardening, spring bud flush, cessation of leader growth

in summer, bud set and frost hardiness (Johnsen 1989, Dormling and Johnsen 1992, Greenwood and Hutchinson 1996, Stoehr et al. 1998, Webber et al. 2005, Besnard et al. 2008). When the temperature is warmer than normal, some of the above processes are delayed in timing and can be decreased in magnitude; the change in performance can last for many years (Kvaalen and Johnsen 2008). This memory effect can be triggered by both temperature and photoperiod, providing a fast response to changes in parental environment (Johnsen et al. 2005, Kvaalen and Johnsen 2008), and has also been reported for clonal offspring produced by somatic embryogenesis (Kvaalen and Johnsen 2008). In wind-pollinated conifers from environments with a high degree of variation in space and time (for example, mountainous terrain), the ability to adjust the physiology of the offspring to the mother's environment will increase survival and growth, and will be advantageous in responding to climate change (Saxe et al. 2001, Kvaalen and Johnsen 2008). Although after-effects seem to be fairly prevalent in the northern conifers tested to date, reports are lacking of similar effects in angiosperm tree species (Rohde and Junttila 2008).

Epigenetic inheritance may also contribute to the ability of tree species to form so-called land races when they are transplanted to areas well outside their current ranges. Land races are populations that adapt physiologically to their new conditions, showing altered characteristics that may differ from populations growing in their native range (Rehfeldt and Gallo 2001, Kremer 2007). Several North American conifers (e.g., *Pinus contorta*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Abies grandis*, *Tsuga heterophylla*) have been planted in Great Britain; *Picea sitchensis* is now the most common British tree, and second-generation collections of British *Abies grandis* outperform newly introduced trees from the same original sources (Peterken 2001). Latitudinal transfers of populations within species can also produce adaptation within one or two generations, suggesting that some tree species may be able to adapt to warming temperatures with relatively low risk (Saxe et al. 2001, Kremer 2007, Rohde and Junttila 2008). Such adaptive changes that occur in one or two generations could result from rapid directional selection or changes in the genetic structure (including epigenetics) of introduced trees (Kremer 2007).

While there is growing evidence for these transgenerational effects on adaptive traits in response to changing temperatures and photoperiod, there is little information on whether epigenetic effects play a role in physiological response of trees to elevated CO₂ levels. There is a report that grass and forb seedlings from parents grown at high CO₂ for 5 years were stimulated by high CO₂ half as much as seedlings from parents grown at ambient CO₂ for 5 years (Lau et al. 2008). This suggests that after-effects may alter physiological pathways and change the impacts of elevated CO₂ across generations. More work in this area is needed to understand the potential consequences for tree species.

In addition to epigenetic effects that can take place during embryo development, there are cultural effects from nursery treatments that can lead to large differences in adaptive traits of seedlings. These nursery effects can persist for several years and affect survival of seedlings after planting (Ying et al. 1989, Hawkins and Shewan 2000, Way et al. 2007). Increasing exposure to one type of stress can build resistance to other stresses. For example, three species of *Cedrus* seedlings preconditioned to drought were also more heat tolerant (Ladjal et al. 2000). Preconditioning may also be effective when applied to tree seed; *Pinus banksiana* seedlings from

seed treated with anti-stress agents showed reduced damage from freezing relative to controls (Borsos-Matovina and Blake 2001). The use of nursery preconditioning to increase seedling resistance to temperature and water stress may lead to higher survival and growth of seedlings planted outside their normal range.

2.2.1.8 Summary of CO₂ and Temperature Effects

Table 1 is a summary of the most common effects of increased CO₂ or temperature on physiological responses of tree species, based on the information summarized above. The direction and magnitude of responses will depend on other environmental factors and biotic interactions.

Table 1. Summary of the most common effects of increased CO₂ or temperature on physiological responses of tree species. Positive effects are shown by +, negative effects by –, and neutral effects by 0. Positive effects are highlighted in green, negative effects in orange.

Process	Increased CO ₂	Increased temperature
Photosynthesis	+	+ or –
Respiration	+ or –	–
Shoot growth	+ or 0	+ or –
Root growth	+	+ or –
Nutrient levels	–	+
Water use	+	–
Shade vs sun growth	+ or –	+ or –
Pollutant effects	– or 0	+ or –
Bud-burst	Earlier	Earlier
Seasonal shoot development	– or 0	+ or –
Bud-set	Earlier	Later
Senescence	+ or 0	+ or 0
Frost hardiness	–	–
Chilling	–	–
Aging	+	?
Reproduction	+	+ or –

2.2.1.9 Summary of Climate Change Effects on Species with Current Range in Canada

Table 2 summarizes physiological responses to climate change for tree species with their current ranges in Canada. Location indicates where the testing was carried out, not necessarily the same as the seed source location in the case of nursery or growth chamber studies. PS = photosynthesis, arrows designate increases or decreases. About 70% of the studies reported some beneficial effects of increased climate change, while 50% reported some negative effects (several studies reported both).

Table 2. Summary of physiological responses to climate change for Canadian tree species. “Factor” includes temperature (T), CO₂ (C) and moisture (M). Colours group genera together.

Species	Factor	Location	Response	Reference
<i>Abies balsamea</i>	M	Québec, greenhouse	Good resistance of cambial meristems during and after water stress, recovery of cell size and shoot growth after drought	Rossi et al. 2009
<i>Abies lasiocarpa</i>	T M	Olympic Mts., mature trees	Growth increase at high elevation and wet sites, decrease at low elevation dry sites	Ettl & Peterson 1995
<i>Chamaecyparis nootkatensis</i>	T	Alaska, mature trees	Declining forests due to reduced snowfall, severe freeze-thaw events, decline may expand	Beier et al. 2008
<i>Pseudotsuga menziesii</i>	T	Oregon, pots	Longest and coldest chilling treatment of seedlings produced greatest spring growth; chilling may be decreased due to global warming, delayed bud burst and more water stress	McCreary et al. 1990
<i>Pseudotsuga menziesii</i>	T C	Oregon, outdoor chambers	↑temp delayed cold hardening and dehardening of seedlings, reduced % bud burst and growth, ↑CO ₂ decreased cold hardening	Guak et al. 1998
<i>Pseudotsuga menziesii</i>	T C	Oregon, outdoor chambers	↑ temp led to higher shoot growth rates but reduced shoot length, delayed or ↓lammas growth, ↑ CO ₂ had no effect on phenology or growth	Olszyk et al. 1998
<i>Pseudotsuga menziesii</i>	T C	Oregon, outdoor chambers	↑ temp led to vegetative bud malformation, ↑CO ₂ had no effect on bud morphology	Apple et al. 1998
<i>Pseudotsuga menziesii</i>	T C	Oregon, outdoor chambers	↑temp ↑photosynthesis (PS) & respiration, ↑CO ₂ increased quantum yield but not photosynthesis or respiration, down-regulation of PS by CO ₂	Lewis et al. 1999
<i>Pseudotsuga menziesii</i>	T C	Oregon, outdoor chambers	↑temp ↑transpiration 37%, ↑CO ₂ decreased transpiration 12%, in both high temp and CO ₂ transpiration increased 19%, no effect on stomata, WUE may decrease	Lewis et al. 2002
<i>Pseudotsuga menziesii</i>	M	Idaho, growth chambers	Seedlings grown with ambient UV-B had 50% higher PS and 40% higher water potential after 15 days drought than seedlings grown without UV-B	Poulson et al. 2002
<i>Pseudotsuga menziesii</i>	T C	Oregon, outdoor chambers	↑CO ₂ did not affect biomass but increased specific leaf mass, ↑temp reduced allocation to leaves, both affected leaf chemistry	Olszyk et al. 2003
<i>Larix laricina</i>	T C	Minnesota, growth chambers	↑temp had no consistent effect on seedling photosynthesis, ↑CO ₂ increased PS by 20-30%, there was down-regulation and decreased leaf area	Tjoelker et al. 1998a
<i>Larix laricina</i>	T C	Minnesota, growth chambers	↑temp led to ↑response to CO ₂ , ↑CO ₂ increased relative growth rate, no ↑allocation to roots, slower effects on conifers than broadleaves	Tjoelker et al. 1998b
<i>Larix laricina</i>	T C	Minnesota, growth chambers	↑temp led to increased seedling respiration but also acclimation, ↑CO ₂ had minimal effects	Tjoelker et al. 1999
<i>Pinus banksiana</i>	C	Alberta, growth room	↑CO ₂ increased biomass	Yakimchuk & Hoddinott 1994
<i>Pinus banksiana</i>	C	Alberta, growth room	↑CO ₂ did not increase survival or growth after cold storage	Hoddinott & Scott 1996
<i>Pinus banksiana</i>	T C	Minnesota, growth chambers	↑temp had no consistent effect on seedling photosynthesis, ↑CO ₂ increased PS by ~20%, there was down-regulation and decreased leaf area	Tjoelker et al. 1998a
<i>Pinus banksiana</i>	T C	Minnesota, growth chambers	↑temp led to ↑response to CO ₂ , ↑CO ₂ increased relative growth rate, no ↑allocation to roots, slower effects on conifers than broadleaves	Tjoelker et al. 1998b
<i>Pinus banksiana</i>	T C	Minnesota, growth chambers	↑temp led to increased seedling respiration but also acclimation, ↑CO ₂ had minimal effects	Tjoelker et al. 1999
<i>Pinus banksiana</i>	T C	Thunder Bay, greenhouse	↓soil temp ↓PS, stomatal conductance and transpiration, ↑CO ₂ increased PS, WUE, foliar N, down-regulation of PS	Zhang & Dang 2005
<i>Pinus banksiana</i>	T C	Thunder Bay, greenhouse	↓soil temp had little effect on growth, biomass, ↑CO ₂ increased biomass, not as much as spruce or birch	Zhang & Dang 2007
<i>Pinus banksiana</i>	T	London ON, growth chambers	photoperiod control of dormancy negated the potential for increased carbon gain from higher temperatures during the autumn season.	Busch et al. 2007
<i>Pinus banksiana</i>	T	Eastern Canada, mature trees	↑temp will cause N shift of optimal habitat, N sources are growing at suboptimal temps, central near optimal will ↓in future, S may be lost	Thomson & Parker 2008
<i>Pinus contorta</i>	C M	Alberta, growth room	↑CO ₂ ↑seedling height, biomass, and leaf area, increased PS, no effect on stomatal resistance, no effect on drought response	Higginbotham et al. 1985

Species	Factor	Location	Response	Reference
<i>Pinus contorta</i>	T	British Columbia, provenance tests	Mean annual temp & mean temp of coldest month best to predict height, ratio of summer temp/summer precip best to predict survival, small changes in climate will have big impacts on growth & survival	Rehfeldt et al. 1999
<i>Pinus contorta</i>	T	British Columbia, provenance tests, modelling	Small temperature fluctuations lead to complex plastic responses, short-term impacts negative in south and positive in north, evolutionary adjustments led to ↑productivity, long-term adjustments could take 1-3 generations in N, 6-12 in S	Rehfeldt et al. 2001
<i>Pinus contorta</i>	T	Sweden, nursery	↑temp in midwinter led to decreased needle sugar and increased freezing damage	Ögren 2001
<i>Pinus contorta</i>	T M	Alberta, mature trees	Growth sensitive to heat and moisture stress in late summer of the previous year, winter cold, and timing of start of growing season, future warming will decrease productivity in Foothills	Chhin et al. 2008
<i>Pinus ponderosa</i>	T	North Carolina, greenhouse	↑temp changed root allocation, ↑CO ₂ increased root biomass	King et al. 1996
<i>Pinus ponderosa</i>	T C	Oregon, modelling	↑CO ₂ and temp increased biomass, ↑CO ₂ increased photosynthesis & reduced stomatal conductance	Constable et al. 1996
<i>Pinus ponderosa</i>	C	North Carolina, greenhouse	↑CO ₂ did not increase N acquisition, but increased NO ₃ absorption and decreased NH ₄ , decreased root respiration rate	BassiriRad et al. 1997
<i>Pinus ponderosa</i>	C	North Carolina, greenhouse	↑CO ₂ increased root surface area due to increased length, root carbohydrates not affected	King et al. 1997
<i>Pinus ponderosa</i>	C	California, open-top chambers	↑CO ₂ increased biomass yield per unit of N in the first 2 y but not year 3, also increased growth dilution	Johnson et al. 1997
<i>Pinus ponderosa</i>	C	California, open-top chambers	↑CO ₂ increased # of mycorrhizal root tips formed but did not increase their lifetime	Rygielwicz et al. 1997
<i>Pinus ponderosa</i>	C M	California, open-top chambers	↑CO ₂ increased seedling diameter, shoot and root volume, and shoot and coarse root weight, mostly in high N, ↑CO ₂ increased drought stress	Walker et al. 1998
<i>Pinus ponderosa</i>	C	California, open-top chambers	↑CO ₂ increased PS by 53%, despite decreased PS capacity, decreased chlorophyll & N, no change in leaf mass per area	Tissue et al. 1999
<i>Pinus ponderosa</i>	C M	Oregon, California, mature trees	↑growth since 1950, especially on dry sites, likely due to ↑CO ₂	Soulé & Knapp 2006
<i>Picea glauca</i>	C	Alberta, growth rooms	↑CO ₂ increased biomass at high N, root biomass at low N	Brown & Higginbotham 1986
<i>Picea glauca</i>	C	Alberta, growth room	↑CO ₂ increased biomass	Yakimchuk & Hoddinott 1994
<i>Picea glauca</i>	C	Alberta, growth room	↑CO ₂ increased survival after cold storage	Hoddinott & Scott 1996
<i>Picea glauca</i>	T	Canada, mature trees, modelling	↑temp of 5°C leads to predicted earlier bud burst of 2 to 4 wks, usually decreased risk of frost after bud burst	Colombo 1998
<i>Picea glauca</i>	T M	Alaska, mature trees	Radial growth has decreased with increasing temperature because of increased drought stress, especially for the fastest growing trees	Barber et al. 2000
<i>Picea glauca</i>	T	Alberta, growth chambers	Seedlings had no change in shoot or root biomass when soil temp increased from 15 to 25°C, only a slight increase from 5 to 15C	Landhäusser et al. 2001
<i>Picea glauca</i>	T	Québec, growth chambers	Families with superior height growth more sensitive to heat stress than intermediate or inferior families, may not grow as well in future	Bigras 2000
<i>Picea glauca</i>	T M	Québec, provenance test	Populations were optimally adapted to local environment for temperature but not moisture, if temp ↑growth will be reduced if moisture increases	Andalo et al. 2005
<i>Picea glauca</i>	M	Québec, growth chambers	Families with superior height growth were more sensitive to drought than intermediate or inferior families, may not grow as well in future	Bigras 2005
<i>Picea glauca</i>	T	Yukon, open-top chambers	↑temp ↑seedling height and PS, seedlings on S aspect grew longer branches and wider annual rings than on N aspect, but had ↓Photosystem-II efficiency and higher winter needle mortality	Danby & Hik 2007
<i>Picea glauca</i>	T C	Thunder Bay, greenhouse	↓soil temp ↓ growth, biomass, high temp had smaller negative effects, ↑CO ₂ increased biomass at all temps	Zhang & Dang 2007
<i>Picea glauca</i>	C	Ontario, greenhouse	↑CO ₂ increased biomass, relatively more under low light, ↑root mass and root:shoot under high light but ↓ under low light	Marfo & Dang 2009
<i>Picea mariana</i>	C	Québec, greenhouse	↑CO ₂ increased biomass of seedlings in March, April, and May, but not in August	Campagna & Margolis 1989
<i>Picea mariana</i>	C	Québec, greenhouse	↑CO ₂ increased frost damage of seedlings and negatively affected bud initiation and development	Margolis & Vézina 1990
<i>Picea mariana</i>	C M	Ontario, growth rooms	↑CO ₂ ↑seedling dry wt by 20-48%, greater increase under drought, effect of CO ₂ decreased with seedling size, down-regulation of PS	Johnsen 1993
<i>Picea mariana</i>	C	Alberta, growth room	↑CO ₂ increased biomass	Yakimchuk & Hoddinott 1994

Species	Factor	Location	Response	Reference
<i>Picea mariana</i>	C	Québec, growth chambers	↑CO ₂ increased seedling survival and growth, especially with added N, no family differences in relative response	Wang et al. 1994
<i>Picea mariana</i>	C	Alberta, growth room	↑CO ₂ did not increase survival or growth after cold storage	Hoddinott & Scott 1996
<i>Picea mariana</i>	C	Ontario, growth rooms	↑CO ₂ increased biomass of seedlings but had no effect on provenance differences in any measured trait	Johnsen & Seiler 1996
<i>Picea mariana</i>	T C	Minnesota, growth chambers	↑temp had no consistent effect on seedling PS, ↑CO ₂ increased PS by 20-30%, there was down-regulation and decreased leaf area	Tjoelker et al. 1998a
<i>Picea mariana</i>	T C	Minnesota, growth chambers	↑temp led to ↑response to CO ₂ , ↑CO ₂ ↑relative growth rate, no ↑allocation to roots, slower effects on conifers than broadleaves	Tjoelker et al. 1998b
<i>Picea mariana</i>	T C	Minnesota, growth chambers	↑temp led to increased seedling respiration but also acclimation, ↑CO ₂ had minimal effects	Tjoelker et al 1999
<i>Picea mariana</i>	C	New Brunswick, greenhouse	↑CO ₂ increased seedling height and diameter, growth performance ranking not affected by ↑CO ₂	Johnsen & Major 1998
<i>Picea mariana</i>	C	Québec, greenhouse	↑CO ₂ led to earlier bud set and cold tolerance, down-regulation of PS, ↑biomass during growing season but less difference by spring	Bigras & Bertrand 2006
<i>Picea mariana</i>	T C	Thunder Bay, greenhouse	↓soil temp ↓ growth, biomass, high temp had smaller negative effects, ↑CO ₂ increased biomass at all temps	Zhang & Dang 2007
<i>Picea mariana</i>	C	Ontario, greenhouse, field	↑CO ₂ increased seedling height but only in seedlings that had been exponentially nutrient loaded, maintained in field for 6 years	Way et al. 2007
<i>Picea mariana</i>	T	Ontario, greenhouse	↑temp ↓seedling height and biomass, root:shoot ratio, PS, also increased thermo-tolerance and mortality	Way & Sage 2008
<i>Picea mariana</i>	C	Ontario, greenhouse	↑CO ₂ increased biomass, relatively more under low light, ↑root mass and root:shoot under high light but ↓ under low light, more sensitive than <i>glauca</i>	Marfo & Dang 2009
<i>Picea mariana</i>	T	Ontario, provenance tests	↑temp will increase height growth of northern sources, central sources will decrease, southern sources should be moved north to avoid extirpation	Thomson et al. 2009
<i>Picea sitchensis</i>	T	Scotland, mature trees	↑temp (2°C) could delay or advance budburst depending on chilling, Sitka spruce would burst buds 5 days earlier in Scotland	Cannell & Smith 1986
<i>Picea sitchensis</i>	C M	UK, growth chambers	↑CO ₂ increased relative growth rate, PS, WUE, and water potential after drought relative to controls	Townend 1993
<i>Picea sitchensis</i>	C M	UK, growth chambers	↑CO ₂ ↑growth in well-watered + fertilizer, droughted + or – fertilizer, but not well-watered – fertilizer, RGR lower in last part of growing season at ↑CO ₂	Townend 1995
<i>Picea sitchensis</i>	C	Scotland, open-top chambers	↑CO ₂ increased root:shoot ratio, relative growth rate, summer extension rate, decreased foliar nutrient concentrations and growth rate in autumn	Murray et al. 1996
<i>Picea sitchensis</i>	C	Scotland, open-top chambers	↑CO ₂ increased instantaneous PS by 62%, there was down-regulation, higher growth stimulation in southern clones	Centritto & Jarvis 1999
<i>Picea sitchensis</i>	C	Scotland, open-top chambers	↑CO ₂ decreased duration of shoot extension, suppressed lammas growth, but increased dry mass, accelerated seedling development	Centritto et al. 1999
<i>Picea sitchensis</i>	C	UK, open-top chambers	↑CO ₂ increased PS and biomass more in high-N than low-N seedlings, increased chlorophyll, no effect on stomatal conductance	Murray et al. 2000
<i>Picea sitchensis</i>	T	Denmark, outdoor nursery	Did not recover frost hardiness after 10 days of warm treatment in early spring	Nielsen & Rasmussen 2009
<i>Betula papyrifera</i>	T	New Hampshire, greenhouse, field	↓temp led to higher root:shoot ratio, at mountain site all seedlings grew at similar rate, warming could reduce growth in mountain populations	Ruel & Ayres 1996
<i>Betula papyrifera</i>	C	Michigan, open-top chambers	Shade-intolerant birch responded to ↑CO ₂ in full sun, not in shade, could alter competitive balance in shade	Kubiske & Pregitzer 1996
<i>Betula papyrifera</i>	T C	Minnesota, growth chambers	↑temp had no consistent effect on seedling photosynthesis, ↑CO ₂ increased PS by 20-30%, there was down-regulation and decreased leaf area	Tjoelker et al 1998a
<i>Betula papyrifera</i>	T C	Minnesota, growth chambers	↑temp led to ↑response to CO ₂ , ↑CO ₂ increased relative growth rate, no ↑allocation to roots, optimal growth at 24/18°C, response to CO ₂ ↓over time	Tjoelker et al 1998b
<i>Betula papyrifera</i>	C M	Massachusetts, greenhouse	↑CO ₂ increased growth most in least watered seedlings, growth may be enhanced on xeric sites in the future	Catovsky & Bazzaz 1999
<i>Betula papyrifera</i>	C	Wisconsin, FACE	↑CO ₂ increased respiration rates in several species, reports of decreased respiration are due to artifacts	Davey et al. 2004
<i>Betula papyrifera</i>	C	Wisconsin, FACE	↑CO ₂ increased the negative effect of O ₃ pollution	Karnosky et al. 2005

Species	Factor	Location	Response	Reference
<i>Betula papyrifera</i>	T	Thunder Bay, greenhouse	↓soil temp ↓stomatal conductance and transpiration and Fv/Fm, ↑CO ₂ increased PS, WUE, foliar N, down-regulation of PS	Zhang & Dang 2005
<i>Betula papyrifera</i>	T C	Thunder Bay, greenhouse	↓soil temp strongly decreased growth, biomass, ↑CO ₂ increased biomass, compensated for low soil temp	Zhang & Dang 2007
<i>Betula papyrifera</i>	C	Thunder Bay, greenhouse	↑CO ₂ increased all growth and biomass parameters, more at high N than Low N	Cao et al. 2008
<i>Populus tremuloides</i>	C	Alberta, growth rooms	↑CO ₂ increased biomass and height in all three N regimes, but only temporarily, possibly due to other nutrient limitations	Brown & Higginbotham 1986
<i>Populus tremuloides</i>	T C	Minnesota, growth chambers	↑temp had no consistent effect on seedling photosynthesis, ↑CO ₂ increased PS by 20-30%, there was down-regulation and decreased leaf area	Tjoelker et al. 1998a
<i>Populus tremuloides</i>	T C	Minnesota, growth chambers	↑temp led to ↑response to CO ₂ , ↑CO ₂ increased relative growth rate, no ↑allocation to roots, optimal growth at 24/18°C, response to CO ₂ ↓over time	Tjoelker et al. 1998b
<i>Populus tremuloides</i>	C	Michigan, pots	↑CO ₂ increased PS and fine root production and mortality in high N but not low N soil, ↑N increased leaf area,	Kubiske et al. 1998
<i>Populus tremuloides</i>	T	Michigan, open-top chambers	↑soil temp ↑PS and biomass but usually in high-N soil, aspen has potential for greater growth in warmer soil	King et al. 1999
<i>Populus tremuloides</i>	C	Michigan, open-top chambers	↑CO ₂ had no effect on ammonium or nitrate uptake, but high soil N decreased N uptake capacity	Rothstein et al. 2000
<i>Populus tremuloides</i>	C	Michigan, open-top chambers	Significant CO ₂ × genotype interaction in PS, stomatal conductance and PS of different genotypes responded differentially to recovery from drought stress	Wang et al. 2000
<i>Populus tremuloides</i>	T	Alberta, growth chambers	At 5°C seedlings had no root growth and limited growth in leaf area and shoot mass compared with the large increases in leaf and shoot mass at 25°C.	Landhäusser et al. 2001
<i>Populus tremuloides</i>	C	Michigan, open-top chambers	↑CO ₂ and O ₃ decreased chlorophyll and carotenoid concentrations in all clones, the CO ₂ +O ₃ treatment had a slight reduction in O ₃ injury but ↑chloroplast damage	Wustman et al 2001
<i>Populus tremuloides</i>	C	Wisconsin, FACE	↑CO ₂ increased respiration rates in several species, reports of decreased respiration are due to artifacts	Davey et al. 2004
<i>Populus tremuloides</i>	C	Wisconsin, FACE	↑CO ₂ increased the negative effect of O ₃ pollution	Karnosky et al. 2005
<i>Populus tremuloides</i>	C	Wisconsin, FACE	↑CO ₂ ↑tree height, diameter, stem volume; ↑O ₃ decreased growth; ↑CO ₂ +O ₃ had no effect on growth; years with higher light levels during July gave more + growth with ↑CO ₂ and more – growth with O ₃ . Mean daily temp in October affected growth similarly next yr.	Kubiske et al. 2006

2.2.2 Response to Maladaptation: Migration

Trees are long-lived sessile organisms that lack the ability to physically move in response to a change in their environment. One potential response to maladaptation is migration through dispersal of genetic material (seeds or pollen) in order to establish new individuals in a more suitable environment (Savolainen et al. 2007). Research on species movements following the last deglaciation provide representative data on the ability of species to migrate. Aitken et al. (2008) report that maximum post-glacial forest migration rates were of the order of 100 m yr⁻¹ (10 km per century), while others suggest much higher rates of dispersal, up to several km per year. McLachlan et al. (2005) have challenged such estimates of rapid migration. They used DNA studies which indicate that it is more likely that remnant populations of some species (e.g. American beech and red maple) persisted during the late glaciation at sites much closer to their modern range limits than previously assumed, and hence provided much closer seed sources for recolonization when conditions improved. McLachlan et al. (2005) therefore concluded that the rapid migration rates reported in older pollen-based studies are generally overestimated. McLachlan et al. (2005) are in agreement with Aitken et al. (2008) in suggesting a theoretical maximum migration rate of up to 100 m yr⁻¹, with most species considerably less than this.

In addition to relatively slow natural dispersal rates, species would have to contend with an inhospitable landscape when attempting to migrate. Barriers to movement across the landscape exist in the form of changes in land cover (e.g. clearing for agriculture), the built environment, and lack of suitable soil conditions to the north of current species distributions, especially for boreal trees (Higgins et al. 2003, McKenney et al. 2009). Changes in natural disturbance regimes and genetic factors will also affect the ability of species to successfully migrate in response to climate change (Barnes 2009). Finally, as species migrate and redistribute themselves, novel combinations of tree species and associated communities of pests and diseases are likely to emerge that may make survival in new locations difficult (Aitken et al. 2008).

How quickly will climate change move across the landscape? Loarie et al. (2009) developed an index representing the horizontal speed of climate change (“climate velocity”) for 14 global biomes. They used the average of 16 GCMs statistically downscaled to 0.5 X 0.5 degrees and forced by the A1B, A2 and B1 SRES emissions scenarios. Table 3 shows representative results for the three forested biomes that occur in Canada. Assuming a maximum tree species migration rate of *ca.* 0.1 km yr⁻¹ (McLachlan et al. 2005, Aitken et al. 2008), temperate broadleaf and boreal species will be unable to migrate fast enough to match the climate velocity given by Loarie et al. (2009). Temperate coniferous species may have the potential to migrate quickly enough but will be affected by the constraints discussed above.

Table 3. Climate velocity and residence time for three forested biomes in Canada. Data from Loarie et al. (2009).

Forest Biome	Mean temperature velocity ¹ (km yr ⁻¹)	Residence time for protected areas (yr)
Temperate broadleaf & mixed	0.35	1.7
Temperate coniferous	0.11	12.7
Boreal	0.43	1.1

¹ Based on the intermediate SRES scenario A1B

Loarie et al. (2009) also note that topography had a very large effect on the outcome of their analysis. They found a strong correlation between topographic slope and velocity from temperature change (correlation coefficient = -0.92). Temperature gradients are steep in landscapes with high relief, so that a large temperature change can occur over a short distance. Hence, species in mountainous terrain may need to migrate relatively short distances in order to keep up with the pace of a changing climate, assuming there is enough “reserve elevation” to accommodate future change. Species on flatter landscapes may need to migrate much greater distances to find a suitable future climate.

Loarie et al. (2009) also recognized the effects of land use change on migration noted above, and suggested that protected areas are important to allow species to migrate to more suitable climates. Table 3 shows the “residence time” for changing temperatures as a function of the average size of protected areas in each biome, expressed as the ratio of protected area diameter (km) to climate velocity (km yr⁻¹). The resulting values can be interpreted as the time required

for the current climate to cross a protected area. Protected areas in temperate conifer forests will experience a somewhat more stable climate (12.7 year residence time) as compared to those in broadleaf and boreal biomes (1.1 - 1.7 years). This is due to a combination of higher climate velocities and generally smaller protected areas in the latter biomes.

Loarie et al. (2009) include three points of clarification. First, they recognize that climate is a complex mixture of temperature, precipitation and other factors. They used temperature as an indicator of climate change, but note that a similar analysis using precipitation yielded almost identical results. Second, an analysis done at finer spatial and temporal scales would provide more detail for a smaller region, but their analysis was carried out at the global scale and precluded a more detailed approach. Finally, this analysis did not include data on migration rates for individual species, which will vary widely among locations.

Given the problems with natural migration outlined above, human-assisted movement of populations or species (i.e. assisted migration) may be an option to be considered by forest managers. We address assisted migration as a management option in Section 3. In the following section we summarize the current state-of-the-art in modeling species and ecosystem range shifts for various species and regions of Canada.

2.2.2.1 Modelling Species and Ecosystem Range Shifts

Contributed by Dr. David Price, Northern Forestry Centre, Canadian Forest Service, Edmonton, AB

2.2.2.1.1 Introduction

Potentially, computer models of the effects of climatic factors on individual tree species, or on forest communities composed of two or more tree species, are powerful tools to investigate effects of future climate change on Canada's forests. Within this premise, however, lie a number of important caveats. First, there are many kinds of tree and forest models available but not all are "climate-sensitive". Climate-sensitive means that the model accepts climatic data (real or simulated) which affect the simulated output to some extent. Secondly, among those models that can be described as climate-sensitive, there are several classes, each designed for different purposes, and none of which can provide "all the answers". Many of these models are "research-oriented", while many others have management applications. Thirdly, the use of ecological models and the interpretation of their outputs is an inexact science. Models are only simplifications of reality and the interacting factors which contribute to overall ecosystem responses to climate and climate change are particularly numerous and complex. Hence, the results obtained from any ecological model should always be treated with scepticism. In practice, modellers try to validate their models by comparing simulation results to real measurements and observations wherever possible and also with other models to determine how and why results may differ.

The US Forest Service organized a workshop in Oregon in January 2008 to discuss the value of climate-sensitive vegetation models to managers needing to make forest management decisions in a changing climate (Robinson et al. 2008). A group of experts identified five distinct classes of

model, of which two have high value in projecting changes in tree species distribution. The first of these two classes is known as “climate envelope” or “statistical species distribution” models. As their second name suggests they are based on statistical relationships which relate the observed natural distribution of a given species to the climatic boundaries (or envelope) of that distribution. The second class is forest “gap” or “patch” models which simulate the ecological processes that determine mortality (leaving gaps in the forest canopy), followed by regeneration, growth and competition of forest species on small (e.g., 0.1 ha) plots (or patches) within the forest.

Three other classes of climate-sensitive vegetation model may have some value to questions about effects of a changing climate on species distribution, but will only be discussed briefly. The first of these are “equilibrium projection models” (e.g., Rizzo and Wiken 1992, Prentice et al. 1992), which are climate envelope models applied to entire vegetation zones (biomes at the global scale) to determine how they might shift in response to a stabilized altered climate. They are not favoured today for several reasons, mainly because the “equilibrium” condition they forecast could take centuries to achieve in reality. They have largely been superseded by dynamic vegetation models (DVM), which are being developed to project transitional changes in distributions of entire ecosystems at large scales over periods of decades to a century. Neither equilibrium projection models nor DVMs explicitly track individual species; instead they represent large-scale vegetation as combinations of inclusive “plant functional types” (PFT) which generally lack species-specific characteristics. Examples of PFTs are evergreen-needleleaf, deciduous broadleaf, etc. Studies using DVMs applied to Canada alone are rare: Lenihan and Neilson (1995) reported one study with the MC1 model (Bachelet et al. 2001) and more recently Price and Scott (2006) coordinated a three-way comparison of MC1 with the SDGVM model of Woodward et al. (1995, 1998) and the IBIS model of Foley et al. (1996) which showed disturbing differences among the models. Price and Scott concluded that DVMs were not yet mature enough for national-scale studies and further effort is ongoing to address the issues raised by their study. The third large group of climate-sensitive models is known generically as “landscape models”. These are very high resolution models often designed to support operational decision-making, and many of them track growth and competition among individual species, often employing forest gap model algorithms. They are computationally intensive, however, and do not appear to provide significant advantages over gap models when projecting potential responses of forest distribution and species composition to climatic change.

2.2.2.1.2 Climate Envelope Models (CEM)

Climate envelope models (also known as Bioclimatic Envelope Models) attempt to correlate the spatial distribution of forest types or species with climatic zones, possibly keyed on specific characteristics of each species (or plant functional type) and using particular combinations of climate variables as the driving factors. Thomas et al. (2004) define climate envelope this way:

“The statistical match between climate variables and the boundaries of a species’ distribution (climate envelope) represents conditions in which a species (normally) shows a positive demographic balance (rarely the absolute physical limits of a species, but the set of conditions under which it survives in at least some multi-species communities). The statistical approach is generic, but specific methods vary between studies” (Thomas et al. 2004, p. 147).

Because climate is spatially variable and generally dependent on latitude, elevation and the degree of continentality, it is attractive to compare the distributions of ecosystems and species with climatic zones that can be defined on the basis of annual or seasonal temperature and precipitation, and potentially of other climate variables or indices (the latter often derived from temperature and precipitation data, such as growing degree day sums and various aridity indices). If good relationships can be established between the observed geographic distribution of a tree species or forest community and the local climate characterized by a combination of variables and/or indices, then in principle it should be possible to project future *potential* distributions of the same climate zone, and hence future potential distributions of the species or communities which are correlated with it. The source of the climate projection could be a simple universal change superimposed on the present-day climate, or it may be generated by a climate model such as a general circulation model (GCM) forced by one or more scenarios of greenhouse gas emissions.

Successful predictions of the distributions of invasive species after arrival in new continents (notably noxious weeds and insect pests, both of which are typically highly mobile and adaptable) have demonstrated the validity of the concept of CEMs. Further validation comes from inferring changes in the distributions of indigenous tree species from fossil records (particularly pollen data) in response to known past changes in climate, such as those following recent deglaciations (Thomas et al. 2004).

As a means of determining the theoretical limits of tree species distributions under projected changes in climate, CEMs are a relatively simple and robust approach. As noted by Robinson et al. (2008), the key strengths of CEMs are that they are easy to implement (since very few parameters are needed) and the output is easy to understand. The output is typically a collection of range maps for individual species that can be interpreted at relatively small scales (1-10 km) and which tell the user where species are likely to be vulnerable to projected changes in climate. When applied to forest tree species, however, the major weakness in this approach is that it provides an *equilibrium* assessment of future distribution—meaning that the future climate is assumed to be stabilized and that the species distribution has fully adjusted to that new climate (the concept of equilibrium in ecosystems is itself contentious). The future projected distributions must assuredly not be interpreted as occurring in synchrony with the changing climate. In reality, it is difficult to conceive of a stabilized altered climate occurring in the foreseeable future, and it might take several centuries for forests to become fully “equilibrated” even if new climate zones were to stabilize within a few decades. Moreover, the projected distributions take no account of other constraints such as soil conditions, tree regeneration rates (particularly seed dispersal distance), landscape fragmentation, or genetic factors (e.g., adaptations to local day length), all of which could affect successful colonization by a new species (or sub-species).

Robinson et al. (2008) and Pearson and Dawson (2003) identify additional criticisms of climate envelope models including: (1) no representation of ecological processes and hence of the biotic interactions which affect species survival or loss; (2) lack of recognition that present-day tree species distributions are often determined by climate in the recent past (hence giving incorrect data for projecting the future); (3) no sensitivity to increasing atmospheric CO₂ concentration;

and (4) no accounting for future changes in natural disturbance regimes which may play a major role in determining “winners” and “losers”.

Davis et al. (1998) reported experiments which demonstrated how climate envelope models might produce incorrect results. They identified two major factors determining present-day species distributions which are not captured by CEMs: (1) distributions are often determined by *interactions with other species* which may be altered by climate change; and (2) distributions may be the result of *seed sources and sinks*. The latter concern is that some species may survive and grow productively in certain areas (sinks) only because seeds are continually arriving from outside (sources). Hence the sinks would disappear if the outside source areas were no longer able to support the species of interest.

The lack of representation of seed dispersal in CEMs led Iverson and coworkers (e.g., Iverson et al. 2002, 2005) to develop a combined modelling approach to address this problem. The DISTRIB model is a well-tested CEM which projects potential changes in forest distribution (Iverson et al. 2002). Its projections are then explored with the SHIFT model which uses dispersal probability functions to estimate how fast seeds can disperse from regions where a species exists to regions where it could exist in the future. These functions account for “seed dispersal ability”, the local abundance of parent trees, the time it takes to produce seeds once parents have occupied a new location, and for barriers in the landscape (as they occur at present). Iverson et al. (2004) used SHIFT to explore the probabilities of successful colonization of new areas for five tree species (four hardwoods and loblolly pine, *Pinus taeda*) along transects across the eastern USA. Their results were of general significance because they showed that migration distances were generally limited for all five species within a 100-year period. Although the model allowed for rare long distance (500 km) colonization events, these appeared insufficient to allow long distance migration. The authors concluded that when parent trees are abundant at the species distribution boundary, there is a relatively high probability of colonization only within a distance of 10-20 km (assuming suitable sites are available), but it decreases dramatically at distances beyond 20 km.

More recent studies by Iverson et al. (2008a, 2008b) have addressed the sensitivity of individual tree species to IPCC Fourth Assessment Report (AR4) climate projections. While not directly relevant to the Canadian situation, some of their general findings are potentially significant. Of 134 species in the eastern USA, they found that 66 would gain at least 10% in area of suitable habitat and 54 would lose at least 10%. With increasing severity of the projected warming trend, the areas lost and gained would also increase, accompanied by shifts of up to 800 km (northeast direction). In general, they found spruce-fir forests would be replaced by southern oaks and pines.

Chiang et al. (2008) investigated potential changes in the distribution of tree species using DISTRIB coupled to the effects of these changes on NPP simulated using the PnET-II model (e.g., Aber et al. 1995) for four study regions in the eastern USA (Maine, Wisconsin, Arkansas and Ohio-West Virginia) which were identified as “focal areas of potential species range shifts”. The NPP simulations were carried out assuming that the future forest distributions were stabilized and there were no limits on species migration. Chiang et al. found the projected changes in species distribution had minor effects on simulated total NPP, whereas the projected

changes in climate had very variable effects (with increases of up to 25% or decreases as large as 60%).

At the scale of individual species, Iverson and coworkers (e.g., Iverson et al. 2008a; Prasad et al. 2006) working in the eastern USA have been the inspiration for much of the Canadian work. Notably, Iverson et al. (2008a) and Prasad et al. (2006) compared different methods of classifying and correlating species distributions to climatic data, and applied these to predicting vegetation distribution under future climate scenarios derived from the Canadian global climate model. They found that two methods, Random Forests (RF) and Bagging Trees (BT) produced superior estimates of present-day species importance value (a measure of basal area coupled to abundance) with RF appearing to give more reasonable results in mapping changes in distribution in the climate change scenarios. Rehfeldt et al. (2006) also concluded that RF produced a better result in predicting present-day species distributions, leading Aitken and coworkers at UBC recently to propose a further study of potential changes in distribution of ecosystems and tree species in B.C. employing statistical approaches based on RF.

Hamann and Wang (2006) reported a new, simpler approach using canonical discriminant analysis (CDA) to define the climate envelopes for ecosystems in B.C., and to model portions of these climate spaces for tree species under current and projected future climates. They found this approach was able to predict existing species ranges at high spatial resolution even beyond the region used to test and calibrate the model. This prediction capacity included the correct locations of outlier populations and southern range limits for many species. This method was adopted by Schneider et al. (2009) to project changes in species distributions in Alberta under different GCM scenarios.

2.2.2.1.3 Forest Gap Models

Forest gap models are more mechanistic in their representation of climate sensitivity than CEMs, but the level of process built into different gap models can vary considerably. Rather than simply correlating the spatial distribution to climatic zones, these models attempt to predict survival, growth and mortality in response to climatic variations, accounting for regeneration rates, competition with other species for resources (light, water, nutrients) and the effects of other environmental drivers, including soil characteristics and disturbance events. They are also *dynamic* simulators, meaning they are capable of simulating transitional changes in forest structure, rather than just “at equilibrium”. In principle, therefore, they can simulate successional stages, and responses to climatic change, over realistic periods of years to centuries. The principles of all gap models follow Botkin et al. (1972) and Shugart (1984) who first developed this approach to simulate the gap-phase dynamics driving succession in eastern US hardwood forests. However, since the original concept, many researchers have developed gap models with more detail, often to address particular problems characteristic of other forest types.

The basic unit of a gap model is a small plot or patch representing a forest site (possibly characterized by other factors, such as soil type) on which a population of individual trees is considered to compete for light, water and nutrients, with monthly or daily climate data driving productivity, respiration and evapotranspiration. Regeneration success, individual tree mortality and exogenous disturbances are treated as random events, so the outcomes of multiple patch

simulations applied to the same ecosystem with the same forcing climate data may vary significantly. Hence in a typical model run, many plots are simulated (often 100 or more) and the averages are used for diagnostic output. Each species considered to be present is parameterized according to measurements or observations of key characteristics such as rates of early height and diameter growth, shade-tolerance, drought-tolerance, deciduous or evergreen habit, nutrient demands and regeneration strategy (i.e., wind or animal borne seed, or vegetative regeneration).

Gap models as a group represent the most comprehensive approach to integrating tree ecophysiology with species-level vegetation dynamics, but there is a wide range of detail in these models, including, for example, how sensitivity to CO₂ concentration is represented. This range of complexity also brings a certain level of flexibility in application (i.e., one can choose a gap model that can be matched to available data!). Most gap models recognize the climatic bounds on presence or absence of individual species in much the same way as CEMs. Superimposed on this is a representation of plant physiological responses to climate and soil conditions, which ultimately determine survival and successful competition with other species. In early gap models, the physiological responses were represented rather empirically, but newer ones are often more detailed. Bugmann (2001) writes: “In spite of all the criticisms..., there is no alternative approach available that would allow one to consider the effects of weather, intraspecific and interspecific competition on tree population dynamics as elegantly, intuitively and comprehensively as forest gap models do.” However, gap models have their own problems and it is difficult to prove they are more reliable than CEMs, at least when used to predict future species distributions. Bugmann (2001) comments that the value of ecological models in general is not that they are able to predict the future, but that they can help us understand ecosystem responses under mathematically prescribed conditions. He argues that the results from modelling studies must be interpreted recognizing the limits of the model (i.e., the knowledge and assumptions of the modeller), particularly when dealing with complex models of complex systems. In this regard, CEMs being demonstrably simpler models, may be better suited to making simple predictions of future forest distribution, but the caveats about CEMs presented earlier must be heeded.

Particular strengths of gap models noted by Robinson et al. (2008) include the following: They can be used at the scale of individual sites and are therefore relatively easy to validate against field measurements. They capture physiological processes that are climate-sensitive, and once properly calibrated, have been shown to provide quite realistic simulations of dynamic ecosystem behaviours in response to climate variations. At the individual tree level, results can be compared to traditional stand growth models and applied to management issues. They are also considered a good class of models for looking at disturbance impacts.

It should be noted, however, that gap models are not really designed for mapping changes in spatial distributions but instead are applied at “point” locations such as climate stations. With thousands of spatially explicit patches spread out over a landscape, it becomes possible to run multiple gap model simulations to investigate changes in composition over time and space, but it appears this has never been attempted within Canada. Researchers interested in the wider scale impacts of climate change have adopted DVMs in place of gap models, to take advantage of the computational efficiency provided by substituting plant functional types for individual species.

Further caveats concerning gap models include: (1) they require proper parameterization and careful calibration to provide plausible results; (2) they may be limited by the availability of ecophysiological data; (3) as with CEMs, most gap models do not account for regeneration constraints on species migration, and instead assume that seeds of all species found in the region are present in every patch (see Price et al. 2001 for a review of this problem and newer models that address it). This last constraint is particularly relevant because there appear to be no published results for a gap model with regeneration controls applied to Canada, though Price et al. (1999a) investigated the importance of mass seed germination from serotinous species (e.g., jack pine) following fire.

Much concern and effort has also been devoted to trying to model the importance of CO₂ fertilization as a mitigating factor for climate change impacts on natural vegetation. It seems clear that increasing CO₂ concentration will increase primary productivity if all other factors are unchanged. However the magnitudes of the response to elevated CO₂, for individual species are still being resolved. For example, Norby et al. (2005) reported a meta-analysis of CO₂ enrichment experiments in North America and the USA which indicated a fairly strong response in several diverse tree species, but a more recent analysis (presented at the American Geophysical Union conference in December 2008) has led Norby to revise that assessment downwards. At the same time, the representation of CO₂ effects in most vegetation models is simplistic at best, so any large-scale projected responses to increasing CO₂ are dubious. Climate envelope models generally ignore CO₂ effects; gap models may use “physiologically-correct” representations of CO₂ responses but detailed data are presently lacking for most forest tree species.

Several researchers have applied “second generation” gap models to Canadian forest ecosystems, mainly boreal. Among these is the model developed initially by Bonan for Alaska and subsequently tested in Québec, New Brunswick and Newfoundland (Bonan 1990, 1992) and applied to central Canada by Nalder (2002). In the Prairie Provinces, Price and coworkers (e.g., Price and Apps 1996, Price et al. 1999a) and Bugmann et al. (2001) used a variant of the FORSKA2 model first developed by Prentice et al. (1993) to investigate changes in productivity and species composition (as determined from simulated biomass) along a transect of 11 climate stations extending from southern Alberta to northern Manitoba. Price et al. 2005 used another variant of FORSKA2 to investigate potential changes in growth rates of key forest types in the central Foothills of Alberta. Nalder and Merriam (1995) developed a model called BOPAS applied to Pukaskwa National Park in central Ontario, and Nalder (2002) compared FORSKA and BORFOR in NWT, northern Alberta, Saskatchewan and Manitoba, primarily to simulate carbon flows in different boreal forest ecosystems. Bugmann et al. (2001) reported a comparison of different gap models including FORSKA2 and yet another FORSKA variant called BOREALIS at Lac Duparquet on the Québec/Ontario border. Burton and Cumming (1995) and Cumming and Burton (1996) adapted the ZELIG model of Urban et al. (1993) for application to temperate and boreal forests in B.C. and Alberta. Most recently, Stratton (2008) carried out an M.Sc. study using FORSKA2 applied to forests in the parkland, boreal and tundra ecozones of the Prairie Provinces and NWT. In general, where climate change scenarios have been imposed in these studies, they were represented as plausible increases in temperature (e.g., +1 °C, +2 °C added to present-day climate records) and plausible changes in annual precipitation (e.g., -10%, 0, +10%) rather than downscaled from GCM scenarios.

Survival of individual species in a changed climate will be governed by two factors: 1) their capacity to produce seeds and have these disperse successfully to the new areas of more suitable conditions (generally at higher latitude or higher elevation); and 2) their ability to grow under changed conditions (temperature, moisture, radiation). Recognition of the importance of regeneration constraints has led to the development of several “third-generation” gap models (see Price et al. 2001), but there have been few (if any) attempts to apply these in Canada. Contributing reasons for this are (1) relatively little information available to parameterize all species adequately for all regions; and (2) the computational demands required to carry out comprehensive studies over large areas. Coates and coworkers have applied the SORTIE gap model to simulate species interactions in natural stands both in B.C. and at Lac Duparquet (e.g., Coates et al. 2003; Canham et al. 2004; Greene et al. 2004), but their focus has been to investigate effects of silvicultural options on stand development rather than to assess effects of climate change.

The potential for attempting large-scale modeling studies within Canada has improved in recent years, mainly because of large scale research programs such as the Canadian Carbon Program (formerly the Fluxnet-Canada Research Network, e.g., Coursolle et al. 2006). These initiatives, supported by the Government of Canada, have greatly increased the amount of information available for key species in a wide range of forested ecosystems, and should lead to new, and more confident, simulations of climate-driven changes in forest vegetation in the near future.

2.2.2.1.4 The Importance of Genetics in Vegetation Models

Few modelling studies of species-level responses attempt to account for population differences as a factor in species capacity to adapt to new conditions—a problem common to CEMs and gap models. For example, black spruce is a boreal coniferous species with a natural range extending from Alaska to Newfoundland. It therefore occurs in a range of distinct climatic zones from mild and moist to sub-arctic (extremely cold winters with low annual precipitation). In most species-level models, the natural range would be considered extremely extensive, suggesting that black spruce is very tolerant of wide ranges in climatic conditions. But it seems unreasonable to suppose that the phenotypic adaptations of black spruce which enable it to survive and grow in north-western Canada are present in subpopulations in New Brunswick or Newfoundland. This presents a potential problem to any model projecting changes in black spruce distribution because there is no explicit recognition of the climatic constraints on the subpopulations that would need to migrate and/or adapt to keep up with the projected shifts in climate zones.

The importance of differences among natural populations is a major focus of current work by Aitken and coworkers at UBC, who recognize that climate change is likely to exert strong pressures on the natural distribution of forest species, and that the rates of shifting of climatic zones will “far exceed maximum post-glacial rates” of forest migration. They are therefore investigating the importance of genetic variability within individual species and its role in adaptation. Factors influencing the extent of adaptation include variability among phenotypes, seed production and dispersal capacities, competition among and within species and biotic interactions (e.g., with insect pests). They find that populations of temperate and boreal species show “moderate to strong clines in phenology and growth along temperature gradients,

indicating substantial local adaptation” (Aitken et al. 2008). The phenotypic traits driving local adaptation appear to be the product of small effects of many genes. This implies there is considerable “genotypic redundancy” in many widespread forest species, which combined with high fecundity could allow relatively rapid local adaptation to rapid changes in climate. The availability of genotypes already adapted to warmer conditions will tend to accelerate migration and adaptation at the leading edge of the existing distribution, whereas maladapted populations at trailing edges (southernmost or lowest elevation) are likely to be extirpated. In general, widespread species with large populations and high fecundity are likely to persist, but they will require several generations to adapt fully to the changed conditions (assuming that these eventually stabilize). As all tree populations will be suffering from maladaptation, interspecific competition may become less strong, which would tend to facilitate survival even when conditions are suboptimal. From the management perspective, species with small populations, fragmented or narrow ranges, and low fecundity, and those in decline due to introduced insects or diseases, should be the primary candidates for “assisted migration” (i.e., human introductions of species and/or varieties expected to be better adapted to future climatic conditions). In Canada this will generally mean matching present-day seed origins with future climate zones projected several hundred km northward, or in mountainous regions, hundreds of metres higher. It may also mean developing site treatments to facilitate establishment and survival of the new arrivals. See also McLachlan et al. (2007) and McKenney et al. (2009) for recent discussion of these issues.

2.2.2.1.5 Review of Modelling Studies

The approach adopted here is to report the results of species-level models of both types, as applicable to different forested regions of Canada. Figure 3 shows the coverage of modelling studies compiled in this report. Of these studies only one by McKenney et al. (2007) covers all of Canada (actually at continental scale), with the remainder focusing on smaller regions or collections of sites. The following section attempts to group the results of these studies into five distinct regional syntheses.

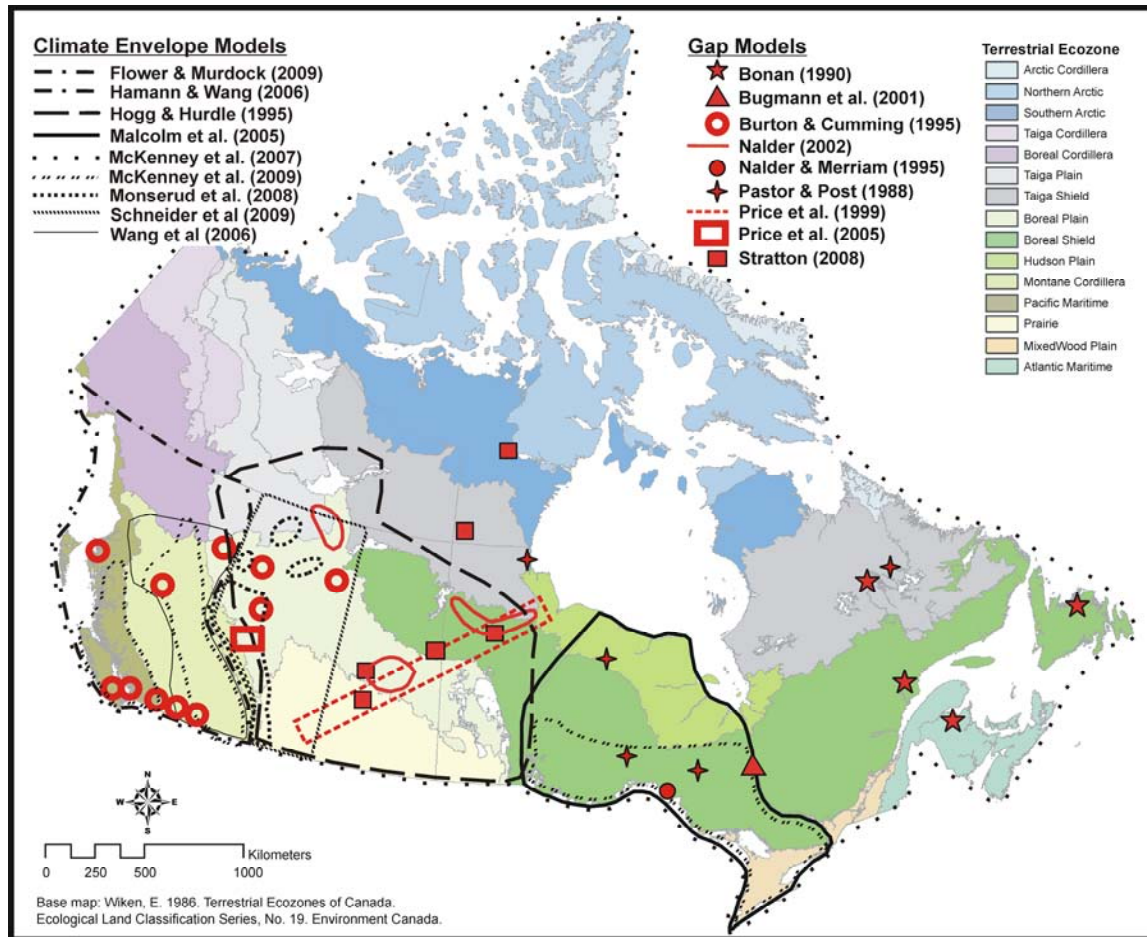


Figure 3. Species-level modelling studies of climate change impacts on forest trees in Canada superimposed on the Terrestrial Ecozones map of Wiken 1986.

McKenney et al. (2007) followed earlier work of Iverson and coworkers using gridded climatological data to define the present-day climatic envelopes for 130 North American tree species throughout Canada and the USA. These climate envelopes were then compared these to projections for three different climate scenarios (Canadian, UK and Australian GCMs forced by the IPCC SRES A2 and B2 emissions scenarios) in 2100. To investigate effects of species dispersal limitations, they reported two extreme scenarios: one where species did not move at all and one where species were assumed able to shift entirely into the future climatic envelope. In the latter “full-dispersal scenario”, future potential ranges were shifted generally northwards by 700 km. Depending on the species, future ranges either decreased or increased in area, on average decreasing by 12%. In the no-dispersal scenario, the average species range contracted by 58% in area, with a northward shift of 330 km (i.e., a shift that overlaps with the present-day distribution range). The general consequence for Canada was that much of the country would be able to support a much wider diversity of forest tree species by 2100, while much of the southern USA would be experiencing a climate that would effectively extirpate most of the species present today (though McKenney et al. emphasized that not all of the 700 or so tree species found in North America were considered in the study). The increase in “climate envelope

richness” was greater in eastern Canada, but there were differences evident between the two emissions scenarios: the more extreme (and potentially more plausible) A2 scenario shifted the climate envelopes further north and reduced their areas compared to the B2 scenario. It was also clear that many of the limitations in CEM simulations discussed previously applied in this continental-scale study. In particular, soil conditions north of the present tree line are likely to present a significant barrier to northward colonization by boreal species.

2.2.2.1.6 Regional Syntheses

2.2.2.1.6.1 *Northern Boreal Treeline*

Pastor and Post (1988) may have been the first to carry out gap model simulations to investigate the interacting effects of climate warming and soil limitations on water and nutrient supplies at forest sites in Canada. In northern Québec, their model projected rather modest increases in productivity of spruce-dominated forests on both silty-clay and sandy sites. In the west, Bonan (1990, 1992; Bonan and Van Cleve 1992) developed a gap model to investigate responses to climate change projections in the boreal regions of Alaska and was able to show that different ecosystems could respond very differently: white spruce stands on south-facing slopes would be likely to suffer from increased water stress, whereas black spruce on colder north facing slopes would be largely unaffected.

Starfield and Chapin (1996; Chapin and Starfield 1997) used a novel dynamic modeling approach to estimate northward expansion of the treeline in Alaska, in response to transient changes in temperature, precipitation, fire occurrence and land use, concluding that it would take 150-250 years for trees to invade the Alaskan tundra. They proposed that rapid warming and drying would lead to the transitional establishment of a boreal grassland ecosystem resembling the aspen parkland of the Prairie Provinces. MacDonald et al. (1993) have also found paleoecological evidence that trees could become established in the tundra in as little as 150 years, supporting earlier modeling studies (e.g., Pastor and Post 1988). More recently, Rupp et al. (2001) used another model (ALFRESCO) to simulate vegetation change in northwest Alaska and concluded that the Brooks Range mountains present a major obstacle to northward migration of forest species into the Alaskan tundra, which could therefore take millennia, but Canada lacks a comparable large trans-continental high latitude barrier. Other studies suggest that dispersal rates will be slower than generally assumed in cold environments (at high elevation and/or high latitude) where slow growth and poor dispersal combine (e.g., Dullinger et al. 2004). Payette et al. (2001; see also Gamache and Payette 2005) argue that northward colonization of the arctic tundra (the zone north of the arctic treeline) in northern Québec is controlled by the interplay of climate, microtopography, soils and fire. The sparse coverage of trees at the northern edge of the forest-tundra is both a cause and a result of infrequent fires, with some trees surviving hundreds or even thousands of years, and relatively few new recruits established from seed. With climate warming, and assuming soil conditions allow, more rapid colonization may proceed, but could be limited to regions within the subarctic forest-tundra transition zone, while northward expansion into the (virtually treeless) arctic tundra would take much longer.

2.2.2.1.6.2 British Columbia

Burton and Cumming (1995) and Cumming and Burton (1996) investigated effects of climate change scenarios on species-level phenology and frost effects using a modified version of the ZELIG gap model applied to forest ecoregions in B.C. and Alberta. The model suggested that lowland coastal temperate forests could undergo catastrophic losses because some dominant species [notably Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and western hemlock (*Tsuga heterophylla*)] would not receive sufficient chilling to induce cold-hardiness and then suffer serious damage from recurrent frosts. Higher elevation coastal forests would generally benefit from longer growing seasons stimulating higher productivity and because more productive species (such as western hemlock) would seed in from below. Interior subalpine forests presently dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann and white spruce would similarly undergo a gradual replacement by more productive lower elevation species including interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and western larch (*Larix occidentalis*). However, interior Douglas-fir forests were projected to remain substantially unchanged, with possible increases of drought-tolerant ponderosa pine (*Pinus ponderosa*). The Interior Cedar-Hemlock zone would see a shift towards dominance by western hemlock with increased productivity. In the B.C. sub-boreal spruce zone, as in much of the Alberta Foothills, lodgepole pine (*Pinus contorta*) was projected to increase in dominance, tending to replace spruces. Similarly the Boreal White and Black Spruce zones of B.C. (and possibly northern Alberta) were projected to give way to domination by lodgepole and jack pine. The rates and magnitudes of change were predicted to be variable, but different climate scenarios did not differ in the direction of change.

Hamaan and Wang (2006) used climate scenarios to determine how the climate envelopes for present-day distributions might change in area, elevation and spatial distribution. Species with their present northern range limit in B.C. were predicted to gain potential habitat at a rate of *at least* 100 km per decade. Some commercial conifer species (notably lodgepole pine) were expected to lose significant areas of suitable habitat whereas the ranges of most common hardwoods were largely unaffected. The simulated spatial redistribution of “realized climate space” for ecosystems in B.C.’s complex topography is considerable, with present-day sub-boreal and montane climate zones projected to disappear particularly rapidly.

Wang et al. (2006) estimated lodgepole pine responses to climate variation and change in B.C., based on mapping of populations and relating these to climate variables (primarily mean annual temperature, MAT). The ultimate purpose was to provide a means of assessing management options for existing geographically defined seed planning units (SPUs) used to define sources of local seed for reforestation programs. Derived response functions identified several populations in central areas of the species’ range exhibiting greater growth potential over a wide range of MAT. They concluded that average productivity of lodgepole pine will increase by up to 7% with moderate warming (approximately 2 °C increase in MAT) and a projected slight increase in annual precipitation, but there would be significant decreases in some SPUs in southern B.C. Greater warming (above 3 °C increase in MAT) would lead to net decreases in productivity compared to present-day with serious reductions in southern SPUs and some local extirpations. Wang et al. (2006) use these results to propose that new strategies are needed to identify the best seed sources for future reforestation, which will not only overcome many of the negative effects

of a warmer climate but may even increase lodgepole pine productivity in some areas compared to present-day. Consistent with these results, McKenney et al. (2009) investigated effects of past and future climate scenarios on present-day seed zones, finding that in B.C., there have already been significant changes in temperature and precipitation with much greater increases in average growing season length and annual precipitation projected for the period up to 2100, particularly in the northeast of the province. The average projected increase in growing season length for B.C. seed zones is approximately 50 days per year while precipitation is projected to increase by 15-50%, depending on location. In many seed zones, however, the increase in precipitation will be insufficient to offset the increase in evaporative demand, implying increased droughts and water stress effects on mature trees and planted seedlings alike.

Most recently, work by Flower and Murdock (2009, in prep.) has focused on the potential changes in distribution of interior Douglas-fir and spruces in B.C. using a CEM based on principal component analysis (PCA) as the method for correlating species presence to a suite of eight climatic indices. When subjected to projections of future climate according to six different GCM scenarios, they found that suitable habitat for Douglas-fir would expand from the central and southern regions of the province to regions at higher elevation and further north. By the 2080s, the overall expansion of area considered climatically suitable varied from 34% to 58% depending on the climate scenario, but the scenarios producing the greatest increases also tend to project the greatest losses of presently suitable habitat (at lower elevations in southern B.C.). Interestingly, in spite of the differences among scenarios, all six projections agreed on the distribution of suitable habitat in the 2080s for 40% of the province, and five out of six agreed for 66% of the province. The story for the white spruce–Engelmann spruce complex is rather different. During the first half of the 21st century, the range of suitable climate is not projected to change greatly, with only minor expansion into higher elevation regions and minor losses of area particularly in the south, presumably where water deficits are projected to become limiting. In the period following the 2050s, however, losses of suitable habitat become more extensive, with much of the southern interior evidently becoming too dry. Agreement among different GCM scenarios for the projected changes in suitable habitat was also stronger: all six models agreed on the distribution of suitable habitat in the 2080s for 54% of the province and five out of six agreed on 76%.

McKenney et al. (2009) also highlighted other effects of a warmer and drier climate in B.C. on the occurrence of fires and insect outbreaks. Flower and Murdock (2009) went further and investigated the potential changes in climatic suitability for two major insect pests: western spruce budworm (*Choristoneura occidentalis*) a pest of Douglas-fir, and spruce bark beetle (*Dendroctonus rufipennis*), which affects spruces. They found overall decreases in projected areas with high “probability of outbreak”, although there were general northward and eastward shifts in the foci of projected outbreaks over time.

2.2.2.1.6.3 *Western Boreal*

In the central Prairie Provinces, Hogg and Hurdle (1995) examined the effects of a projected 2×CO₂ stabilized climate on the southern boundary of the boreal forest, previously found to approximate an isoline where annual potential evapotranspiration (PET) approximately balances annual precipitation (P_{ann}). Although this was not strictly a CEM study, they created a

generalised climate projection derived from the Canadian GCM 2×CO₂ scenario (warming of about 4.5 °C in MAT and 11% increase in P_{ann}) and applied these changes to the 1951–1980 climate normals. They found the projected increases in P_{ann} were insufficient to offset the projected increase in average PET, which implied that aspen and mixedwood forests would have to die back (reduced leaf area, lower productivity and eventual death) to re-establish the annual water balance. The transitional ecozone, known as the aspen parkland, which extends between the boreal forest and the prairies, would similarly undergo extensive dieback, possibly exacerbated by insect defoliation, causing both the forest and the aspen-parkland to retreat northwards to be replaced by grassland ecosystems as drier conditions prevail. The process of dieback would cause tree species impoverishment because different boreal species have different levels of drought tolerance. Given that aspen is the major species occurring in the transition zone, it would presumably be the last species to remain after boreal conifers disappeared from the forest (spruces, followed by pines). This northward retreat of the forest was also projected using the IBIS DVM (Price and Scott 2006), with a significant northward expansion of grass and shrublands in the drier regions of Alberta and Saskatchewan, in response to a climate warming scenario. Gap model projections by Burton and Cumming (1995) for this region produced somewhat similar results, mediated by possible survival of pine species on moister sites.

Price and Apps (1996) first investigated effects of climate change scenarios on biomass accumulation and species composition using a modified version of FORSKA2 (Prentice et al. 1993) at station locations along a transect extending from southern Saskatchewan to northern Manitoba using four GCMs. They found little impact on either except in the south where higher minimum temperatures allowed new species to survive (though these invaders were unrealistically far from existing populations) but low annual precipitation limited significant increases in biomass. Further work with an improved version of the model that accounted for interannual climate variations (Price et al. 1999a) suggested that increasing drought stress at the southern boundary would reduce productivity of existing species with little prospect of new arrivals compensating for these losses. In northern Manitoba, however, longer growing seasons were expected to increase productivity while leading to shifts in species composition from communities dominated by black spruce to mixtures of white spruce and aspen.

Monserud et al. (2008) carried out a study on lodgepole pine productivity and distribution in Alberta using the SRES A2 climate change projections for three GCMs. All three models projected significant warming in Alberta, with negligible changes in precipitation, implying a major increase in the water limitations to forest trees in a region already subject to relatively low annual precipitation. Projected increases in growing season (measured in growing degree days above 5 °C, GDD₅) generally benefitted lodgepole pine productivity (measured in terms of site index, SI) but the area suitable for pine growth changed substantially with projected increases in Dryness Index (DI, defined as GDD₅ / P_{ann}). Areas suitable for growth expanded by as much as 67% during the 2020s, according to one GCM projection (this area includes regions already occupied by jack pine and jack/lodgepole hybrids). Further warming and drying reversed the trend with decreases (compared to present-day) of 6 to 34% in suitable area by the 2050s, and of 40-67% by the 2080s, depending on the GCM.

Most recently, Schneider et al. (2009) carried out a study for all of Alberta, following the approach developed by Hamann and Wang (2006) for B.C., and were able to reproduce the

present-day vegetation with very high accuracy using canonical discriminant analysis. The Schneider et al. study also investigated the likelihood that existing vegetation would persist until the occurrence of natural disturbance (primarily wildfire), thereby delaying the projected changes in established tree cover implied from a simple correlative approach. Even so, their results were consistent with earlier studies, suggesting a significant replacement of forest by parkland, and of parkland by grassland, within 50 years—even under the relatively benign SRES B2 emission scenario. The major driver of this change was increasing drought, caused by higher evaporative demand exceeding projected increases in annual precipitation.

2.2.2.1.6.4 *Eastern Boreal*

Figure 3 shows that eastern Canada has received very little attention from CEM studies and only slightly more from gap modellers. Our knowledge of national climatology shows that the influence of the Great Lakes and Atlantic storm systems results in annual precipitation much greater than that occurring in the western boreal, so that sustained and widespread droughts in present-day forested regions are less likely in the east in the near future, even with a warmer climate. This suggests that for the eastern boreal zone, there is likely to be an increase in productivity and relatively little species loss, though we might expect spruces and birch to be out-competed by pines and aspen on drier sites. However, Malcolm et al. (2005a) projected major losses of area suitable for black spruce, jack pine and sugar maple (*Acer saccharum*) in central Ontario, with the potential for replacement in the longer term by hardwood species from the south.

Pastor and Post (1988) found that simulated impacts of climate warming in this region were very dependent on soil type. At the present-day boundaries between eastern hardwood forests and the boreal, the general trend on soils without moisture limitations was for a transition to more productive temperate hardwood species. Increased productivity occurred because temperate species were considered to be intrinsically more productive and because the warmer conditions also enhanced nutrient availability. For a site at Kapuskasing in northern Ontario, a silty-clay site supported a transition from boreal species to more productive hardwoods including maple and birch, but a site with sandy soil incurred frequent water deficits resulting in a transition to a “stunted pine-oak forest of much lower carbon storage”. Overpeck et al. (1990) simulated changes in a boreal ecosystem (balsam fir, spruce and birch) in southern Québec, finding that an increase in disturbances coupled with relatively mild increase in temperature or reduction in precipitation could precipitate dramatic shifts towards hardwood–pine mixtures.

2.2.2.1.6.5 *Southern Ontario, Québec and Maritimes*

An early example of a climate envelope analysis was carried out for red pine (*Pinus resinosa*) by Flannigan and Woodward (1994). Their study investigated the relationship between climatic variables and the abundance (expressed as volume per hectare) of red pine across its range in eastern Canada and north-eastern US (this study is not shown in Figure 3). A model was developed to fit the present day range and abundance of red pine using available climatic variables in the expectation of better understanding the processes controlling distribution. Next,

general circulation models were used to explore the implications of a $2 \times \text{CO}_2$ environment on the range and abundance of red pine. Using a response surface, growing degree-days (base 10 °C), and precipitation explained 54% of the variance in an independent data set of red pine volume per unit area. Possible explanations for the present day boundaries of red pine are competition for the southern limit, insufficient moisture for the south-western limit, and insufficient warmth during the growing season at the northern limit. The greenhouse warming simulation suggested a dramatic north-eastward shift of 600–800 km in the potential range of red pine and a decrease in total area, but also suggested higher volumes per unit area.

In their study of climate change effects on Ontario seed zones, McKenney et al. (2009) found that January average daily temperature minima have increased by approximately 5 °C since 1950 in these regions, with the greatest increases occurring in the northwest of the province. Depending on the GCM scenario, January minima were projected to increase further during the 21st century, by as much as 10 °C in eastern Ontario. Trends in growing season length were somewhat differently distributed because these are tied to changes in spring and fall temperatures: increases of 30-45 days are projected by 2100, with the greatest extensions occurring in the south.

The consequences of these climatic changes for Ontario forests are likely to be dramatic. Malcolm et al. (2005a,b) concluded that by 2050, there will be an *average* annual warming of 2°C (based on six different GCM scenario projections in the range 1.4- 3.4°C). These researchers then projected the corresponding changes in climate zones across the province, and used regression tree analysis to model potential shifts in forest tree species distribution, accounting for soils, topography and present-day land-use. The general northward shifts of the modeled climate envelopes resulted in major losses of conditions suitable for today's dominant commercial species (black spruce, jack pine and sugar maple) through much of the province. The authors also inferred that species composition will be impoverished in the near future by the mortality of less tolerant species (notably sugar maple), with only the more climatically tolerant species (e.g., jack pine) surviving. Although the projected conditions in 2050 would likely become suitable for more southerly species (many of which are not naturally present in Ontario today), the authors recognized that limited dispersal rates and landscape fragmentation, particularly in the south, would effectively prevent significant colonization.

It is expected that the less tolerant species will be constrained to refugia where conditions are cooler and/or moister than average. On the other hand, increased stresses due to more frequent and/or intense heat waves and drought events will presumably make many species more susceptible to disease and pest problems. Malcolm et al. (2005b) also explored the potential effects of increased occurrence of natural disturbances related to warmer climate, pointing to losses of biodiversity, habitat and timber supply resulting from generally younger forests. These disturbances would therefore precipitate the losses of the more climatically sensitive tree species.

The work of Iverson and coworkers in the eastern USA (e.g., see Iverson et al. 1999) suggest that climate zones will shift northward by 250–600 km, with much of Québec and the Maritime Provinces becoming suitable for many hardwood species by 2100. Similarly McKenney et al. (2007) report that Ontario, Québec and the Maritimes would develop climate zones in some areas suitable for more than 60 new species (mainly hardwoods). At present, many of these

hardwoods only occur naturally in the USA. Whereas Malcolm et al. (2005a) suggested that present-day sugar maple stands are at serious risk of decline, McKenney et al. (2007) indicates the core range for this species would be preserved under most climate model scenarios. The climate zone suitable for yellow birch (*Betula alleghaniensis*) would be likely to shift from its present range in southern Québec and New Brunswick northeastward into central Québec.

2.2.2.1.7 Concluding Remarks

Canada's forests are already exposed to serious threats, many of which can be attributed at least partially on ecosystem responses to climate warming that has already occurred during the second half of the 20th century. With continued increases in atmospheric greenhouse gas concentrations, it is only logical to assume that these threats will worsen and others may manifest. To date, most of the concern derives from the likelihood that warmer conditions will increase the frequency and intensity of natural disturbances, more than that they will adversely affect primary productivity and forest distribution. However, there is ample evidence, supported by numerous modelling studies, that a warmer climate will shift the optimal climatic conditions for most Canadian tree species away from their present locations: in general northward and/or upward. The rate of warming and the consequential shifts in suitable climate zones will be far faster than any natural colonization process. Species losses are likely to be accelerated by disturbances, though regeneration of disturbed areas by colonizing species may be more rapid. But we can reasonably expect sensitive species to be lost at the southern or lower-elevation edges of their present-day ranges faster than new individuals will be able to colonize at the northern or upper-elevation limits. Human interventions, generally to "assist migration" of tree species into new areas of suitable climate, appear to be the only real option if forest resources are to be managed successfully for the future. Models of species-level responses to climate can help in forward planning, but it is important to recognize they cannot provide all the answers. Part of the reason for this is that local projections of future climate change (how much? how fast? and where?) are extremely uncertain, because detailed understanding of climatic processes, as captured in global climate models, is still very incomplete. Climate model forecasts are unlikely to become much more trustworthy in the foreseeable future (Dessai et al. 2009). Therefore, projections of species level models like those reviewed here should be used only as a guide. The differences among species model projections, and among scenarios of future climate, must be used to develop flexible management plans, which will need to be reviewed and revised frequently as new knowledge about future trends in climate and ecosystem responses emerges.

2.2.3 Response to Maladaptation: Species Adaptation

In addition to migrating in response to climate change, populations of trees may also adapt to their new climates through natural selection (Kawecki and Ebert 2004). The ability to adapt depends on the amount of genetic variation and number of individuals in the selection pool. Rapid adaptation requires high genetic variation within populations for traits of adaptive importance, and populations must be large enough to sustain high selection intensities (Aitken et al. 2008). Adaptation in a particular trait may occur rapidly in a population with high phenotypic variation, high heritability, large number of individuals, and strong selection pressure (Savolainen et al. 2007).

Species that have high fecundity, long distance pollen flow and short generation times are likely to be more successful in adapting to a changing climate. These characteristics are often associated with pioneer species, which in turn are promoted by disturbance events (Aitken et al. 2008). In many regions of Canada, higher levels of disturbance are expected with a changing climate (e.g., Flannigan et al. 2005), so successful pioneer species may thrive in the future due to a combination of relatively rapid adaptation and increased disturbance. For example, in boreal mixedwood forests increased fire frequency and severity may favour populations of trembling aspen over those of white spruce in regions where disturbance rates increase (Johnstone et al. 2010).

Populations on the edge of a species' geographical range are less likely to adapt to a changing environment because of compromised fitness and reduced genetic variation in the relatively extreme environment (Savolainen et al. 2007). However, a warming climate would be expected to cause less stress to high-latitude or high elevation populations because gene flow from central populations would introduce genetic material pre-adapted to a warmer climate. Conversely, populations on the low-latitude or low-elevation edge of the range are likely to be stressed by a reduction in fitness due to receiving genetic material from the colder regions of the species range resulting in further maladaptation. In general, density of populations tends to be higher close to the centre of a species' range and other things being equal, more long-distance pollen will reach populations closer to the edge of a species' range from the direction of the centre of the range than from other directions (Aitken et al. 2008).

Phenotypic plasticity is the production of multiple phenotypes from one genotype in response to changes in environmental conditions, and is an important characteristic of tree species because of the longevity of individual trees and their sessile nature (Miner et al. 2005). Trees survive extreme climatic events with a variety of strategies due to phenotypic plasticity. The current level of phenotypic plasticity largely determines the longevity of extant population survival under changing conditions. Migration and adaptation require time, so the more time available due to phenotypic plasticity, the greater the chance of survival of a population's genes through adaptation or migration (Rehfeldt et al. 2001).

As indicated above, current research on local adaptation of tree populations indicates that migration of trees is slow relative to climate change. Even if populations have extensive genetic variation, limited dispersal and establishment possibilities may hamper an evolutionary response to climate change (Savolainen et al. 2007). However, even common, widely distributed tree species need special consideration in the following situations (Mátyás 2007):

- where there are isolated populations on the southern or continental fringes of the distribution area;
- where there are isolated mountain populations with no 'reserve altitude';
- in locations where conditions in the potential colonization area are unsuitable (e.g. unsuitable soils in high alpine or boreal conditions); and
- where the areas were regenerated with reproductive material of obviously low adaptability

Adaptation, like migration, is a lengthy process for long-lived tree species. As an example, Rehfeldt et al. (2001) developed climate response functions for two subspecies of lodgepole pine (*Pinus contorta* ssp. *contorta* and *latifolia*) based on an extensive provenance test established throughout BC in 1974. The objective was to assess the impact of several climate change scenarios on forest productivity (volume per hectare at age 20). Impacts were governed by physiological plasticity in the current generation and long-term evolutionary adjustments that provide adaptedness and optimize productivity in future generations. Global warming scenarios produced short-term impacts that were negative in the south and positive in the north, but subsequent evolutionary adjustments projected substantial increases in productivity. The long-term adjustments may require only one to three generations in the north but six to 12 generations in the south, i.e. between 100 and 1200 years. Clearly this will not be sufficient to allow tree species to adapt given the velocity of climate change described by Loarie et al. (2009).

Populations at the southern or continental distribution limits are threatened in particular due to strong productivity loss, i.e. weakened competitive ability and hindered sexual reproduction (Mátyás et al. 2009, Mátyás 2010). A good example of this is the Island Forests in the Prairie Provinces. These are isolated patches of forest along the southern edge of the boreal forest, often surrounded by agricultural land. These forests occur on wind-deposited sands and are slightly higher than the surrounding landscape and therefore intercept sufficient moisture to support tree growth (Henderson et al. 2002). The Island Forests support primarily jack pine and aspen with some white spruce. The sandy soils, in combination with a semi-arid climate, result in frequent droughts which will likely increase in a warmer, drier future (Hogg and Bernier 2005). Johnston et al. (2008) describe additional sources of vulnerability for the Island Forests including the likelihood of mountain pine beetle spreading from Alberta, increased frequency and severity of fire and losses of productivity due to increased droughts.

2.2.4 Index of Vulnerability

Recent work by the Canadian Forest Service has provided a preliminary approach to determining the vulnerability of tree species to climate change based on aspects of tree genetics. The following section outlines recent work undertaken by J. Loo, Canadian Forest Service, Atlantic Forestry Centre and K. O’Leary, New Brunswick Department of Natural Resources (Loo and O’Leary 2009, unpublished).

Loo and O’Leary set out to develop an index of tree species’ vulnerability to climate change based on three factors:

- Ability to adapt in place: this is a function of genetic variance, population size, seed production, and gene flow between populations. It also includes a factor that reflects location relative to the centre of a species’ range (north, central, or south), and the level of external threat to populations (e.g. insects or disease).
- Ability to migrate: this is based on the method of seed dispersal and seed size combined as a single dispersal score; the age at which reproduction begins; and habitat specificity and availability, which is influenced by degree of habitat fragmentation and isolation.

- Phenotypic plasticity: indicated by degree of heterozygosity and evidence of tolerance range in traits that are likely to influence adaptation.

Each group of factors was assumed to have the same over-all weight; i.e., the risk of population extirpation is equally influenced by ability to adapt in place and ability to move, and both of these depend to the same extent on phenotypic plasticity. If accurate measures of plasticity were available, it might be reasonable to identify a “plasticity threshold” necessary for survival of populations while adaptation or migration occur, but it is not clear which surrogates best capture the concept and regardless of which are chosen as such data are not readily available.

The index is calculated as

$$V = 1 - (A + M + P)/3,$$

where V is the index of vulnerability, A = the ability to adapt in place, M = the ability to move, and P = plasticity. A , M and P each take a value between 0 to 1 based on the following calculations:

Ability to adapt in place (A) is a function of genetic variance (VG , expressed as a scale from 0 to 1) multiplied by the product of population size (N) and fecundity (F); the quantity of gene flow between populations (P), weighted by quality expressed as (L) a factor reflecting location relative to centre of species’ range (north, central, or south); and level of external threat to populations (T).

Ability to move (M) is a function of method of seed dispersal and seed size combined as a single dispersal score (D); age at which reproduction begins (R); and habitat specificity and availability, which is influenced by degree of fragmentation and isolation (H).

Plasticity is easily and directly quantified using provenance test data to develop transfer functions and calculating their width. Transfer functions relate the climate or latitudinal distance populations are moved to population growth. Alternatively, Rehfeldt (1994) calculates the climate distance between genetically distinguishable populations to quantify plasticity and seed transfer distances, noting large differences among species. For example, genetically differentiated populations of western white pine occupy locations that differ by 80 frost free days, while only 18 frost free days separate genetically distinguishable populations of Douglas-fir.

Plasticity may also be inferred from standardized heterozygosity determined with allozyme studies (divided by maximum value) and evidence of tolerance range in traits that are likely to influence adaptation (expressed on a scale of 0 to 1). Such data are not available for all species of interest. Note that the degree of confidence in the predictions depends on available data which varies widely for Canada’s commercial tree species. Loo and O’Leary’s analysis used published reports in determining the values for A , M and P .

Species vulnerability ranking is as follows:

0.0 – 0.19 = Low

0.2 – 0.39 = Low-Medium

0.4 – 0.59 = Medium

0.6 – 0.79 = Medium-High

0.8 – 1.00 = High

2.2.4.1 Results

To illustrate the calculation and interpretation of the vulnerability index, nine Canadian tree species were chosen for evaluation: sugar maple (*Acer saccharum*), red spruce (*Picea rubens*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), trembling aspen (*Populus tremuloides*), red oak (*Quercus rubra*), western larch (*Larix occidentalis*), butternut (*Juglans cinerea*) and beech (*Fagus grandifolia*). These species were chosen to illustrate how different life histories will influence outcomes. Table 4 shows the results:

Table 4. Index and ranking of nine species' vulnerability to climate change. Data from Loo and O'Leary (unpublished).

Species	Vulnerability Score	Ranking
Trembling aspen	0.00	low
Sugar maple	0.20	low
White pine	0.35	low-medium
Western larch	0.40	medium
Red oak	0.40	medium
Beech	0.40	medium
Red spruce	0.55	medium
Butternut	0.60	medium-high
Red pine	0.75	medium-high

Trembling aspen has the lowest vulnerability score due to its high mobility and therefore its ability to keep up with changing climate. Its potential for adapting in place is tempered by the fact that it will not regenerate under its own shade. Aspen's genetic variation is high, populations are large and fecundity is very high. Populations in southern Canada are in the central or southern portion of the species' range so long-distance pollen migrants would be expected to come from other directions more frequently than from the south, indicating that although the rate of gene flow is high, quality is relatively low. Resilience and buffering against environmental change appears to be high, although estimates for heterozygosity vary greatly among studies.

Overall trembling aspen has low vulnerability because of the high ability to move and high genetic diversity.

Other species with high capacity for moving are the relatively heavy-seeded oak and beech because birds are known to carry such seeds at least 4 km. The capacity of these species to adapt in place appears to be approximately equal because although mature beech is threatened by beech bark disease, the disease does not prevent seed production or regeneration. Both produce relatively low quantities of large seeds and are moderately site specific. Red oak tolerates soil moisture changes to a greater degree than beech, and both have relatively high heterozygosity and gene flow, coming from the south. Both have intermediate vulnerability.

Three species are particularly vulnerable: red spruce which has relatively low genetic diversity, small species range, small populations over much of its range, short distance dispersal, and low tolerance to drought; red pine, largely because of low genetic diversity and short distance seed dispersal; and butternut because of very large seed, with short dispersal distance, relatively low genetic diversity and high potential threat from introduced disease, butternut canker (*Sirococcus clavigignenti-juglandacearum*) (Harrison et al. 1998).

The great advantage of this approach is that jurisdictions can begin to assess the climate change vulnerability of important commercial or conservation species using data available today. While the index does not account for all sources of vulnerability, and data may be lacking for some species, it does provide the opportunity for beginning the process of species-level vulnerability assessments.

2.3 Disturbance

In addition to maladaptation, change in disturbance regimes is one of the most important factors that will determine the impacts of climate change on Canadian tree species (Lempriere et al. 2008). The following section provides an overview of species-level impacts of disturbance agents (fire, insects, disease) and how these are expected to change under a changing climate.

2.3.1 Fire

The effects of climate change and fire at the landscape level will be considered in detail in the Phase 2 of the CCFM climate change project. Here the species-level impacts of fire and its interaction with climate change are considered.

The effects of fire at the species level can be characterized by tree species' ability to survive fire and the ways in which they regenerate following fire. Rowe (1983) characterized boreal forest tree species as invaders, evaders, avoiders, resisters, and endurers in order to examine presumed adaptive traits such as seeding from a distance, seed storage in 'banks', sprouting from protected tissues, and resistance to burning. The categories can assist in forecasting forest succession under current climate and fire regimes, and can be used to suggest likely shifts in species composition under future fire regimes. This characterization is based on the Vital Attributes model of Noble and Slatyer (1980), particularly their "regeneration niche" which includes reproduction and shade tolerance.

Species' regeneration niche is defined as follows (after Rowe 1983):

1. Mode of regeneration and reproduction
 - a. Vegetative-based
 - i. *V* species: able to resprout if burned in the juvenile stage
 - ii. *W* species: able to resist fire in the adult stage and continue growth after burning (fire kills juveniles)
 - b. Disseminule-based
 - i. *D* species: highly dispersed seed
 - ii. *S* species: seed stored in soil
 - iii. *C* species: seed stored in the canopy
2. Communal relationships
 - a. *T* species: shade tolerant, establish immediately following fire and persist thereafter
 - b. *R* species: shade tolerant, cannot establish immediately after fire but require shade later in the successional sequence
 - c. *I* species: shade-intolerant, establish immediately after fire but do not persist in shade of later successional species.

These characteristics can be combined to describe a species response to fire and its ability to establish afterward. Rowe (1983) uses these characteristics to define invaders, evaders, avoiders, resisters, and endurers.

2.3.1.1 Invaders

These species have wind-dispersed seeds and rapidly invade recently burned areas, i.e. *DI* species. They are shade-intolerant pioneers that, once established usually flower or fruit profusely or spread vegetatively. Common forest tree species in this category include paper birch (*Betula papyrifera*) and trembling aspen. Aspen may reproduce primarily through wind-dispersed seed on rocky terrain (e.g. the Canadian shield) but reproduces vegetatively elsewhere.

2.3.1.2 Evaders

Evaders store seed in the canopy (*CI*) or the soil (*SI* or *ST*), thereby evading the high temperatures of fire near the ground. These species rapidly germinate in the charred forest floor following fire. The best know examples are jack and lodgepole pine, both having serotinous cones with heat required to open the cone scales and release seed. Black spruce has semi-serotinous cones in clumps near the top of the canopy. It should be noted however that extremely

severe crown fires can destroy seed in the cones of jack and lodgepole pines, preventing on-site regeneration. Tree species that store seed in the soil are fewer, but pin cherry (*Prunus pensylvanica*) is a common example in eastern hardwood forests.

2.3.1.3 Avoiders

As suggested by the name, avoiders are very susceptible to mortality from fire and tend to occur late in the successional sequence (*DT* or *DI*). They are found more frequently in areas with long fire cycles, and generally occupy mesic sites and are shade-tolerant. Examples include balsam fir and white spruce.

2.3.1.4 Resisters

These species become increasingly tolerant of fire as they get older, with thick bark and rapid self-thinning which reduces ladder fuels and therefore the risk of crown fires. Jack and lodgepole pine and some mature Douglas-fir are examples.

2.3.1.5 Endurers

Species that resprout following fire make up the last category (*WI*). The best-known species in the group is trembling aspen, although birch may resprout if fire is not too severe.

Table 5 summarizes these strategies with respect to the length of the fire cycle.

Table 5. Adaptations of species groups to fire cycles (modified from Rowe 1983).

Short fire cycle	Intermediate fire cycle	Short, intermediate or long fire cycle	Very long fire cycle
Endurers (<i>VI</i>): aspen	Resisters (<i>WI</i>): jack pine Evaders (<i>CI</i>): jack pine lodgepole pine black spruce Evaders (<i>ST, SI</i>) pin cherry	Invaders (<i>DI</i>): aspen	Avoiders (<i>DT</i>): balsam fir white spruce

Short fire cycles favour sprouting, shade-intolerant species such as aspen. Intermediate fire cycle length allows species that are resistant in the adult stage to mature and survive, along with those that store seed in the canopy or the humus layer. Pioneer invaders prosper under all fire cycles and the disseminule-based shade-tolerant species do well in climax communities.

De Groot et al. (2003) carried out a quantitative analysis of the effects of future fire regimes on boreal tree species using the Vital Attributes approach of Rowe (1983). The Vital Attributes

approach was incorporated into a simulation model called BORFIRE. These authors simulated the effects of fire under current (1975-1990) and future climate (2080-2100) using data from the first generation Canadian general circulation model (CGCM1) as input to BORFIRE. Changes in forest composition and biomass due to future altered fire regimes were determined by comparing the effects of present and future fire regimes on forest stands over a 400-yr period. As compared to current climate, CGCM1 showed more severe burning conditions under future fire regimes including fires with greater intensity, greater depth of burn and greater total fuel consumption. Shorter fire cycles estimated for the future generally favoured species which resprout (Endurers) or store seed (Evaders). Species with no direct fire survival traits (Avoiders) declined under shorter fire cycles. The moderately thick bark of Resisters provided little additional advantage in crown fire-dominated boreal forests. Species with multiple fire survival traits (e.g. being both Evader and Avoider) were adapted to the widest range of fire cycles. There was a general increase in biomass under future fire regimes caused by a shift in species composition toward fast-growing re-sprouting species. Long-term biomass storage was lower in fire exclusion simulations because some stands were unable to reproduce in the absence of fire.

This characterization can be applied to any species of interest as a means to predict (in a general way) the effects of future fire regimes on species composition. For example, climate change projections suggest that western Canada will experience a doubling to tripling of area burned and more frequent fire events by 2100 (Flannigan et al. 2005, Balshi et al. 2009). Under this scenario it is likely that aspen (both an Endurer and Invader) will increase in dominance on the landscape (Johnstone et al. 2010). In contrast, Flannigan et al. (2001) suggest that fires will become less frequent in eastern Canada, thereby favouring long fire-cycle species such as balsam fir and white spruce.

2.3.2 *Insects*

Contributed by Dr. Rich Fleming, Great Lakes Forestry Centre, Canadian Forest Service, Sault Ste. Marie, ON

2.3.2.1 Introduction

This section provides a description of the current state of understanding of how climatic change is expected to influence insects in Canada's forests. The report focuses on insect impacts on forest productivity to coincide with what is assumed to be the main interest of the readership, the Canadian Council of Forest Ministers.

In this section, species are identified by only their common names (unless Latin names are needed to avoid confusion). In addition, an attempt has been made to remove jargon, and reduce the number of cited references. Consequently, the reader is often referred only to earlier reviews of related subject areas with the understanding that those cited reviews can be used as gateways for further reading for those wishing to delve deeper into particular subjects. A number of topics are given only cursory mention. These include carbon budgets, pest control methods, a number of important pest species, and industrial considerations.

The first section describes why insect impacts on Canada's forests are important. Next the report

discusses some generalities (and complications) regarding how insects can be expected to respond to climate change. The third section deals with some representative examples of Canada's prime suspects – the insect species likely to be the most damaging to Canada's forests as the effects of climate change mount. The final section discusses a number of considerations in the management of forest insect populations in a changing climate.

2.3.2.1.1 Why Are Insect Disturbances in Canada's Forests Important?

2.3.2.1.1.1 *Disturbances Drive Ecosystem Change in Canada's Forests*

Besides timber, healthy forests provide a variety of non-timber products and many ecosystem services including maintenance of biodiversity, clean water, and carbon storage (Gitay et al. 2001). Forests are normally highly dynamic so separating normal forest change from changes caused by changes in forest health is not always easy.

In Canada's forests, change comes primarily in the form of "disturbances" which can be defined as any relatively discrete event in time that disrupts the successional development of a forest stand, ecosystem, or landscape, by affecting its population structure and changing resources, substrate availability, or the physical environment. Disturbances are often thought of as destructive events which setback, or even change the direction of, the successional processes of regeneration and recovery. Disturbances occur in many forms (e.g., storms, fire, insects, disease, and logging) and over a wide range of scales (Ayres and Lombardero 2000, Dale et al. 2001). Disturbances leave ecological legacies which are critical in conserving biodiversity and influence future species composition, age structure, and spatial heterogeneity of the area (Radeloff et al. 2000), and consequently, facilitate or impede the occurrence of future disturbances (Kulakowski et al. 2003).

The concept of disturbance regime is typically used to classify disturbances of a particular type (e.g., insect outbreak) in terms of their areal extent, severity, duration, and frequency. Since many areas are prone to multiple kinds of disturbances, focusing on a single type of disturbance may not lead to a complete analysis of a site's disturbance history. Hence, it is also important to consider how different disturbances interact (Bouchard and Pothier 2008, Parker et al. 2006). In short, it is the disturbance regime complex, which ultimately results in large scale alterations of forest ecosystems and their environments.

Disturbance plays a fundamental role in the development of forest ecosystem structure and function in Canada (Johnson and Miyanishi 2007). In sustaining itself at a site, a forest ecosystem goes through repeated cycles of maturation and renewal. In Canada, disturbances are the principal agents in these 'renewal' cycles for releasing the tightly bound accumulations of biomass, energy, and nutrients that characterize a mature forest ecosystem (Gunderson and Holling 2002). This sudden release produces a pulse of available resources, which opportunistic species exploit as they effectively invade the site and launch another successional sequence. This is a critical time in forest recovery. The next successional sequence could retrace previous successional pathways at the site and thus culminate in a mature forest with much the same properties (in terms of species composition, spatial distribution, soil qualities, etc.) as the one which existed on the site immediately before the disturbance. In this sense, the original forest

ecosystem has effectively retained the site. However, there are natural situations that result in the original forest ecosystem not retaining the site, and another, sometimes radically different ecosystem may start to dominate (Folke et al. 2004). Depending on the mix of available resources and micro-environments available at the site, and the variety of species with the opportunity to exploit them, the new successional sequence may veer away from the successional pathway leading back to the forest ecosystem originally situated at the site, and move in a pathway culminating in an entirely new ecosystem with its own unique disturbance regime complex (Raffa et al. 2008). For instance, mountain pine beetle outbreaks have caused the replacement of lodgepole pine ecosystems by Douglas-fir in British Columbia (Heath and Alfaro 1990) and forest tent caterpillar attacks during droughts have contributed to forest retreat in the prairies' aspen parkland (Hogg et al. 2002). The adoption of a successional sequence leading to a totally new ecosystem is most likely after a forest is subjected to disturbances outside its historical range of experience (e.g., rapid climate change, large-scale land-use-change, or logging).

2.3.2.1.2 Insect Outbreaks are Dominant Disturbances in Canada's Forests

Insects are the most diverse class of organisms on earth and the major natural cause of depletion of Canada's forest productivity. Past outbreaks have covered extensive areas (Volney and Fleming 2000). In 1985, the jack pine budworm defoliated 5.8×10^6 ha of pine forest in Ontario and the prairie provinces. The forest tent caterpillar damaged roughly 15×10^6 ha of aspen parkland and adjacent boreal forest in the prairie provinces in 1982. In Ontario, this insect defoliated more area (19×10^6 ha in 1992) than any other hardwood-feeding insect, but typically causes little direct tree mortality (although it is suspected of sometimes contributing to subsequent declines). In 1975, at the peak of the last spruce budworm outbreak, 71×10^6 ha of forest in eastern North America were defoliated. Since then, spruce budworm populations have declined, but Canada's western forests are now experiencing "the largest insect outbreak in Canadian history" (Ono 2003). The mountain pine beetle has been killing mature lodgepole pine over an area extending up to 13 million ha since 1999 (Raffa et al. 2008). The resultant decline in carbon uptake through photosynthesis and increase in emissions from decaying trees has changed Canada's western forests from a small net carbon sink to a large net atmospheric source (Kurz et al. 2008).

Until relatively recently, the technology to assess wood volumes lost during insect outbreaks over large areas was lacking. Now, geographical information systems can be used to overlay digitized maps of the historical patterns of defoliation on maps of the characteristics of the forest affected, so that the total volumes lost to pests can be estimated. The last period for which these estimates are available was 1982 to 1987 (Hall and Moody, 1994). The average annual loss for Canada during this period due to the spruce budworm was 27.3×10^6 m³, that due to jack pine budworm damage 2.2×10^6 m³ and for the tent caterpillar 2.4×10^6 m³. To put these losses in perspective, the average annual total of depletions from Canada's forests from 1982 to 1987 was 298×10^6 m³. Insects and diseases accounted for 106×10^6 m³ of these depletions; fire, 36×10^6 m³; and harvest, 160×10^6 m³. During this period the estimated annual allowable cut (which approximates the estimated forest growth in Canada), was between 244 and 346×10^6 m³.

These estimates suggest that overall, Canada is close to the limits of sustainability, and probably

beyond it in some areas. One approach to improving this balance would be to reduce losses due to pests. Although it is likely impossible to change the course of outbreaks, the repetitive patterns evident in outbreak development and spread (e.g., Candau et al. 1998) suggest that with current harvest levels, one might be able to pre-empt pest-caused mortality in some situations by harvesting the most vulnerable stands before an outbreak reaches them.

2.3.2.2 How Will Insects Respond to Climate Change?

Climate expresses itself in many interacting physical dimensions (e.g., temperature, humidity, precipitation, cloudiness, severe storm frequency). Nonetheless, this paper focuses largely on temperature because, of these climate variables, it is the one for which there is most confidence in forecasting future climate change scenarios, and for which we have most evidence from which to infer insect responses. The rate of population growth of many insects is strongly dependent on temperature, and their survival is impaired at low and high temperatures. Changes in both mean temperature and the extent and frequency of extremes can have major impacts on insect populations.

Normally, individual insects of any species have negligible impacts on forest productivity (although there may be trade and tariff implications). Only when their populations grow to damaging densities do they pose a direct threat. Since population growth is determined by the net effects of survival, reproduction, and dispersal, the key to determining how insect populations will respond to climate change is in determining the net effect of how these three processes will respond. (Of course, insect impacts on the forest in future climates also depends on how these climates affect the forest directly through forest productivity and forest structure [Cohen et al. 2001] and through the sensitivity of the forest to insect attack).

Unfortunately, we lack a complete picture of how climate (even just temperature) affects any of the three key population processes for any important forest insect in Canada. Survival may be the best understood of the three, but even with survival, how climate affects interactions with the collections of natural enemies and host trees and potential host trees remains almost totally unknown.

Two approaches have been adopted for this situation. A classical, reductionist one would delve into the most accessible biological sub-processes which influence survival, reproduction, and dispersal. Forecasts of how climate will affect the future impacts of forest insects are based on the knowledge gained about these sub-processes (e.g., seasonality), and a variety of implicit assumptions about the state of the myriad unstudied components of the forest insect outbreak system. Alternatively, a holistic, and more empirical approach uses historical, geographic data on outbreaks, forest conditions, and climatic variation in process-oriented statistical analyses to infer how the forest insect outbreak system has responded to climate variation over its range in the past. This approach implicitly assumes the system will maintain the historical relationships between outbreaks, forest condition, and climate in making forecasts about future insect impacts on the forest. By comparing how the system as a whole responds to the different climates encountered over its range, one is able to infer how the system responds to climatic variation, and hence forecast how the system is likely to respond in future climates. Both approaches have their short-comings and in many situations, it may be the available data which dictates which

approach is applied. Ultimately, the two approaches will likely converge as the proponents become better informed about alternatives and more data becomes available.

Three aspects of insect population behaviour for which there is suggestive evidence of how a broad rise in temperature might affect them are insect physiology, seasonality, and geographical distribution. This section starts with these three, and then discusses how other factors might complicate the expectations.

2.3.2.2.1 Physiological Responses to Climate Change

In Canada where temperatures affecting physiological processes tend to be below species optima for most of the year, increases in temperature may be expected to speed up these processes and lead to more rapid development, shorter generation times, more movement, and reduced mortality from abiotic factors. For example, Yamamura & Kiritani (1998) estimated the potential decrease in generation time for a range of insect orders with a 2°C temperature rise. In Canada's forests, likely candidates for shorter generation times are the hemlock woolly adelgid, certain bark beetles, and the two-year cycle budworm. Some insect species are constrained through responses to other stimuli (e.g., day length) to a fixed number of generations each year, and changes in generation time must be compensated by increases in the duration of a dormancy period.

Winter mortality from lethally low temperatures is a key factor in the dynamics of many temperate insects, especially those that do not enter diapause but continue activity throughout the winter as temperature permits. Warmer winters, or reduction in the frequency of extremely cold periods, may thus improve the prospects for survival of such species (Cooke 2009). However, insects display a range of strategies in relation to the threat from low temperature (Bale et al., 2002) and these will, in part, determine the impact of warmer conditions. Survival of insects that can tolerate freezing may not be increased as much by warmer winters as survival of those that cannot, and within the latter group, physiological and behavioural attributes will be influential in determining the impact of climate change. Species which are quiescent in winter may even be disadvantaged by periods of unusual warmth because activity increases, possibly in the absence of food, and depletes energy reserves critical for survival until food supplies are replenished.

2.3.2.2.2 Seasonal Responses to Climate Change

For insects whose life-cycle events are controlled by temperature, those events may generally be expected to occur earlier, and higher temperatures are likely to facilitate extended periods of activity at both ends of the season. (This is subject to constraints that other factors such as day length and drought might impose. For instance, insects often enter diapause in response to photoperiodic cues). Unless the duration of food availability is also extended, insects will not be able to gain from the opportunity given by changes in temperature alone. There is some evidence that adults of insects which normally have a single generation and fly late in the season, such as the winter moth, might emerge even later under climate warming (Buse & Good 1996).

2.3.2.2.3 Changes in Distribution in Response to Climate Change

In Canada's forests, warmer conditions can be expected to promote a northward extension of the range of species currently limited by low temperature and an increase in the altitude at which they can survive (Logan et al. 2003). For instance, a modest 2°C rise in temperature in northern temperate latitudes over the next century is equivalent, on average, to shifting current conditions approximately 6 km per year north or 3.3 m per year higher in elevation (Harrington et al. 2001). Most insects would be capable of tracking such changes but some host plants may not be. Hence the spread of some insect species may be limited by the spread of their host trees. In the case of invasive insects, if conditions during transport are suitable they can, of course, be moved by humans. International trade and tourism offer the opportunity for species to spread. Insects may come into contact with new potential hosts, and these hosts may already be under some stress, for example as a result of drought, and hence less able to defend themselves. This increases the likelihood of host switching. If any host plants are not under stress then any impact will be determined by the balance of advantages and disadvantages conferred on the insect. For example, phloem sap becomes more concentrated at higher temperatures, and thus acts as a richer source of amino acids for sap feeders, but the concentration of a range of secondary plant compounds tends to increase under drought stress, leading to changes in the attraction of plants to insects. The physical nature of the host plant may also change. Leaves may become thicker or waxier, or may change colour, which could make them less palatable or attractive to insects.

It is not necessarily the case that, if a species which is a pest in one area arrives in a new location, it will be a problem there as well. The reverse is also true. As numerous examples of exotic biological invasions attest (Niemela and Mattson 1996), a species that is not a pest in one location may become one if it establishes, for example, in an area relatively free of natural enemies or where hosts have not evolved adequate defensive mechanisms.

2.3.2.3 Complicating Factors

There are complications that affect how predictably the responses of insect physiology, seasonality, and distribution to a general rise in temperature percolate up to the population and community levels. Specific complications include facets of the interactions between climate variables, the possibility of separation in time and space between species which currently interact directly, and factors affecting the ability of species to adapt physiologically to changed conditions.

2.3.2.3.1 Complicating Factor: Changes in Multiple Variables

Temperature does not act in isolation to influence pest status and it is important to consider interactions with other variables. Rainfall, for example, is also critical to survival. Some insects are unable to tolerate extremes of drought, whilst others are disadvantaged by extremes of wetness.

Atmospheric chemistry (e.g., CO₂ levels) is also changing. Increased concentrations of carbon dioxide produce increases in the carbon:nitrogen ratios of plants. This requires insects to eat more in order to obtain adequate dietary nitrogen, and plants may respond through increases in

plant biomass or levels of carbon-based defences (Bezemer and Jones 1998). For insects, the net result may be slower larval development, longer exposure to natural enemies, and hence increased mortality.

Besides changes in temperature and rainfall, other climate variables expected to change include snowfall, humidity, wind, and cloudiness. In addition, even where each of these variables is well within their historical ranges, their combinations (interactions) may present forests and their insects with climates never experienced before (Harrington et al. 2001).

Economic and other considerations may lead to changes in land use, forestry practices, or human population distribution. Increasing transportation leads to increased risk of invasion by exotics. Such considerations may dominate or override any effect of climate on insects.

2.3.2.3.2 Complicating Factor: Separation in Time and Space

Changes in climate may affect interactions between species by disrupting temporal synchrony. For example, many plant-feeding insects are dependent on synchrony between the time of bud burst (or flowering) and the emergence of their feeding stages. However, there is little evidence of feeding stages being cued directly by bud burst. Instead, similar external cues often affect both bud burst and the appearance of feeding stages. These external cues are often complex combinations of day length and specific combinations of periods and extents of chilling and warming. Requirements are rarely identical for the plant and insect, and have developed over evolutionary time. It is quite conceivable that when rapid changes in climate occur, the synchrony between bud burst and the emergence of feeding stages could become decoupled due to subtle timing differences in the response to cues determining the seasonality of the species concerned (Harrington et al., 2001). Pest problems may then be reduced. The decoupling of one synchronous food web interaction may initiate others. This can occur when a participant of the original interaction (e.g., an insect species) later falls into synchrony with different members (host tree species) of adjacent levels of the local food web. Such switches in synchrony allow pre-adapted exploiters immediate access to new host trees although it may take time for the insect to evolve the ability (if it has the capacity for such evolution).

It seems highly improbable that all members of a community will respond in the same way to climate change, and this is likely to lead to rearrangements of current communities. Evidence suggests that species may move north separately rather than as fully integrated components of an entire ecosystem which is moving in unison. In fact, the conifer species which comprise today's boreal forest in North America migrated northwards separately in the Late Glacial. Separate movement under future climate warming could result from (a) basic differences in the migratory potential of different tree and different insect species, (b) the appearance of 'green bridges' (plants which, once the climate warms, become hosts or provide favourable overwintering sites for exotic insects which previously were incapable of surviving the winter in that region), and (c) the destabilization of resident ecosystems.

2.3.2.3.3 Complicating Factor: Differential Adaptability

Differential effects of increasing temperatures on forest insects, their host trees, and their natural enemies may lead to changes in pest potential at higher temperatures even if temporal and spatial synchrony is maintained. For instance, it is expected that rapid climate change will impose more stress (e.g., through drought) on the relatively immobile host trees than on the forest insects which feed on them (and can more easily avoid environments which have become stressful for them). Stressed trees are often less resistant to attack, so insect population densities which typically only damaged the trees before the climate warmed, may become host tree killers after some climate change.

Differential adaptability could have a genetic basis. The extent to which species genetically adapt to change will be dependent on the strength of the selective forces for change acting on the species and the genetic capacity of the species to respond. This capacity can be expected to increase with the species' genetic variability, geographic range, reproductive rate, migratory ability and competition with other biotic components of the changing environment. The more adaptable species are likely to be the more mobile species (because pre-adapted phenotypes are more likely to be able to move in from elsewhere) and the faster reproducing species (which are likely to give rise to appropriate genotypes more frequently). Unfortunately pests tend to show these characteristics. For instance, as outlined in the following sections, the spruce budworm, the mountain pine beetle, and the gypsy moth all have potential for genetic adaptations which could make them more serious problems in the future.

2.3.2.4 Which Insect Species are the Prime Suspects for Future Damage to Canada's Forests as a Result of Climate Change?

Doubtless, the mountain pine beetle is the prime suspect among insect species as a future threat to Canada's forests as a result of climate change. Then there are the usual suspects. These are species which have always ranked among the most damaging in Canada, and will likely remain so in a changing climate. These species include the forest tent caterpillar, and the budworm species, headed by the spruce budworm. Finally, invasive species are included as a group, not because any particular one deserves this notoriety, but rather because there are quite a few of them, their number is increasing rapidly, and there are especially large uncertainties about the threat that any one of them pose to Canada's forests.

2.3.2.4.1 Mountain Pine Beetle

The mountain pine beetle (MPB) is currently the dominant cause of mortality in mature pine forests in western North America. Mountain pine beetle can successfully attack most western pines, but lodgepole is its primary host throughout most of its range.

Although widespread – occurring from northern Mexico, through 12 U.S. states and 3 Canadian provinces – mountain pine beetle outbreaks in Canada have been mainly restricted to the southern half of British Columbia and the extreme south-western portion of Alberta. [In 1979, an outbreak occurred in the Cypress Hills at the southern junction of the Alberta-Saskatchewan border (Ono 2003)]. This restriction is not due to MPB's host tree. Lodgepole pine extends north

into the Yukon and Northwest Territories, and east across much of Alberta. Rather, the potential for mountain pine beetle populations to expand north and east has historically been limited by winter cold and mountainous terrain. The substantial shift by mountain pine beetle populations into formerly unsuitable habitats during the past 30 years as a result of climate change has recently enabled the beetle to overcome the natural barrier of the high mountains (Carroll et al. 2004).

Pre-requisites for a mountain pine beetle outbreak to occur are an abundance of large, mature pine trees and several years of favourable weather. Fire suppression and selective harvesting of species other than pine during the latter half of the previous century have more than tripled the area of mature pine in western Canada. Moreover, mountain pine beetle survival has increased as a result of climate change over much of western Canada, allowing populations to invade successfully into pine forests in areas that formerly were climatically unsuitable. Thus, both conditions for an outbreak have coincided, and with enough force to produce the largest MPB outbreak in recorded history. Given the rapid colonization by mountain pine beetles of areas that formerly were climatically unsuitable in recent decades, continued warming in western North America associated with climate change will likely allow the beetle to expand its range further northward, eastward and toward higher elevations.

Surprisingly, MPB densities have decreased in some areas that formerly were extremely supportive of infestations. It was expected that if climatic conditions improved in historically unsuitable areas, then conditions should also do so in the more suitable habitats, and the overall number of infestations should increase. This used to hold in areas that historically had had climates that were moderately to highly favourable for MPB. However, by the mid-1980s the number of infestations in the habitats that were previously the most climatically favourable for mountain pine beetle had fallen sharply. In very hot summers there, parts of the mountain pine beetle populations were forced into a second generation. This caused cold-susceptible stages (eggs, pupae, adults) to overwinter and thus interrupted flight synchrony, and consequently, mass attack success in the following year. This apparent disruption of mass attack in areas with very hot summers suggests that southern and low-elevation regions may become less favourable for the currently resident mountain pine beetle populations. However, in the longer term, mountain pine beetle populations that are genetically better adapted to warm temperatures (Bentz et al. 2001) may move north from their present location in the U.S.

In the past, large-scale mountain pine beetle outbreaks collapsed due to localized depletion of suitable host trees in combination with adverse weather (e.g., an unseasonably cold period or an extreme winter). The current outbreak may be different. In the absence of unusual weather, this outbreak may persist by continually moving into new habitats as global warming allows access to a small, but continual supply of mature pine, thereby maintaining populations at above-normal levels for some decades into the future (Carroll et al. 2004).

A recent series of benign winters has allowed mountain pine beetle populations to extend their ranges along the northeastern slopes of the Rockies in Alberta – areas in which the beetle has not been previously recorded. This has created a very dangerous situation. The MPB is now approaching the jack pine forests of northern Alberta and Saskatchewan. There is no known biological barrier to populations of the beetles colonizing jack pine if its range expands north to

the zone of overlap between jack and lodgepole pines. Because jack pine is susceptible and extends through the rest of the boreal all the way to the east coast, the MPB may be about to gain access to the whole extent of Canada's boreal forest (Raffa et al. 2008). For this reason, MPB is the forest insect species which poses the greatest threat to Canada's forest resources as a result of climate change.

2.3.2.4.2 Spruce Budworm and Jack Pine Budworm

Most forest insects which attack trees specialize in feeding on particular tissues on a particular tree species or a group of closely related species. Such attacks rarely kill trees unless the trees are already experiencing stress from something else (e.g., drought). The spruce budworm (SBW), which feeds on balsam fir and spruces, and the closely related jack pine budworm (JPBW), which feeds on jack pine are two exceptions.

The spruce budworm is present in every province and territory of Canada. It is the most destructive insect defoliator of forests in North America. The JPBW is among the next most important insects in this regard. Both SBW and JPBW are members of a complex of 15 conifer-feeding *Choristoneura* "biotypes" which hybridize naturally, have overlapping host tree ranges, and lack distinguishing morphological traits (Volney and Fleming 2007). Another member of this complex is the western spruce budworm, which has had serious outbreaks in the southern Rocky Mountains. Its principal host is Douglas-fir. Another *Choristoneura* species which has occasionally had substantial impacts is the large aspen tortrix. It attacks trembling aspen and has reached outbreak levels in the prairie provinces. All four of these insects are likely naturally prone to large outbreaks. Evidence suggests that SBW outbreaks have probably occurred since shortly after forests followed the last glacial retreat.

Outbreaks of the JPBW typically last two to three years. SBW outbreaks last several years, with their after-effects remaining for up to two decades in the same stand. Defoliation intensity varies markedly from one year to the next. In spruce-fir stands, spruce survival after SBW outbreaks is normally greater than that of balsam fir.

The periodicities of the outbreak cycles of both SBW and JPBW vary geographically. In eastern Canada, SBW outbreaks have a well-documented cycle with a period of 30-35 years. In western Canada, SBW outbreaks occur much less regularly. JPBW defoliation fluctuates with an average period of 10 years in Manitoba and Saskatchewan. In northwestern Wisconsin densities of some populations also cycle with a 10-year period. However, several populations in stands on xeric and nutrient-poor sites cycle with a higher frequency (five or six years) and maintain a higher mean density. This observation has led to the suggestion that a warmer, drier climate may cause a change in population behaviour in which JPBW outbreaks occur more frequently with an elevated mean population density. If so, tree mortality in jack pine stands would be expected to rise above historically observed levels (Volney and Fleming 2007).

The persistence of episodes of SBW and JPBW defoliation also varies geographically. SBW occurs throughout the range of its host trees, but the extended periods of defoliation which characterize outbreaks seem to be confined to the southern margins of this range. In the western boreal forests, both JPBW and SBW defoliation persist longest at the southern margins and are often associated with drought. The collapse of outbreaks, at least for parts of the range, is often

associated with the catastrophic loss of suitable foliage caused by spring frosts. For the two budworms, the normal collapse of the outbreak in the host's core range is associated with mortality driven by natural enemies late in the larval stage.

In eastern Canada, because of the dominance of the 30-35 year cycle in SBW outbreak dynamics, the limited length of the insect survey records, improvements in survey technology, and changes in survey protocols over time, it is no simple task to determine whether outbreaks have been getting larger. However, these survey records have been used as a basis for developing holistic models (Gray 2008, Candau and Fleming 2008) to forecast SBW-forest-climate system responses to future climates. The results suggest that outbreaks will extend further north, but lose some ground on the southern margins. Overall, defoliation will increase.

In western Canada, where SBW outbreaks occur more sporadically than in the east, the areas affected have increased dramatically. The areas affected in successive JPBW outbreaks in the west have been increasing since the 1930s (Volney and Hirsch 2005).

Climatic influences on budworm life history are considered a major factor in restricting the extent and intensity of outbreaks (Volney and Fleming 2007). Recent population trends for SBW have been associated with recruitment to the feeding stage. On white spruce, more than 85% of the total SBW mortality in a generation occurs before the larvae establish feeding sites and moult to their third instar. Dispersal in the autumn following egg hatch and again in the spring before establishing feeding sites accounts for many of these losses. Two indicators of recruitment, egg weights and seasonality, are both climate dependent. Among spruce budworm populations, those from locations with long, cold winters tend to have fewer, heavier eggs than those from environments with milder winters. This genetically based adaptation allows SBW populations to increase their potential recruitment substantially where winters are mild. By contrast, where winters are harsher, such as at higher elevation, reduced SBW recruitment is expected. This may help explain the decrease in the number of spruce budworm outbreaks with increasing elevation reported by Burleigh et al. (2002).

The success of both JPBW and SBW populations in establishing feeding sites in the spring depends on the synchrony of their development with that of their host trees. JPBW is critically dependent on the development of the male and female strobili for survival of the early instars. By contrast, SBW second instars possess an array of morphological and behavioural adaptations that allow them to mine needles, and thus tolerate some asynchrony between their spring emergence and vegetative shoot development. The seasonal window of spruce budworm, which spans from at least 3 weeks prior to, and one week after budbreak, opens gradually and closes abruptly. The population consequences for late-emergers is severe: larval survival is depressed (from 60% to 10%), the pupal mass of both males and females is 50% below that of the segment of the population that synchronizes emergence with the opening of the seasonal window, and development is delayed. This is a critical period in the life history of both of these insects.

The seasonality of SBW in the field after establishing feeding sites is quite predictable. However, the heat sum needed to develop from 2nd instar to moth varies substantially with latitude. The geographic variation observed in this trait appears to be almost completely under genetic control and the rates are buffered to accommodate variations in the bioclimatic conditions that a wide-

ranging species such as the spruce budworm might encounter.

Genetic control of spring emergence is weak so SBW larvae from a single family typically exit from hibernacula over a prolonged period. This 'spreading of the risk' guarantees SBW populations some synchronization with budburst. However, hybrid populations display high heritabilities which enable rapid adaptation to new conditions (e.g., mixed host species stands). Geographic variation in seasonality after establishing feeding sites is largely genetically controlled.

2.3.2.4.3 Forest Tent Caterpillar

The forest tent caterpillar (FTC; *Malacosoma disstria*) is an early season defoliator of a taxonomically diverse group of broadleaf trees, especially species of *Quercus*, *Acer*, and *Populus*. Its vast range goes from the Gulf of Mexico to northern Canada, and from coast to coast.

Outbreaks generally last 3-4 years, and the repeated defoliation can kill trees although the loss in wood volume is much less than that from a SBW outbreak. Little is known about what causes outbreaks, but two possible climatic factors are suitably warm temperatures during larval development and seasonal synchrony with the leaf-out of host trees. Population collapse is often attributed to natural enemies and occasionally to harsh winters (Dukes et al. 2009).

As with many other early season insect defoliators, synchrony between larval emergence and host plant budbreak is important for survival and growth. Optimal growth depends on access to young foliage. Larvae that emerge before budbreak starve. Those that emerge too late grow slowly, have reduced female fecundity, and longer larval stages (and consequently more exposure to various mortality agents).

Climate warming is already showing discernible effects on the occurrence of first leaf dates (Schwartz et al. 2006). However, many forest insects are quite capable of adjusting their egg hatch to the timing of leaf out despite substantial year-to-year variation in it. Given the large number of environments FTC has successfully dealt with as evidenced by its vast range, FTC is likely very adaptable in this regard. If leaf maturation is less responsive to temperature than insect development rate, larval FTC will be able to complete more of their development while feeding on nutritious immature foliage. Other things being equal, this would tend to increase the population growth potential of FTC and increase the severity, frequency, and duration of outbreaks.

In the aspen parkland of the prairie provinces, FTC damage combined with drought and extreme weather in spring have increased tree mortality and reduced growth to the point that, in some places, forest is being replaced altogether (Hogg et al. 2002). The occurrence of outbreaks at a higher frequency toward the warmer margins of the host range is also evident with some other defoliators and seems to be associated with drought (Volney and Fleming 2000). Together, defoliation and drought can cause the decline and ultimate extirpation of some stands at the southern margins of the host's range (Hogg et al. 2002). This is a generalization of the theme

developed earlier for the spruce budworm (Fleming and Volney, 1995) and applies to the other major defoliators that affect boreal forest tree species.

2.3.2.4.4 Invasives

Invasive forest insects are non-native insects that spread when introduced outside of their natural distribution and cause serious and often irreversible damage to forest ecosystems and forest industry. The increased movement of goods and people around the world has correspondingly increased the likelihood of introduction of invasive forest insects. For reasons discussed above, climate change will likely make it easier for many introduced insects to become established in Canada's forests.

However, there are too many uncertainties to pinpoint exactly which invasive species will become the most damaging at this stage because of climate change. Accordingly, number of invasive species are briefly described (CFIA 2009) with the idea that, as a group, invasive species should be included as a prime suspect. In some cases (e.g., Asian longhorned beetle), the immediate threat has declined and may be disappearing altogether. In other cases (e.g., emerald ash borer), the immediate threat is mounting but a paucity of relevant information precludes forecasting the insect's response to climate change. More detail is provided for the gypsy moth and hemlock woolly adelgid as examples for explaining some of the complexities involved in such forecasting.

2.3.2.4.4.1 *Asian Longhorned Beetle*

The Asian longhorned beetle (ALHB) is an invasive insect that attacks and kills a wide variety of deciduous tree species. This beetle was detected for the first time in Canada in September of 2003. The infestation occurred in an area along the municipal border between the cities of Vaughan and Toronto, Ontario. An eradication program was launched in November of 2003. In 2008, a broad scale survey was conducted. No signs or symptoms of ALHB were observed during these surveys. It seems that the immediate threat from this insect is subsiding.

2.3.2.4.4.2 *Emerald Ash Borer*

The emerald ash borer (EAB), is an introduced wood boring beetle which attacks and kills living ash trees. This exotic insect pest was positively identified for the first time in North America in the summer of 2002. This insect has been spreading in Ontario and was first reported in Québec in 2008. In 2008, surveys were conducted in the four Atlantic provinces but no signs or symptoms were observed.

This insect is considered a major threat to ash trees in central Canada and adjacent US states. A major research effort has been launched to develop better understanding of the insect's life history and population dynamics. However, there is not enough information yet to make well-founded forecasts about how EAB is likely to react to a changing climate (B. Lyons, Canadian Forest Service, pers. comm.).

2.3.2.4.4.3 *European Wood Wasp*

On July 5, 2005, the first established population of the European woodwasp in North America was reported in Fulton, New York. It has been spreading ever since. The European woodwasp feeds on many species of pine and is a serious pest of plantations in Australia, South America and South Africa. In Ontario, there were a number of positive finds in 2006 and 2007, but no adults were captured during the 2008 survey. In Québec, surveillance began in 2006 and the first case was not detected until two years later. No observations have been reported in the Atlantic provinces.

2.3.2.4.4.4 *North American Gypsy Moth*

The gypsy moth is native to the temperate forests of Europe and Asia where occasional outbreaks occur. A European strain of this insect was introduced accidentally to North America (Massachusetts) in 1869 and has since become established in much of the susceptible forest of northeastern North America: west to the Great Lakes region, north to south-western New Brunswick and south-western Nova Scotia, southern Québec and southern Ontario (and south to North Carolina).

In 2008, gypsy moth males were also captured in Newfoundland (2) and Prince Edward Island (501) and at two or more sites in all four of the western provinces. DNA analysis found no evidence that the Asian biotype has become established in Canada: all moths examined were of genotypes well known within the North American populations. The Asian strain is a greater threat because its female moths can fly and the larvae have a much broader host plant range, including conifer species, than does the European strain. Some years ago the Asian strain was detected in BC's lower mainland but it was reportedly exterminated in control programs.

Spread of the gypsy moth further north and west in Canada has so far been prevented by climatic barriers and host plant availability, as well as by aggressive eradication of incipient populations. Climate change is expected to increase the area of climatic suitability and result in greater overlap with susceptible forest types throughout Canada, especially in the west. At the same time, the gypsy moth is spreading west in the USA into states bordering western Canadian provinces. These circumstances all lead to a greatly increased risk of further invasion into Canadian forests by the gypsy moth (Regniere et al. 2009).

Given the broad host range of the gypsy moth, including abundant northern hardwoods such as birch, aspen and a variety of ornamental plants, defoliation is likely but the ecological and economic impacts are less predictable. On the one hand, the historical pattern in Ontario and elsewhere suggests that leading-edge populations can reach damaging levels quickly. On the other hand, the substantial mortality that often quickly follows a gypsy moth invasion could dampen those damaging effects.

2.3.2.4.4.5 *Brown Spruce Longhorned Beetle*

The brown spruce longhorn beetle (BSLB), an introduced wood boring pest, is native to north and central Europe and Japan, where it uses stressed and dying conifers as hosts, most notably

the Norway spruce. In 1999, the beetle was recognized in Halifax, Nova Scotia, and subsequent investigations confirmed that beetles collected there as early as 1990 were, in fact, BSLB. Studies conducted by the Canadian Forest Service since 1999 indicate that the wood-boring beetle is killing healthy spruce trees by feeding on the cambium and phloem and eventually girdling the tree.

In 2008, the detection survey for the BSLB resulted in 8 new positive locations in Nova Scotia outside of the current BSLB containment area, bringing the total to 26 sites. Extensive trapping was continued in Eastern Canada and again produced no evidence of spread to other provinces.

2.3.2.4.4.6 *Pine Shoot Beetle*

The pine shoot beetle (PSB) is native to Asia, northern Africa, and Europe. It was first found in North America in 1992 in Ohio, USA. A serious pest of pines, the beetle attacks new shoots, stunting the growth of the tree. The PSB is thought to have been introduced in solid wood packing material and has since been detected in the Great Lakes region of Canada and throughout the northeastern United States. Surveys suggest that the infested area expanded in 2008 in both Ontario and Québec. There were no captures elsewhere in Canada.

2.3.2.4.4.7 *Hemlock Woolly Adelgid*

The hemlock woolly adelgid (HWA) is an introduced, aphid-like insect native to India, Japan, Taiwan, and China. This insect is a destructive pest of susceptible species of hemlock. In 1919, HWA was first reported in North America in British Columbia and now attacks both western hemlock and mountain hemlock along the west coast of North America from Alaska to California. Damage on these two species is usually minor.

Hemlock woolly adelgid was first identified in eastern North America in Virginia in 1951. Since then it has spread rapidly and now ranges from Georgia to Maine. In the eastern US, HWA has killed both eastern hemlock and Carolina hemlock and now threatens the existence of these two species in many locations. In 2008, no signs of HWA were observed during visual surveys conducted in and around importing nurseries in New Brunswick (3 sites), Nova Scotia (8 sites), Québec (18 sites) and in Ontario (10 sites).

Several studies have shown that HWA survival is reduced at increasingly lower temperatures. Paradis et al. (2008) suggest that a mean winter temperature below -5°C is required to prevent HWA populations from spreading. Consequently, the most recent climate projections suggest that warming will expose hemlock across the Canadian border from Maine and New Hampshire which was previously protected by winter cold. In addition, recent evidence suggests that HWA may have the ability to develop even greater cold tolerance at the northern extent of its range (Butin et al. 2005). More important than relaxing range constraints, milder winters may lead to increased survival and fecundity, thus producing higher population densities and more rapid decline of infested hemlocks (Pontius et al. 2006). If warming occurs in the future as forecast for the winter months, HWA may spread unimpeded throughout the range of hemlock's distribution in eastern North America (Dukes et al. 2009).

2.3.2.4.5 Surprises

There will undoubtedly be surprises. Climate change is already causing some disruption to forest ecosystems (Gitay et al. 2001). This will likely allow populations of a few, currently relatively harmless insects to escape from their controlling factors, and grow to densities that threaten the products and services we derive from our forests. Such surprises will probably be relatively rare among native insect species which have become deeply embedded in their native forest ecosystems over the millennia. These insects are likely subject to multiple controlling factors so even if climate change disrupts a few of them, there are other factors to maintain control.

In contrast, simpler or simplified forest insect ecosystems where there are relatively few effective controlling factors are likely more prone to such surprises. Although it has always been a threat, the recent MPB outbreak provides a vivid example of how simplifying a forest ecosystem (by reducing its variability in tree species composition and age structure) made it vulnerable to outbreak. When warmer winters then disrupted the key remaining control on MPB population growth by reducing winter mortality from cold, an outbreak developed that was more catastrophic than any ever recorded before.

Simpler forest insect ecosystems would include those around insect species which were originally considered invasive when introduced but which have recently become controlled. These forest insect ecosystems are relatively young so it is unlikely that many different controlling factors have yet had time to develop effectiveness. Consequently, in these ecosystems, climate change need only disrupt one or two key controlling factors to allow the insect populations of concern to reach dangerous levels again. The satin moth and European spruce sawfly are both showing signs that they may be following this scenario (J. Volney, Canadian Forest Service, pers. comm.). The satin moth is native to Europe but in 1920 it was discovered on both coasts of North America. Native enemies and introduced parasites now effectively control this insect most of the time, but when the climate is favourable, it continues to spread, albeit episodically. The European spruce sawfly was found in North America in 1922 and through the 1930s was responsible for outbreaks in NB, ON, QC and adjacent US states. Two introduced parasites and an introduced virus have controlled the European spruce sawfly populations since the mid-1940s. However, this insect has recently extended its range into Manitoba, albeit at low population densities. Thus, climate change may be making it easier for the satin moth and the European spruce sawfly, both established and previously 'controlled' invasives, to expand their ranges by partially countering the effects of their controlling factors.

2.3.2.5 SO WHAT (Are Key Issues for Management to Consider in this Context)?

Traditionally, management of forest insect outbreaks has been viewed as one aspect of the larger problem of total forest management. This has involved federal and provincial forestry organizations, but the many goods and services produced by forests and the controversies surrounding forest insect management in the past have drawn in many other organizations with a variety of interests including aboriginal concerns, biodiversity, communities, economics, employment, environment, fisheries, forest industry, human health, land use change, parks, tourism, urbanization, and wildlife. The issue of climate change has focussed attention on yet another issue: the importance of the vast amount of carbon stored in Canada's forests (Cohen et

al. 2001). This has given Canada a stewardship role of global dimension to play on the international stage.

In this context, future insect management in Canada's forests during a changing climate faces two broad challenges (Fleming 2000). The first is how best to manage insect disturbance regimes in order to sustain the benefits currently gained from the forest resource in a future climate change environment (Montréal Process 2009). The second is how to manage insect disturbance regimes so as to maximize carbon storage within Canada's boreal forests and support the international agreements and obligations which will undoubtedly be coming, even if temporarily lacking at the moment (Cohen et al. 2001). Responses to these problems involve both preparatory activities which anticipate the future and the development of reactive capacity to deal with the unforeseen surprises that are certain to arise as the climate changes.

Some of the changes brought about by climate change will not be smooth transitions from one state of the forest insect ecosystem to another, but rather abrupt, unforeseen disruptions as the system passes over previously unrecognized 'tipping-points'. (MPB is certainly one example of this, JPBW is likely another). In such cases, it will be advantageous to have any renewable resource system designed with as much 'resilience' already embedded in it as possible before the threshold or 'tipping-point' is passed. Because of the primitive state of our ability to predict with any precision how insect disturbance regimes will respond to climate change, it is premature to make specific recommendations for a suite of management actions. Consequently, only the general concepts behind some proposed management approaches are commented on below.

2.3.2.5.1 Insect Management for Sustainable Forest Benefits

Climate change will likely alter the patterns of damage caused by many insects and the resulting uncertainties directly affect a number of aspects of forest insect management. As the frequency and duration of outbreaks changes in response to climate change, it will become increasingly difficult to forecast where, and when, and how great the depletions will be. This will make current pest hazard rating procedures dated and reduce the predictability in long-term planning for harvest queues and insect control.

Under these circumstances of increased uncertainty, it becomes increasingly important to design renewable resource systems which are resilient to unexpected perturbations and surprises. For instance, direct control through larvicide application has protected high value stands from defoliators in the past, but this strategy does little to alter the stand conditions under which outbreaks develop and the adoption of this strategy is subject to much political uncertainty. Silvicultural methods provide a possible alternative approach (Volney and Hirsch 2005), although it remains to be seen whether they are feasible at acceptable scales and at acceptable costs. The goal is to modify stand structure through thinning with different retention levels and cutting patterns such that conditions within stands become less conducive to outbreaks. For instance, such modifications might increase the impact of the natural enemies of the pest by changing the understory vegetation in their favour so that they would increase their presence in the stand, and consequently, their attacks on the pest population. An additional benefit is that such modification would reduce intra-specific competition within treated stands. The dynamics of the insect population can also be altered through changes in mortality rates and dispersal in

these new stand environments. Population densities five years post-treatment in one such experiment (Volney and Hirsch 2005) now seem to be showing positive results.

In a changed climate, a few of what were once innocuous forest insects may thrive and suddenly become major disturbance agents. Potential examples include the satin moth and the European spruce sawfly). Similarly, there is no guarantee that all of today's major insect herbivores will remain important in the new environment. In addition, insects play a fundamental role in sustaining forest ecosystems (Volney and Hirsch 2005) and some of these species may be threatened by climate change (Harrington et al. 2001). It may be difficult to distinguish the relatively permanent changes in population density that such scenarios imply from the long population cycles exhibited by some insect species (e.g., SBW: 30-35 yrs) until long after the fact (Fleming and Candau 1998), and this complicates the management of forests for ecological values (e.g., biodiversity) and services (e.g., fresh water).

Changes in disturbance regimes which re-route successional pathways and produce rapid changes in forest landscapes are likely to disrupt certain wildlife species and aboriginal peoples following traditional lifestyles. Such changes may also lead to large unanticipated releases of carbon, especially in the less intensively managed areas of Canada's forests.

The emergence of new insect disturbance regimes also introduces additional difficulties in forecasting future requirements for insect control products. Since such products typically take years to develop and are becoming increasingly target-specific to meet environmental requirements. As in the past, if the demand from forestry becomes unreliable, some companies may become discouraged altogether and shift their research on forest insect control products into areas with a more certain future demand such as agriculture. At the same time, demands for insect outbreak suppression may grow.

2.3.2.5.2 Interactions with Other Disturbance Types

Interactions between different types of disturbance are probably the rule rather than an exception. This is an important consideration for management: it implies that management actions taken to deal with one type of disturbance will indirectly affect other types of disturbance. Since these indirect effects can sometimes work against management goals, and in a very big way (witness the contribution of fire suppression to the current MPB outbreak), it behoves management to be cognizant and wary of such interactions.

Insect disturbances interact with most other disturbance types including logging, extreme weather (e.g., drought, storm effects), and forest diseases (Fleming 2000). Diseases caused by root rots such as *Armillaria spp.* and *Tomentosus (Inonotus tomentosus)* are chronic problems in older stands of both conifers and hardwoods in the boreal forest. These diseases do not cause extensive damage but kill individual trees, or pockets of trees, and cause gaps in the canopy. Such diseases are often most active after prolonged insect defoliation or drought has weakened the trees (Mallet and Volney 1990). In other cases (e.g., hypoxylon canker [*Entoleuca mammata*] of aspen), insect vectors are crucial to the dispersal of the pathogen.

Extreme weather strikes Canada's forests in a variety of forms including drought, wind-storms, ice-storms, lightning, floods, and heavy snowfall culminating in avalanches. The resulting damage often leaves stressed and injured trees which offer little resistance to opportunistic insects. For instance, drought stress is directly harmful to forest vegetation but more often acts in concert with secondary organisms to cause tree mortality. Drought conditions can also increase the level of stress to which defoliated trees are subjected during insect outbreaks and can result in higher than normal tree mortality (FTC is one example). JPBW and SBW are other examples (Volney and Fleming 2007). While drought does not directly predispose jack pine to insect defoliation, drought conditions stimulate flowering on jack pine and this, in turn, increases the survival of jack pine budworm, and hence the likelihood of damage during an outbreak. There is also evidence suggesting that spruce budworm reproduction and survival increase directly as a result of the warmer and drier conditions of drought. Indirect effects are also important for the spruce budworm. At high temperatures the vulnerable larval stages can escape many natural enemies because (a) the larvae develop faster than at normal temperatures and thus reduce the duration of their exposure, and (b) they develop more quickly at high temperatures than do many of their natural enemies.

Wind-throw, caused by strong surface winds which can uproot extensive areas of forest, is a common feature of Canada's forests and plays an important role in determining their structure. It is frequently reported that wind-thrown trees provide bark beetles with a staging ground from which to mount attacks on neighbouring healthy trees. Ice-storms, late spring frosts, and floods are other kinds of extreme weather which can affect successional pathways in the Canada's forests or affect the progression of forest insect outbreaks.

Since insect defoliation and fire are the major disturbances that affect the succession of northern forests, some interaction can be expected. In Ontario's boreal forests, after severe crown fires, post-fire stands can be dominated by birch due to the ability of that tree species to colonize extensive areas by wind-disseminated seed. Where extensive crown fires have not occurred, shade tolerant species, such as balsam fir and white spruce are likely to dominate, creating a forest composed largely of tree species susceptible to spruce budworm. Where fire does not occur after a SBW outbreak, the tree mortality resulting directly from SBW or secondary insects and disease-causing tree pathogens (beetles, root rots) produces gaps in the canopy. Deciduous (non-host) species such as birch and aspen, which require ample light, rarely establish in the smaller openings. Instead, the shade tolerant host species of the SBW, balsam fir and white spruce, eventually occupy the gaps and thus maintain a forest susceptible to spruce budworm.

Often, SBW defoliation does not result in stand-replacing tree mortality. Rather, the nature of the damage to the stand increases fuel loads and their vertical continuity so that it becomes easier for a surface fire to climb into the canopy. Once in the canopy, the fire has the potential of becoming much more intense and spreading very quickly as a continuous crown fire. The time over which the elevated probability of a dangerous crown fire persists depends on local moisture regimes because they affect the rate of decay of the fuel load.

A recent study in Ontario found that fires were disproportionately more likely to occur three to nine years after an outbreak than at any other time in SBW damaged stands. In the western areas

of Ontario, fires occurred more often after SBW outbreak and longer periods of susceptibility to fire were evident than in the eastern part of the province.

These regional differences in the elevated fire risks in budworm-damaged stands that are associated with different moisture regimes give us an estimate of the changes that might be expected with future climate regimes. For instance, the drier warmer climate scenarios projected for the west could result in more fire activity and more damage (social, economic, and even environmental). On the other hand, in eastern Canada where mild cooling and precipitation increases are forecast, fire frequency is consequently expected to decrease. This will allow the coniferous forests there, which support the more extensive insect outbreaks, to survive into the particularly susceptible older age-classes. Under these circumstances, aggressive silvicultural regimes such as those mentioned above, might pre-empt the losses caused by insects (Volney and Hirsch 2005). Careful application of this approach to produce a spatial arrangement of age-class cohorts over the landscape (Harvey et al. 2003) would likely help reduce losses when the next inevitable insect, or other type of, disturbance arrives, perhaps brought on by climate change.

Other disturbance-causing insects such as JPBW and MPB also interact with wildfire. For instance, improved fire control in the prairie provinces reportedly allows more jack pine stands to reach the older ages at which they are most susceptible to JPBW. This helps explain the increased extent of JPBW outbreaks over time in recent years. The jack pine killed by JPBW in defoliated stands leave gaps in the canopy that expose the forest floor and its litter layer to increased direct sunlight and air circulation. The consequent drying may promote ground fires which provide the heat required for the cones of jack pine to open. As a result, jack pine seed is deposited on an exposed mineral bed while competing tree species (which are less tolerant of ground fire) are simultaneously burnt back. Under these circumstances, jack pine successfully regenerates and retains its dominance on the site (Volney and Hirsch 2005).

Overall, this interaction between insect disturbances and fire points to a significant positive feedback that might be working to further drive climate warming (Volney and Hirsch 2005, Fleming 2000, Kurz et al. 2008). With the increased release of carbon to the atmosphere from outbreaks and elevated fire activity, comes an increase in the global concentration of atmospheric carbon dioxide. The vastness of Canada's forests may give these processes the potential of affecting the atmospheric carbon balance, with the consequence of an even higher risk of outbreaks and fires. In Canada's forests, the net effect would be to reduce the area and distribution of old-growth stands, convert the forested landscape to earlier successional stages, and allow the grassland/forest border to move farther north.

2.3.2.5.3 Carbon Storage

Suppression of insect outbreaks is occasionally considered as one way to combat the tendency of insect disturbance regimes to limit the carbon sequestration capacity of Canada's boreal forests. The vast spatial scales involved, however, make broad-scale suppression prohibitively expensive and environmentally controversial using current conventional insecticides.

Using insecticides to protect old growth stands, which store a disproportionate amount of carbon, or areas which have recently been afforested (or reforested) to sequester carbon, has also been suggested. This approach must demonstrate durability of benefit. For instance, there is little gain in protecting an overmature old growth stand from insect attack only to see it blown down the following year by heavy winds. Nor is there any point in protecting a recently afforested or reforested area if the net greenhouse effect of all gases released in producing, transporting, and applying the insecticide exceeds the net greenhouse effect of the additional sequestration gained through protection.

Protection may also be feasible in conjunction with harvesting. Where harvest rotation lengths exceed the length of the natural disturbance cycle, whether the agent be fire or insect, carbon storage is enhanced by suppressing the disturbances and letting the forest reach the older ages at which it is harvested (Price et al. 1997). Ideally, the economic gains of the harvest alone would justify the expense of protection. A possible additional benefit is that some wood products have very long life-spans and thus further slow the release of carbon back to the atmosphere.

The encouragement of suitably pre-adapted non-host tree species in some selected areas is another option. This may involve aerial seeding or other means of planting on a large scale. Genetic improvement of the stock may also be cost-effective. An unresolved issue is the trade-off implicit in any approach, be it large-scale planting or protection from insects and fire, which uses fossil fuels. Any short-term increase in the sequestration of atmospheric carbon by the forest comes at a cost of additional carbon imported into the modern biospheric system for the long term.

In summary, insect population suppression is potentially useful for particular species in select areas under certain circumstances to protect stored carbon. The vast scales at which some insect disturbance regimes operate, however, are liable to overwhelm any efforts to manage or alter their course.

2.3.2.6 Research Directions

A number of key information gaps also limit confidence in forecasts of how insect disturbance regimes in particular will respond to climatic change in Canada's forests, and what the consequences of this response will be (Fleming 2000, Volney and Hirsch 2005). These include the effect of insect outbreaks in a climate change environment on: (a) other disturbance regimes (i.e., those involving different insects or altogether different agents, such as fire), and the reciprocal effects, (b) post-disturbance successional pathways and tree growth and carbon sequestration rates, (c) the rates of net forest decomposition, respiration, and carbon transfer among the soil carbon pools. An ongoing challenge will be to scale-up the innumerable effects of increased CO₂ and temperature on the physiology and ecology of individual insects at various stages of their lifecycle, first to the level of insect population dynamics, and then beyond that to the even larger scales of disturbance regimes.

The ability of forest insects to adjust their life history traits quickly in response to a change in climate needs more attention. Genetic changes driven by quantitative selection on populations can affect the structure and diversity of local species assemblages within roughly 7-70

generations. Where hybridization is involved, e.g. among different budworms, substantial change can occur within a generation (Volney and Fleming 2007). Since many insects can go through seven or more generations a year (and this will probably increase for some insects in a warmer climate), it is clear that forest insects can adapt genetically to a change in climate much more quickly than their host trees. In addition, the great mobility of many insects allows them to move away from an unfavourable climate, although they will need to find suitable host trees in their new environment. Specific evidence has been provided above of avenues by which natural selection could play a role in the adaptation of MPB, SBW, and gypsy moth in the near future.

Natural selection could also have important, although indirect effects on forest insect disturbance regimes. For instance, a complex of disease organisms drive the spruce budworm's outbreak cycle. Since many insect pathogens can have many generations each year, they are subject to the forces of natural selection on short time scales. Hence, through changes to the natural enemy complex, natural selection could bring about changes to the budworm's outbreak cycle and disturbance regime.

Finally, the poor resolution of global climate models and the uncertainties inherent in their performance at regional scales present a major difficulty to acquiring suitable scenarios of how future climates will develop. These scenarios will provide the climate input data for the models used to forecast future insect and other disturbance regimes. Because the models will probably be quite sensitive to variations in these scenarios (for reasons discussed above), it is important to improve the realism of these scenarios.

2.3.3 Tree Diseases

Kliejunas et al. (2009) recently published a comprehensive review of climate change and forest diseases in western North America. The reader is strongly encouraged to consult this volume for detailed discussions of forest diseases and climate change in this region. Here we summarize the main points of their review.

There is large uncertainty concerning how forest pathogens will respond to climate change. In general, the factors affecting forest pathogens and their relationship to climate change include: 1) disease type, 2) host specificity, 3) pathogen aggressiveness, 4) host importance, 5) functional uniqueness of host, and 6) phytosociology of host (i.e. competitive interactions with co-occurring species).

Several general conclusions emerged from the review by Kliejunas et al. (2009):

- In a rapidly changing environment, host resistance to pathogens may be overcome more rapidly due to accelerated pathogen evolution.
- Interactions between biotic and abiotic (e.g. drought stress) diseases may represent the most important effects of climate change on plant diseases.
- When combined with climate change, trends in increasing invasions by non-native pathogens mean that new epidemics may occur.

- Greater overwintering success of pathogens will likely increase disease severity. Because temperatures are expected to increase more in winter than in other seasons, this population bottleneck may be removed for many pathogens.

Most plant pathogens are strongly influenced by environmental conditions and the condition of the host. Climate change will directly affect the pathogen, the host, and the interaction between them (see Figure 1 above). Global climate change is ultimately expressed at the microclimatic scale which controls the reproduction, dispersal, and infection by many fungal pathogens. Host condition is also affected by temperature, moisture, and by variations in their cycles and extremes; pathogens may then take advantage of either increased host susceptibility or availability. In addition to demographic and epidemiological interactions, hosts and pathogens also respond genetically with consequences on community structure and ecosystem function.

The following summarizes the expected implications of climate change for several disease types of importance in western North America.

Abiotic Diseases: Drought-stressed trees experience greater damage by pathogens, as shown in the recent prairie-wide drought in 2001-2003 (Hogg et al. 2008). A general conclusion is that interactions between biotic and abiotic (e.g. moisture stress) diseases may represent the most important effects of climate change on plant diseases.

Declines: Forest declines are predicted to increase as stands become less adapted to prevailing conditions; see section above on maladaptation.

Canker Diseases: Very few stem canker and dieback pathogens attack vigorous trees. Climate change will result in more water/drought-stressed trees and, therefore, more outbreaks or disease epidemics will be associated with canker pathogens.

Root Diseases: Hot and dry conditions (e.g., prolonged drought) are expected to increase incidence and spread of root diseases in forests. However, it is difficult to specifically predict how climate change will affect diverse root diseases under various projected climate scenarios.

Phytophthoras: Recent climate change modeling efforts in Europe indicate that increases in winter temperatures of 0.5 to 1.5°C allow for increased survival of *Phytophthora cinnamomi* propagules, resulting in increased impacts from *P. cinnamomi*. Future climate scenarios for Canada generally project greater warming in winter (Lemmen et al. 2008) so that results similar to those found in Europe may also occur here.

Foliar Diseases: The majority of foliar diseases are likely to benefit from climate change as a result of their increased activity in the spring and summer where warmer temperatures and increased moisture are expected and reduced winter mortality allows populations to increase.

Rusts: Although spread and intensification of many rust fungi are favoured within narrow limits of high moisture and cool temperature, their complex life cycle provides a long-term survival strategy for years with favourable conditions and for adaptation to a rapidly changing environment.

Mistletoes: The genus of mistletoes common to the western region (dwarf mistletoe *Arceuthobium* spp.) can infect otherwise healthy host trees. When severe, infection can induce stress and predispose hosts to serious damage in combination with other biotic agents and drought. Mistletoe reproduction is often limited by cold temperatures, so warming could allow for geographic range expansion. For example, Brandt et al. (2004) found that temperatures below -38 °C prevented germination of *Arceuthobium americanum* seeds. Johnston et al. (2008) have shown that near Prince Albert SK, a region heavily infested with dwarf mistletoe, the frequency of days with minimum temperatures of less than -38 °C have declined substantially since the 1960s.

Wood Decays: Decay of wood in both living trees and ‘dead’ trees is intimately dependent on moisture and temperature regimes and thus could be heavily impacted by future climate change.

Kliejunas et al. (2009) provide the following general conclusions:

- Climate change will alter forest ecosystems primarily by its affect on the frequency, intensity, duration and timing of disturbance factors, including fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. Although significant as stress factors, pathogens will probably play a lesser role than other disturbances such as fire and drought in some ecosystems. However, agents such as pathogens may ultimately have a greater impact—by causing selective mortality of susceptible hosts—on forest ecosystems than the initial stress or disturbance.
- Disease risk assessment developed previously for invasive and emergent diseases can provide a framework for organizing and presenting information on forest disease–climate change interactions. Components include assessments for environmental suitability, dispersal potential, and impacts/effects. Comprehensive assessment depends on an adequately supported and responsive infrastructure that includes research, stakeholders, and decision-makers at various agencies and levels.
- The most likely impact of climate change on forest pathogens will be felt in three areas: in losses from plant diseases, in the geographical distribution of plant diseases, and in the efficacy of disease management strategies. Climate change could have positive, negative, or no impact on individual plant diseases. Changes will occur in the type, amount and relative importance of pathogens and diseases. Currently, insufficient information is available to quantify these effects.

More research is needed to obtain fundamental understanding on different disease systems and supporting various potential mitigations. The research agenda should include for hosts and pathogens: 1) estimation and monitoring of distributions, 2) biogeographical and hazard modeling, 3) community interactions and ecosystem reactions, 4) dispersal, and 5) genetic diversity.

Climate change may cause a surpassing of an environmental threshold, resulting in irreversible changes to ecosystems. Ecosystems may be able to withstand individual stresses, but multiple stresses occurring together could seriously impact forest health and sustainability. Forests on

marginal sites may deteriorate if climatic change makes conditions less conducive to host survival.

Plant pathologists have a critical role in providing input to other disciplines and various publics on the effects of climate change on forest ecosystems. Pathologists are uniquely trained to understand host–pathogen–environment interactions as integrated systems. They need to actively provide information on, and the importance of, those interactions to other disciplines working on effects of predicted climate change and how to deal with them.

Modeling efforts would benefit from active networking among multiple disciplines working across scales from genomes to ecosystems. Pathologists need to especially work with modellers, to provide information on the interactions of various disturbance factors in forest ecosystem dynamics, to help insure that these factors are incorporated into models. Although the complexity of host–pathogen interactions with climate change may be difficult to model, pathologists need to provide information so the synergistic impacts of climate change and other environmental stresses are considered in models.

Managers and policymakers will need input and guidance from pathologists, in the form of viable management alternatives, in order to guide decisions on management as expected climate change occurs. Because managing climate change and forest ecosystems are complex problems, multiple conceptual approaches and rational policies are required. Pathologists can begin now to formulate ways for adapting to climate change and forest disturbance by maintaining forest ecosystem diversity and resilience.

The review by Kliejunas et al. (2009) applies to forests of western North America. Several recent reviews have been also been published dealing with eastern North America. In this section we have extracted the main points from reports by Boland et al. (2003) for Ontario and Dukes et al. (2009) for the eastern US and Canada.

As in western North America, the expectation for Ontario is that the interactions that occur between biotic and abiotic diseases may represent the most important effects of climate change on plant diseases (Boland et al. 2003). Interactions of biotic and abiotic factors can cause susceptible species to deteriorate gradually, often resulting in plant death. Such diseases are referred to as decline diseases and primarily affect forest tree species but can also affect other perennial woody species in agriculture and horticulture.

Boland et al. suggest that management of plant diseases will be affected by anticipated changes in climate. The research priorities of plant breeding programs may have to adapt to increased duration of growing seasons and to focus on developing drought and stress tolerance in crops and commercial forest species. Some drought-prone areas used for commercial agriculture and forestry may have to be abandoned. Changes in climate may allow new species and cultivars to be introduced and grown in Ontario, but effective systems must be in place to prevent new pathogens from accompanying these new crops. Due to the long-lived nature of trees, forests are slow to adapt, and forest management plans will need to consider the impacts of climate change and how forest management can reduce the vulnerability of forest stands, e.g. through removing susceptible trees and managing stand density to reduce conditions likely to encourage disease.

Table 6 summarizes the relationship between climate change and the main tree diseases in Ontario. In general, factors encouraging diseases are warmer, drier conditions, increased overwintering of inoculum, trees under stress from drought or other factors, and increased survival of insect vectors. In a few cases (blister rust, scleroderris canker, larch canker, conifer-aspen rust), warmer and drier conditions discourage development of the disease.

Dukes et al. (2009) provide a review of insect pests and diseases and their response to climate change in eastern North America, with an emphasis on how basic ecological principles can be used to predict pest species response to climate change. In addition to listing a wide variety of current diseases of north-eastern forests, they highlight the same concern as Klienjunas et al. (2009), i.e. the difficulty of predicting how pathogens will respond to climate change. Dukes et al. suggest that the direct effects of climate change on pathogens are: increased growth and reproduction, altered propagule dissemination and transmission rates and changes in overwinter survival. Indirect effects include host nutrient status, distribution and life history of insect or other vectors, the distribution of alternate hosts, maladaptation of host species and the creation of novel community assemblages. They also stress the importance of multiple interacting factors in determining susceptibility to pathogens. For example, rust fungi may be encouraged by more intense precipitation events which create moist foliar surfaces for establishment and are also encouraged by higher humidity. Mechanical damage from lightning or windthrow can provide entry points for disease organisms.

Table 6. Tree diseases in Ontario and estimated effect of climate change. For Pathogen Group: F = fungus; N = nematode; PL = parasitic plant. Note that oak wilt does not yet occur in Ontario but may easily spread from wide-spread locations in the US. Modified from Boland et al. 2003.

Tree/Disease	Pathogen (Group)	Estimated effect for the disease (+/-)
Pine		
Armillaria (affects all tree species)	<i>Armillaria</i> spp (F)	+
Blister rust	<i>Cronartium ribicola</i> (F)	-
Blue stain	<i>Ophiostoma</i> spp (F)	+
Diplodia tip blight	<i>Sphaeropsis sapinea</i> (F)	+
Fomes root rot	<i>Heterobasidium annosum</i> (F)	++
Scleroderris canker	<i>Gremmeniella abietina</i> (F)	-
Pine wood nematode	<i>Bursaphelenchus xylophilus</i> (N)	+
Dwarf mistletoe	<i>Arceothobium americanum</i> (PL)	+
Spruce		
Tomentosus root rot	<i>Inonotus tomentosus</i> (F)	+
Larch		
Larch canker	<i>Lachnellula willkommii</i> (F)	-
Poplar		
conifer-aspen rust	<i>Melampsora medusae</i> (F)	-
hypoxylon canker	<i>Entoleuca mammata</i> (F)	+
Oak		
Oak wilt	<i>Ceratocystus fagacearum</i> (F)	+
Beech		
Beech bark	<i>Nectria coccinea</i> (F)	+
Elm		
Dutch elm disease	<i>Ophiostoma ulmi</i> (F)	+
Forest Declines		
Ash		++
Maple		++
Oak		++

3.0 MANAGEMENT OPTIONS FOR ADAPTATION

The preceding sections describe the main sources of vulnerability for Canadian tree species. This section provides some preliminary suggestions for forest management options that may enhance the ability of the forest sector to adapt to the species-level impacts of climate change. In the following we present a general approach to adaptation planning. We then address assisted migration and related policy issues in some detail, as there has been more research in this area than most others with respect to species-level analyses of climate change impacts and adaptation. We also discuss silvicultural options that may confer adaptive capacity, and other suggestions that are still in the realm of untested ideas. It must be kept in mind that the scientific understanding required to implement these options varies considerably among tree species and regions. For example, there have been extensive analyses of lodgepole pine provenance data in BC which might allow some degree of assisted migration to occur now. For the most part this level of understanding is absent for other species and areas of the country.

Woods (2009) provides a conceptual model that links climate change impacts, forest stand growth, and economic benefits of timber harvest (Figure 4).

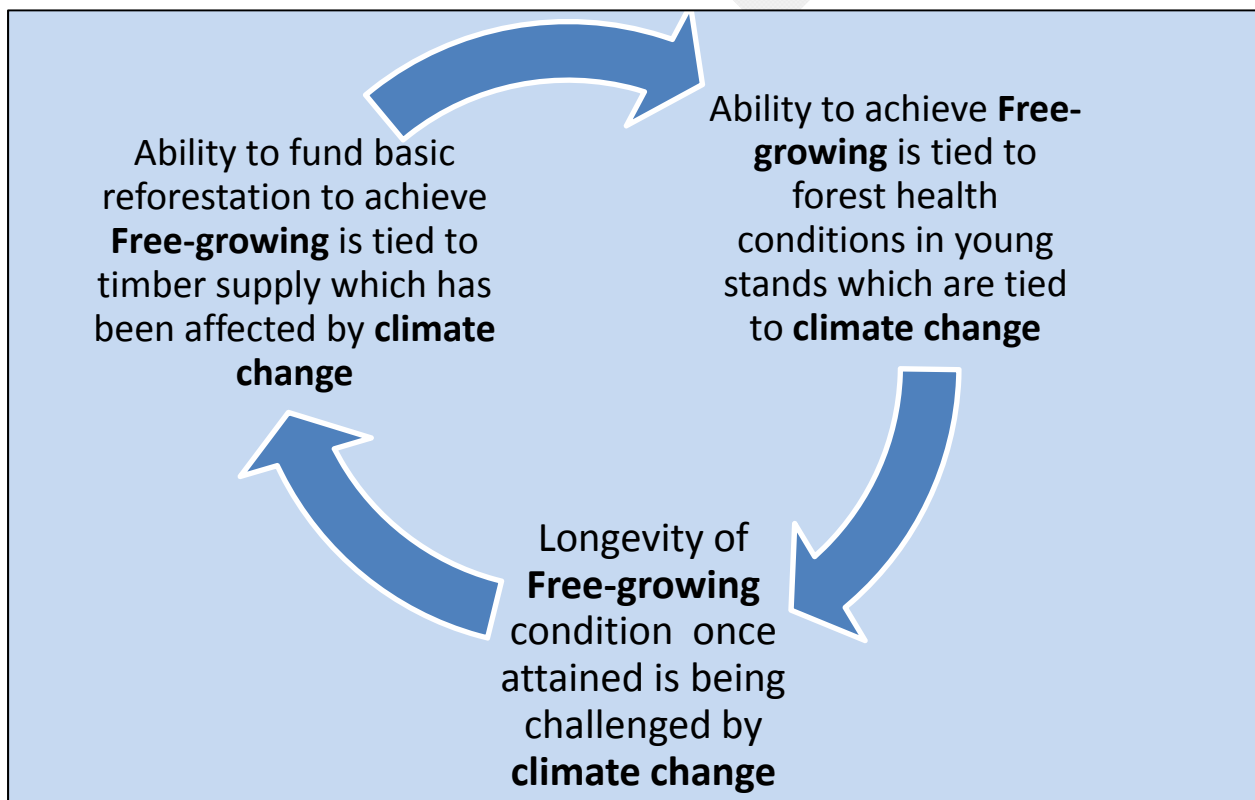


Figure 4. Conceptual linkages among climate change and free-growing standards, stand growth and economic benefits from timber harvest (from Woods 2009).

Starting at the bottom of Figure 4, the final harvest volume (and hence revenues) are a function of how climate change (and other factors) have affected growth through the rotation. Revenues, in turn are re-invested in reforestation. Regeneration can be significantly affected by climate

change and the likelihood of it reaching free-growing. In early stand development the ability to reach free-growing is affected by climate change, which in turn will determine the future development of the stand and the final volume at harvest. This will again determine revenues available for reforestation, etc. In this way it is clear that climate change affects not only the stand throughout its rotation but also in the longer term as it determines management options and economic benefits, part of which will fund good forest management and silviculture.

3.1 Adaptation Planning

In Figure 5 we provide a general approach to planning adaptation actions. We begin with the assumption that the overriding goal of forest management is to achieve Sustainable Forest Management as defined by the CCFM Criteria and Indicators of Sustainable Forest Management (Canadian Council of Forest Ministers 2003). The process begins by carrying out a vulnerability assessment with respect to the SFM objectives as described in Section 1. If adaptation is determined to be necessary (highly likely under future climate scenarios), adaptation options, strategies or portfolios are identified and implemented. Monitoring is carried out to determine the success of the adaptation actions, in which the primary question is whether the adaptation increase the ability to deliver SFM under climate change. The results of implementing the adaptation options are screened with respect to the SFM Criteria and Indicators as defined by the CCFM (Canadian Council of Forest Ministers 2003).

If SFM is achieved by implementing the adaptation options, monitoring and feedback is continued. If not, two choices are available. If the policy or technical options are available, adaptation can be expanded or modified and the implementation step repeated. If adaptation options are limited, or if adaptation is not sufficient to cope with extreme climate impacts, the SFM objectives may have to be modified so that realistic outcomes are possible.

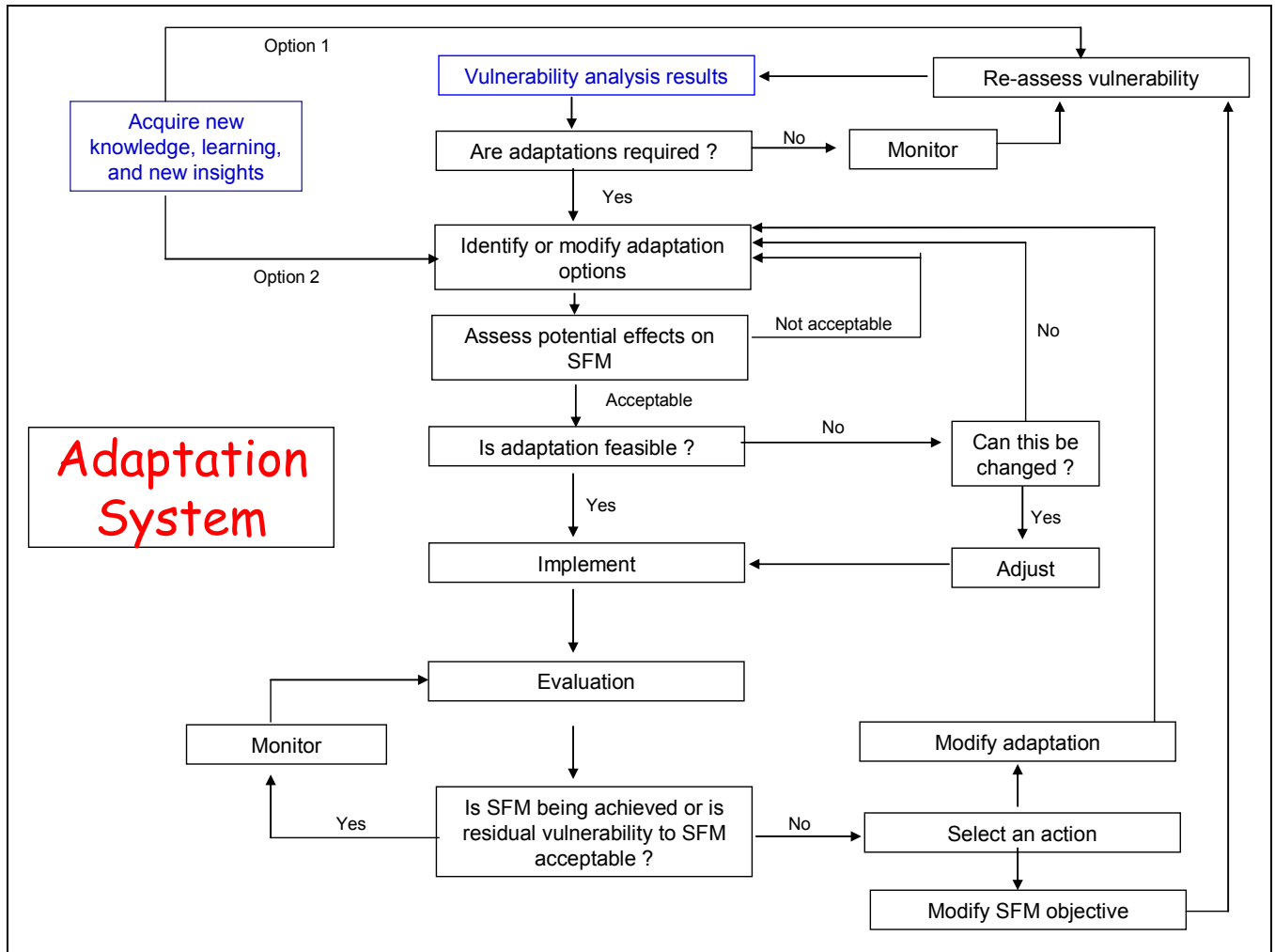


Figure 5. An approach to climate change adaptation planning in the context of Sustainable Forest Management.

3.2 Assisted Migration

The inability of migration or adaptation to occur rapidly enough in response to climate change was described previously. This suggests that some form of assisted migration will be required in order for species to continue to grow under conditions to which they are adapted. The key question for assisted migration is: which is the best population to establish in each planting site in order to anticipate the changing climate? Analysis of provenance test data is beginning to provide an answer for some species.

Provenance tests are based on planting seed from a variety of populations (provenances) at a number of test sites that sample the range of conditions across a species' geographic distribution. Most or all provenances are planted at all test sites to assess the performance of each provenance under a range of climatic conditions. Observations from provenance tests in the past several decades have shown that variation is often large and often associated with adaptation to cold and drought, e.g., growth phenology, cold hardiness, winter desiccation (Rehfeldt et al. 1999). Provenances moved northward are often damaged by cold while provenances moved southward often grow slower than local provenances because they are adapted to lower temperatures and a shorter growing season or they are damaged by insects or disease (Rehfeldt et al. 2001).

One of the largest provenance tests in the world is the Illingworth provenance test for lodgepole pine undertaken by the BC Ministry of Forests and Range. In this trial, 140 provenances were planted at 62 sites across BC. The provenances ranged from southern California (34°N latitude) to central Yukon (64°N latitude). The test sites are located in interior BC and at two sites in the Yukon, encompassing 12 degrees of latitude, 21 degrees of longitude and 1220 m of elevation (O'Neill et al. 2007).

Data from provenance tests can be used in several ways. **Transfer functions** relate the growth of provenances to geographical or climatic distance they were transferred to at the test site. Impacts resulting from climate change are interpreted as the productivity difference between a local provenance (i.e. zero transfer distance) and the transferred provenances. Alternatively, **growth response functions** characterize growth of an individual provenance as a function of the climate across the range of test sites in which it was grown. More recently, an approach called the **Universal Transfer Function** has been developed in which both ecological factors (the test site climate) and genetic factors (population adaptation) are combined (O'Neill et al. 2008b). This allows forest productivity in current and future climates to be predicted for any provenance in any location as a function of the regional climate at the planning site and the climate of the provenance.

These approaches have been applied to a range of species across the country including lodgepole pine in BC; white spruce, black spruce and tamarack in Alberta; and jack pine and white spruce in Québec and Ontario (see Table 7 for a more complete list). This work provides some indication of how species will respond to climate in the future at a range of locations and will provide a guide for redefining seed transfer guidelines in terms of climatic factors for both current and future conditions. However, it must be kept in mind that for the most part these provenance tests were established several decades ago to identify sources of superior germplasm; consequently, the range of provenance or test site climates sampled in older provenance tests is

often insufficient to develop reliable transfer or response functions. In addition, there is still a dearth of information available for the majority of Canada's commercial tree species. As a result, these data have a number of limitations (Rehfeldt et al. 2001, Aitken et al. 2008):

- No ability to test enriched CO₂ effects: in addition to changes in climate, the future will bring higher concentrations of atmospheric CO₂. This has been shown experimentally to be important in determining tree growth rates and other ecological processes but is not addressed in provenance tests.
- Lack of extreme test sites: most of the existing provenance tests were not designed to sample the complete range of climatic conditions under which a species might grow. If future climate brings relatively extreme conditions, current provenance test data do not represent these conditions.
- Lack of populations from across species range: many tests only include data from populations in the central portion of the species range. If species may migrate north, data representing these outlying populations could be important but are not represented.
- Bypassing important early stages of selection in seed germination and seedling establishment: most provenance tests are established in nursery-type environments where seedlings are raised in artificial conditions and do not experience selection processes related to soils and topography, insects, diseases and intra- and interspecific competition that would occur in a wild stand environment.
- Establishing new provenance tests is expensive and will take at least a few decades to bear useful results.

Even in cases where provenance test data are adequate, there is a more general concern related to the length of a tree's life span. Managers wishing to undertake assisted migration will be faced with a trade-off: the climate distance that populations or species are migrated will have to be small enough to allow for good survival at establishment, but large enough to ensure good adaptation toward the end of the rotation when mean annual increment is maximum. O'Neill et al. (2008a) suggest that to account for future climate change, planting populations best adapted to the climate expected at a site at 1/3 of the rotation (i.e., approximately 0.5 °C warmer than present) will achieve the best balance of tree volume growth and survival. This is because tree volume growth is greatest among populations adapted to end-of-rotation climates when mean annual volume increment is greatest, and survival is highest in populations adapted to early rotation climates when trees are most sensitive to stress.

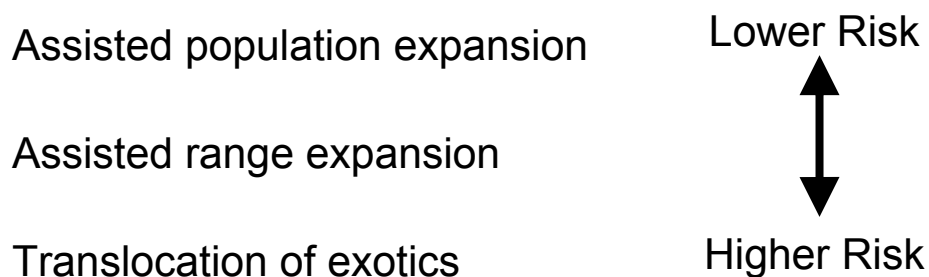
In addition, assuming that populations were locally adapted to climates in the last 3-10 tree generations, and that migration and adaptation have been negligible during recent climate change (i.e., in the last 100 years), it will be necessary to further migrate populations to account for recent climate change. In BC, this distance is estimated at 1.0 to 1.6 °C mean annual temperature (O'Neill et al. 2008a). Therefore, total migration distances of 1.5 to 2.1 °C are recommended for BC, and comparable distances could be expected for the rest of Canada.

Other concerns include the effects on biodiversity if exotic species are included in assisted migration, and the fact that large uncertainties exist concerning the extent and pace of climate change and the interactions between climatic change and the influence of local site conditions.

Table 7. Summary of main Canadian literature on species and transfer functions

Species	Reference
Lodgepole pine	Rehfeldt et al. 1999, 2001, (Wang et al. 2006), (Monserud et al. 2008), (O'Neill et al. 2007, O'Neill et al. 2008b), (Rweyongeza et al. 2007a)
White spruce	(Li et al. 1997), (Andalo et al. 2005), (Beaulieu and Rainville 2005), (Rweyongeza et al. 2007b)
Black spruce	(Beaulieu et al. 2004), (Thomson et al. 2009)
Jack pine	(Savva et al. 2007), (Thomson and Parker 2008), (Rweyongeza et al. 2007a)
Douglas-fir	St Clair and Howe 2007, (Flower and Murdock 2009)
Western larch	(Rehfeldt and Jaquish 2010)

Aitken² has suggested that there are three types of assisted migration, each associated with a different level of risk, where risk refers to the likelihood of species becoming invasive or being planted in a non-suitable location. Assisted population expansion refers to moving populations within the current species range to improve productivity and health as the climate changes. Since species remain within or close to their historic ranges, risk is considered to be low. For example, St. Clair and Howe (2007) recommend assisted population expansion for Douglas-fir in the Pacific Northwest US.



Assisted range expansion involves expansion of northern, inland or elevation limits of a species for reforestation. This involves moving populations to locations near the current species' distribution and where the climate in the near future is expected to be suitable for growth of the species. Provenance data are less helpful in this option because they do not generally include plantings outside of species historical ranges. In this case other species will already be

² Dr. Sally N. Aitken, Department of Forest Sciences, University of British Columbia, personal communication, July 2009.

established in the new location and will compete to some extent with the introduced populations (Rehfeldt et al. 2001). In addition, it requires a sophisticated understanding of how species climatic envelopes will change, which currently is at an early stage for most species (McKenney et al. 2007). However, if sufficient data are available, this would allow the species to track its climate niche as the climate changes. An example of this concept is the change in seed transfer zones now under discussion by several jurisdictions. The BC Ministry of Forests and Range modified its seed transfer guidelines effective April 1 2009. Seed can now be transferred 100-200 m higher in elevation depending on the species and seed source. This change in provincial policy was based on analysis in which the current and future climate envelopes for most commercial species were calculated and related to the province's seed transfer zones. For details see O'Neill et al. (2008a).

The riskiest option for assisted migration is translocation of exotics, which entails moving a species far outside its current distribution to a location in which it has not occurred in the past, e.g. to a new continent. While the new species may be adapted to conditions expected to occur in the future at the new location, the understanding of how climatic conditions will change in the future is highly uncertain, especially at the scale of individual stands where reforestation decisions will be applied (O'Neill et al. 2008a). In addition, exotic species may become invasive, and are likely to bring along associated pests and diseases which may react differently (i.e. higher virulence, population outbreaks) in the new location (Rehfeldt et al. 2001).

Some conservation biologists are strongly opposed to the translocation option except in the case where the invasiveness and pest issues are well understood; they point out that this is generally not the case for most tree species. Ricciardi and Simberloff (2009) represent the extreme perspective on the inadvisability of assisted migration of exotics. Their primary concern is that scientists do not have a sufficient understanding of the impacts of species translocations. They state:

“Even if preceded by careful risk assessment, such action is likely to produce myriad unintended and unpredictable consequences. ... [T]he impacts of introduced species vary over time and space under the influence of local environmental variables, interspecific interactions and evolutionary change. (Ricciardi and Simberloff 2009, p. 248).

McLachlan et al. (2007) provide a simple framework for guiding the discussion on the introduction of exotics. They suggest three policy options: 1) Aggressive Assisted Migration, 2) Avoidance of Assisted Migration and 3) Constrained Assisted Migration. The options can be assessed using three criteria: confidence in ecological understanding, perceived risk of assisted migration and perceived risk of no assisted migration. Option 1 is focused on conservation of species faced with highly probable extinction under climate change, in particular those that have particularly high ecological or economic value. Advocates of this option feel that the risks of inaction are manageable and the ecological understanding is sufficient to take action. Option 2 arises from a perceived lack of data on the ecological consequences of establishing exotics and a preference for facilitating the spread of natural populations instead, similar to the first two lower-risk options identified by Aitken. Proponents of this option must also accept the risk of species extinction should the low-risk strategies fail (McLachlan et al. 2007). An intermediate position is

represented by Option 3. The main assumption in this option is that some degree of assisted migration is necessary to preserve biodiversity, notwithstanding the risks involved.

Richardson et al. (2009) build on the discussion in McLachlan et al. (2007) and provide a more sophisticated framework for evaluating managed relocation (= assisted migration) opportunities. They suggest there are four impacts associated with managed relocation (MR): 1) Focal Impact, the impact on the species to be translocated and its community from climate change and exacerbating effects of MR; 2) Collateral Impact, the effect of the exotic species in the recipient region; 3) Feasibility, the constraints on or opportunities for MR; 4) Acceptability; the societal willingness to pursue MR. These authors argue that due to the many interacting and values-based considerations involved, a more inclusive approach is required in decisions about MR. They go on to show that various groups of stakeholders can reach quite different conclusions regarding MR, even when all are using the criteria listed above. Richardson et al. (2009) conclude by suggesting that this approach will help decision-makers to capture the uncertainty in the evaluation criteria, create transparency in the evaluation process, and recognize the inherent tradeoffs that different stakeholders bring to evaluation of MR and its alternatives.

Hoegh-Guldberg et al. (2008) provide a decision pathway for determining whether to implement species translocation. Figure 6 shows their decision tree in which the authors consider such factors as the risk of species' decline or extinction, the technical feasibility of translocation and whether the benefits outweigh the social and biological costs. As mentioned previously, for many species these data are not yet available.

Thorpe et al. (2006) carried out an analysis of the ecological and policy implications of introducing exotic trees for adaptation to climate change in the Canada's western boreal forest. Based on a global review of past introductions, they found the most important problem with exotic forestry species is invasiveness. These species tend to be rapidly-growing, prolific seeders and can overwhelm local populations, e.g. by forming dense canopies which prevent native species from regenerating. Thorpe et al. (2006) considered a number of species: lodgepole pine, ponderosa pine, Douglas-fir, red pine, Scots pine, Siberian larch and hybrid poplar. They concluded that the future climate would be too dry for red pine and too warm for lodgepole pine. Ponderosa pine and Douglas-fir were considered to be likely candidates for establishment in the western portion of the prairies as long as moisture was not limiting. Their review of invasive behaviour indicated that the relative risk of invasiveness was lodgepole pine>Scots pine>Douglas-fir>ponderosa pine>red pine. Thorpe et al. (2006) recognized the need for biological assessment, benefit/risk analysis, and controlled field trials prior to widespread introduction of exotics. However, they note that most governments do not have strong policies against the introduction of exotic species.

Thorpe et al. (2006) also consider some of the philosophical issues related to existing concepts of "naturalness" and ecological communities. They suggest that the new ecosystems that result from climate change can be expected to be different from those that exist now, and probably different from those seen previously. The idea of protecting representative examples of natural ecosystems may become meaningless, and may need to be replaced by a focus on maintaining resilience, diversity and connectivity. Climate change may require abandoning the "hands-off"

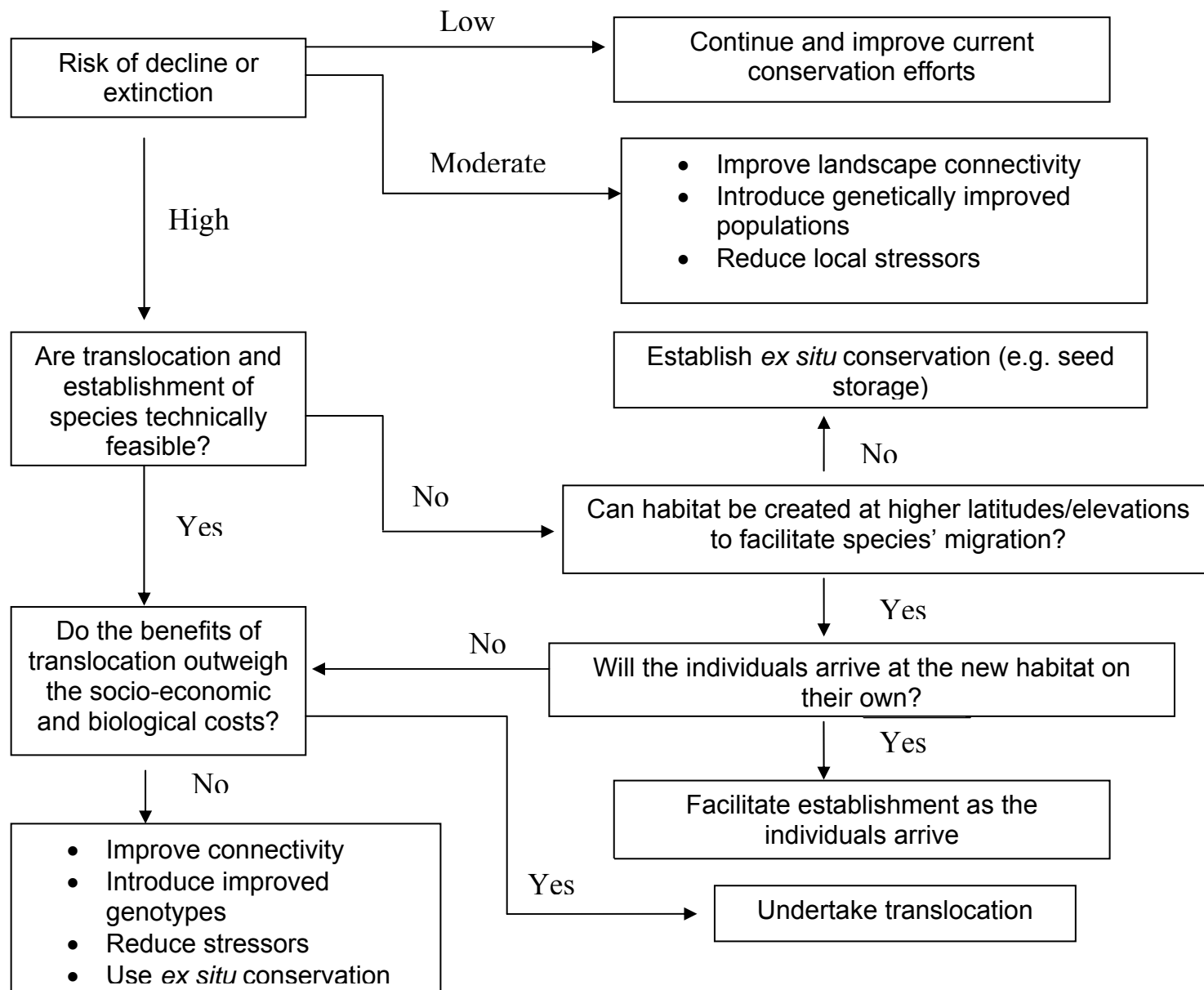


Figure 6. Decision pathway for implementing species translocation (modified from Hoegh-Guldberg et al. 2008).

management approach and assisting the movement of species to newly suitable habitats. The key question then becomes not whether species is exotic, but whether it contributes to biodiversity preservation, or causes problems because of invasiveness. Thorpe et al. (2006) recommend that limited planting trials, with appropriate monitoring and evaluation, should precede widespread planting. In the case of species and situations where widespread planting has already happened, a comprehensive assessment should still take place. Plantation planning guidelines should be developed to reduce risks associated with planting exotic species, and governments should review their current policy on exotic trees and develop new policy to address exotic species issues.

Tools are being developed to assist forest managers in making decisions about movement of seed to facilitate assisted migration. McKenney et al. (1999) have developed a software tool called “Seedwhere” to support decisions on moving plant material across environmental gradients. Seedwhere is a pun on the word “software”, and is designed to help forest managers answer the question "Where can I move seed"? The model maps climate similarity across large geographic regions using the Gower similarity metric. A web-based version is in development which will allow users to access several North America-wide climate models and investigate the similarity of current climate to projected future climates. The climate models are approximately 10 km in resolution, although higher resolution models are possible. While not a panacea, the Seedwhere tool provides an intuitive approach to visualizing how far forest managers might risk moving seed or other plant material away from its maternal climate in the absence of detailed population genetics work. The types of questions this might be addressed by Seedwhere include:

- How similar are the environmental conditions at a seed collection site to other areas?
- How similar are the environmental conditions at a regeneration area to potential seed collection sites?
- How similar are the environmental conditions at a regeneration area to seed already in storage?
- How similar are the environmental conditions at areas where seed lots have been collected?
- Where are the environmental conditions similar to a particular seedlot source?
- How similar are the environmental conditions between two particular sites?
- How similar are the environmental conditions between two particular seedlots that have already been collected?

3.3 Silviculture: Regeneration, Stand Management, Landscape-level Management and Planning

Assisted migration has received perhaps the greatest attention as a species-level adaptation option. This is due to the renewed interest in revisiting provenance test data and the development of transfer functions that allow a quantitative assessment of how genetic material can be moved in anticipation of climate change (O'Neill et al. 2008b). In the following we discuss a range of additional adaptation options for forest managers. Many of these are based on theoretical

arguments of modeling studies and lack verification from field testing. Much of the discussion is based on a workshop held by the Taskforce on Adapting Forests to Climate Change in Portland OR in November 2008 titled “Managing Climate Change Risk in Forests: How Can We Use Silviculture and Genetics to Minimize Potential Problems?”. In particular we summarize material presented by G. Howe and B. St. Clair (presentation titled “Genetic Options for Adapting Forests to Climate Change”) and by P. Anderson and D. Chmura (presentation titled “Silvicultural Approaches for Adapting Forests to Climate Change”). All presentation are available on-line at http://tafcc.forestry.oregonstate.edu/workshop_presentations.html.

3.3.1 Regeneration

As a preliminary step toward large-scale assisted migration, managers could begin to mix seed from warmer locations with current seedlots, e.g. as suggested by St. Clair and Howe (2007) for Douglas-fir in the US Pacific Northwest. However, analyses would be required such as the development of climate-based seed transfer zones and perhaps climate envelop modeling using approaches similar to McKenney et al. (2007) or O’Neill et al. (2008a). This also highlights the need for well-documented seed sources and providing a legacy of information and tracking data for future forest managers. Related to this is to use data on genotype characteristics to match seedlots to site conditions. This would pay benefits under current conditions and the expertise gained could be used to then extend the genotype-site matching analyses to future site conditions. An example of this kind of work currently underway is the Tree Species Selection Tool (TSS) being developed by the BC MOFR (see <http://www.for.gov.bc.ca/hfp/silviculture/TSS.htm> for further detail). The TSS is based on the following questions regarding selection of tree species for reforestation:

- What are the ecologically suitable species and potentially suitable species choices in the context of climate change and increased management complexity?
- What is needed to inform species selection decision-making for forest management plans;
- What information do practitioners need to make tree species selection decisions at the stand-level and to understand desired outcomes over time, i.e. cumulative effects at the landscape-level?

The TSS will be a decision-support tool that combines information on species ecological characteristics with up-to-date understanding on how site conditions will change under future climate scenarios. For a given ecological unit, it will include information on environmental conditions, forest health, genetics and management objectives; this will be used to provide recommendations on species to be used in reforestation.

Several authors have recommended increasing species diversity in reforestation as a general “insurance policy” for coping with climate change (Spittlehouse and Stewart 2003, Spittlehouse 2005, Ogden and Innes 2007). While this may provide a wider range of options for maintaining productivity under future climate, careful screening and climate envelope analyses would need to accompany such a decision.

Breeding improved planting stock for future conditions, e.g. drought tolerance, insect and disease resistance has also been recommended by several authors (Spittlehouse 2005, Ogden and Innes 2007). However, traditional breeding is slow and expensive and may not be able to produce appropriate genotypes quickly enough given the expected pace of climate change. More recent techniques based on clonal forestry approaches may be better suited to a rapidly changing environment, but gaining the required social license for this technology will likely be a constraint.

A constraint to “climate-proofing” the managed forest landscape is the relatively small area affected by forest management. While approaches such as assisted migration hold much promise for adapting the forest to climate change, the ability to affect large areas of forest is limited by the relatively small footprint of forest management. According to the National Forestry Database Program, slightly more than 1 million hectares per year were harvested annually between 1990 and 2007, and about 43% of this area was planted, or 430,000 ha. According to the National Forest Sinks Committee, managed forest land that contributes to the Annual Allowable Cut is 197 million ha. This suggests that implementing assisted migration through planting could be applied on about 0.2% of the forest annually. At this rate of planting it would require about 460 years to reforest the managed forest land base, not including forest land that lies outside of the currently managed area. While this is an admittedly simplistic analysis, it points out the large disparity between the size of the forest land base in Canada and the ability of forest management to affect a significant portion.

The area burned annually by forest fires averaged 2.3 million ha during 1990-2007, and several authors have suggested that this could double or triple by the end of the century (Flannigan et al. 2005, Balshi et al. 2009). Ogden and Innes (2007) suggest that forest managers could use large disturbance events as an opportunity to establish better-adapted populations, given that this represents a much greater level of disturbance than harvesting. However, managers would need to make sure that they have reforestation plans available before fires occur, e.g. ensure seed supply of appropriate provenance is available. This could allow relatively rapid deployment of better-adapted genotypes over large areas, as well as ensuring that the site is occupied soon after disturbance. Of course this will be constrained by the level of resources available for reforestation, which in turn will be affected by market conditions and other economic factors.

Establishing a small number of tree species and provenances adapted to future climates near the existing natural forest may increase the resilience of the forest landscape. As recommended by Thorpe et al. (2006), experimental plantings of new populations and species could be carried out where proper biodiversity screening has occurred. This would begin to form a database of species response to climate change under experimental conditions, including careful monitoring. Potentially useful species could be identified, and this would also provide an opportunity to collect relevant physiological data to improve our scientific understanding of biological adaptation. Assuming these trials are successful, small populations of genotypes adapted to future climates could be established near native forests to facilitate pollination and seed dispersal, i.e. ‘genetic outposts’ (Ogden and Innes 2007). Careful documentation of treatments, seed sources, and outplanting locations will be increasingly important in order to learn from both failures and successes of such efforts (Thorpe et al. 2006).

3.3.2 Stand Management

Spittlehouse and Stewart (2003) and others have suggested thinning stands to maximize efficient use of water, light, nutrients and reduce susceptibility to insects and disease. As an illustration of the potential for reduction in water use, Papadopol (2001) reports data from a thinning experiment in a 46-year old red pine plantation (*Pinus resinosa* Ait.) on sandy soils near Sault Ste. Marie, ON. Soil water content was measured at the beginning and end of a 26-day dry period in a stand that had been heavily thinned (HT) and in an unthinned control (UC). In the 0-30 cm soil layer, available soil water was reduced by 56% in HT as compared to a reduction of 87% in UC. A similar, but milder, effect occurred in the 31-150 cm soil layer, with reductions of 36% and 43% for treatments HT and UC, respectively. The more pronounced reduction in layer 1 is most likely due to the superficial rooting habit of red pine. Thinning will only be a realistic option in cases where growth rates and economic conditions justify the additional cost and effort. However, as part of a general strategy to increase the health and resilience of forest stands thinning may have a role in some locations.

Making an appreciable change in the population structure of the forest estate in Canada is severely constrained by the long life times of most tree species. One step that might reduce this constraint is adopt shorter rotation ages and replant with more robust genotypes in an effort to hasten forest adaptation to future conditions (Ogden and Innes 2007). As with the other options mentioned, such a change will have to be economically viable and may be applied more readily in environments with faster growth rates. Alternatively, technology that can make use of smaller-diameter material might assist in adopting shorter rotation ages. However, the impacts of reducing rotation ages on the landscape-level carbon balance must also be considered (Kurz et al. 1998).

3.3.3 Landscape-level Management and Planning

A common recommendation from the forest genetics community is to avoid forest fragmentation and maintain corridors that facilitate migration (i.e. gene flow), e.g. Aitken et al. (2008). This in turn calls for a more landscape-level view of harvest planning and infrastructure layout (e.g. roads). For example Rempel et al. (2007) use advanced spatial modeling techniques to determine the optimal configuration of forest management activities over decade time-scales in order to provide maximum habitat retention for 13 species of songbirds. Similar analyses could be combined with climate model simulations and forest ecosystem models to project the best forest management practices that would reduce forest fragmentation and provide habitat for gene flow at the landscape level.

Forest management at the species level can reduce landscape-scale fire risk. Changing species composition from high flammability conifers to lower flammability hardwood species and using this approach to break up contiguous blocks of highly flammable fuel types (i.e. FireSmart planning) can reduce the likelihood of fire ignition and spread (Volney and Hirsch 2005). Similarly, establishing low flammability species near forest communities can reduce the risk of fire and damage to human settlements.

Species will respond individually to climate change. We should expect species to move independently across the landscape, forming new communities not seen previously (McKenney et al. 2007). Therefore, a management objective that stresses conservation of existing communities is likely to fail. Instead, a focus on maintaining ecosystem functions (e.g. productivity, biodiversity, nutrient cycling, etc.) rather than current ecosystems is more likely to be successful. As part of this approach, *ex situ* conservation of endangered species will become more important, since without artificial regeneration, genetic options are limited (Chourmouzis et al. 2009).

Forest productivity will change in complex ways as climate change occurs. There is some potential for increased productivity due to warmer temperatures and the CO₂ fertilization effect, e.g. Norby et al. (2005). However, research has shown that if other resources are limiting (e.g. water, nutrients), the potential for increased growth may not be realized (Oren et al. 2001). As our understanding of these effects increases, managers may need to focus forest management activities on currently productive sites and those likely to remain more productive under future climates, and reduce efforts on poor sites (Johnston and Williamson 2005). The ultimate expression of this approach is to adopt some form of the TRIAD approach for forest management (Nitschke and Innes 2008). In this approach the forest management land base is divided into portions devoted to intensive timber production, extensive multiple use management and protected areas. This may offer forest managers the opportunity to focus more effort on a smaller land base for timber production, allowing climate change impacts to proceed on protected areas and the extensively managed forest land base (Ogden and Innes 2007).

Many forest companies across North America are seeking to certify their forest management practices under one of several certification systems (e.g. Canadian Standards Association, Sustainable Forest Initiative, Forest Stewardship Council). Recently both CSA and SFI have included general recommendations in their standards for companies to include climate change considerations in forest management plans, research activities and communication plans. See CSA (2008) and SFI (2010) for details.

3.3.3.1 Adaptive Capacity

The ability of tree species to adapt has a biological component (e.g. migration and adaptation as described previously) as well as a human component (i.e. forest management) (Johnston et al. 2010). While the understanding of climate change vulnerability and potential adaptation options is rapidly increasing, there is still a deficit of adaptive capacity among forest managers and forest management institutions. Adaptive capacity can be enhanced by:

- sharing adaptation best practices across jurisdictions;
- incorporate knowledge of species vulnerability in decision-making on reforestation and silviculture;
- encourage changes in society's expectations towards future forest values and benefits so that they include tree species vulnerability to climate change;
- develop technology to make use of different wood quality and tree species composition;

- reduce reliance on historical observations and plot measurements to predict what will happen in the future; and
- develop reliable species- and stand-level process models for predictions of future growth and yield.

A comprehensive assessment of the adaptive capacity of the Canadian forest sector will be a major focus of Phase 2 of the CCFM climate change project.

4.0 RESEARCH NEEDS

Given the large amount of variability in Canada's forest landscape, and our relatively limited understanding of the impacts of climate change on forests, the potential scope of research needs is nearly unlimited. Here we provide a more focused list of suggested research needs based on the preceding discussion on tree species vulnerability.

4.1 Adapted Genetic Material

Of the management options presented in the literature and summarized above, assisted migration and related activities is the most recurrent and seems to be one of the most promising areas for climate change adaptation. However, it is clear in reviewing the literature that there is a great deal known about a few species (e.g. lodgepole pine, Douglas-fir), limited data on several species and virtually nothing known about the majority of Canada's 93 commercial tree species. The most valuable source of information on how populations are adapted to variations in climate come from provenance tests (O'Neill et al. 2008b). This leads to three important research needs: first, that provenance tests for more commercial species need to be established, specifically so that they sample the full range of climates currently occupied by the species and with some plantings in areas that may lie outside of the species current range. They should also include source populations that currently lie to the south of the existing range (e.g. northern USA). However, to be effective, this would require an expensive, interprovincial and international undertaking and will require at least two decades to yield useful data. Therefore, the second research need is to undertake analyses (or re-analyses) of existing provenance tests and interpreting these data in light of potential climate change.

The third research need is related to the relatively small footprint of forest management in Canada. Implementation of assisted migration is most easily achieved when forest plantations are being established. However, the amount of planted each year is a small fraction of Canada's forested area. Further, much of Canada's forests are not managed for timber production, and therefore, are left to naturally regenerate. To ensure that adapted genotypes are present across the Canada's forested landscapes, it will be necessary to devise and implement systems of assisted migration for areas not managed for timber production (Aitken et al. 2008). This will first require population genetics research to identify effective deployment strategies (i.e., the size, frequency and genetic composition of 'genetic outposts').

Related research includes developing a better understanding of the role of genetic variation in climatic tolerances of tree species. Deployment of better-adapted genetic material will require

the development of climate-based seed transfer zones and mechanisms to ensure that the best adapted seed sources are used in reforestation. Experimental plantings of better adapted populations and perhaps species could be established under careful control and monitoring following a comprehensive biodiversity assessment.

4.2 Tree Physiology

Improved information on tree physiology can increase managers' ability to better match species characteristics to site conditions, e.g. drought tolerance, frost tolerance etc. Physiological thresholds to changes in temperature, moisture CO₂ etc. should be identified. In particular, research is required to better understand the effects of higher atmospheric levels of CO₂ on tree species. The potential effects include fertilization (through enhanced photosynthesis) and increased water use efficiency. Both of these mechanisms provide the possibility of increased adaptive capacity for tree species, but the scientific understanding of how they will function in the "real world" of forests stands is lacking. There is an expectation that good sites may improve and bad sites get worse in the future; if so, thinking about reallocating management efforts could begin now. We need more research on how phenology will change with climate change and variability, and its implications for pests and diseases. Research on how climate change will affect seedling growth and survival following planting is essential for other strategies such as assisted migration to succeed.

4.3 Insects and Disease

It seems that diseases are more poorly understood than insects with respect to potential effects of climate change. However, in both cases we require further information on the complex relations between host, insect (vector) and disease organisms. Climate-related physiology of insects, phenological changes in both host and insect, and how environmental change affects disease establishment are all required.

4.4 Fire

Using the Vital Attributes approach described by Rowe (Rowe 1983), managers can now begin to assess the likely impacts of fire at the species level, and how this may determine post-fire successional pathways under climate change. The BORFIRE described in de Groot et al. (2003) provides one approach for these analyses.

4.5 Silviculture

We need better information on how silvicultural interventions (e.g. thinning) may provide a short-term strategy for assisting existing stands to cope with the immediate effects of climate change until better adapted genetic material is deployed. Economic analyses will be an essential component of this work.

4.6 Genetic Diversification

Increasing genetic diversity on the landscape may help buffer some of the impacts of climate change and the uncertainty present in all climate and genetic models, by increasing the probability that plantations contain a threshold proportion of adapted species and populations. Genetic diversification could be achieved by planting a wider range of species and populations of species than is currently planted. However, much remains to be learned before this strategy can be implemented effectively. Field trials and forest growth modelling research could contribute greatly to help identify suitable species compositions for uncertain future climates.

Further work on species distribution modeling is required. While newer climate envelope modeling approaches are yielding interesting and valuable results, e.g. McKenney et al. (2007), these models do not account for increased CO₂ levels and other factors important to seedling establishing and growth under climate change. The next generation of dynamic global vegetation models offers a more comprehensive analytical approach but can be difficult to parameterize and require significant computing resources. Further development of both of these approaches is essential for a better understanding of Canada's tree species vulnerability.

5.0 CONCLUSIONS

Canada's commercial tree species are vulnerable to a variety of climate change impacts. At the species level, maladaptation and disturbance are the most important factors causing this vulnerability. Species occurring at the southern or xeric edge of their range may be particularly vulnerable due to the combined effects of climate change impacts and lack of genetic potential for adaptation. Areas of particular concern in this regard are the forest-grassland boundary in the Prairie Provinces, and portions of the southern interior of BC. A critical need to address this issue is further work in analyzing provenance test data, and establishing new provenance tests designed to determine the genetic basis of forest productivity-climate relationships. Forest managers can use the index of species vulnerability recently developed by CFS researchers to identify which species may be particularly vulnerable based on genetic and life-history attributes.

Disturbance regimes are likely to change in the future. Species life-history attributes can be used to develop a general sense of how the species will respond to changes in fire regimes. The impacts of climate change on insects and disease are not well understood, but indications are that warming will generally be beneficial to insects and have varying influences on disease organisms. The occurrence of invading species from warmer climates will likely increase. The de-coupling of insect and host phenology will result in new host-insect relationships that are difficult to predict. Similarly, complex disease-vector-host relationships will change in ways that cannot be predicted at this time. In general, good SFM practices that maintain forests in a healthy and productive condition is the best long-term strategy given the uncertainty in future conditions. Management options for assessing vulnerability and identifying adaptation options need to become part of day-to-day activities, i.e. mainstreamed into forest operations and planning. A framework for guiding managers on these activities is in production by the CCFM's Climate Change Task Force.

Assisted migration has been identified as an action that, for some species, can be considered now. Where adequate provenance data exist, transfer functions can be developed and seed transfer policy changed accordingly, as was done for some species in BC in 2009. However, the deployment of better adapted genetic material is constrained by the relatively low level of harvesting as a proportion of the total forest area in Canada. Managers may consider using large-scale disturbance events (e.g. fires) as windows of opportunity for introducing better adapted genotypes on the landscape. Assisted migration is still controversial among some groups within the forest sector, and a broad social consensus on using this tool will need to be developed before it can be applied widely.

Some options exist in silvicultural operations, including increasing intra- and inter-species diversity in reforestation, thinning high value stands at risk from moisture stress and scheduling harvest operations to target susceptible stands before they are attacked by insects or disease. Climate change considerations can be incorporated into forest management plans as has been done in a few cases in the past decade. The most recent versions of the CSA and SFI standards for SFM provide guidance on including climate change in planning, communications and research activities.

6.0 ACKNOWLEDGEMENTS

We thank the many dedicated forest managers and scientists across Canada for their support and contributions to this report. Special gratitude is extended to those who took the time to review major sections or the entire report and provided helpful and constructive comments: Ms. Kathy Hopkins, BC Ministry of Forests and Range; Dr. Greg O'Neill, BC Ministry of Forests and Range; Dr. Jan Volney, Canadian Forest Service, Northern Forestry Centre; and Dr. Steve Columbo, Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research. R. Fleming would also like to thank fellow CFS researchers Rene Alfaro, Jean-Noel Candau, Allan Carroll, Barry Cooke, Barry Lyons, and Vince Nealis and Jan Volney for discussion and development of contributing ideas. We appreciate the guidance and feedback we received from the Climate Change Task Force of the Canadian Council of Forest Ministers. We acknowledge funding from the Canadian Council of Forest Ministers, Canadian Forest Service, BC Future Forest Ecosystem Science Council, Prince Albert Model Forest, the Canadian Model Forest Network, the Sustainable Forest Management Network, and Natural Resources Canada's Climate Change Impacts and Adaptations Program and Regional Adaptation Collaborative Program.

7.0 REFERENCES

- Aber, J.D., S.V. Ollinger, C.A. Federer, P.B. Reich, M.L. Goulden, D.W. Kicklighter, J.M. Melillo and R.G. Lathrop Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* **5**: 207–222.
- Adams, H.D., M. Guardiola-Claramonte, G.A. Barron-Gafford, J.C. Villegas, D.D. Breshears, C.B. Zou, P.A. Troch and T.E. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global change-type drought. *Proceedings of the National Academy of Science* **106**: 7063–7066.
- Ainsworth, E.A. and S.P. Long. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *The New Phytologist* **165**: 351–372.
- 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.
- Ali, A.A., H. Asselin, A.C. Larouche, Y. Bergeron, C. Carcaillet and P.J.H. Richard. 2008. Changes in fire regime explain the Holocene rise and fall of *Abies balsamea* in the coniferous forests of western Québec, Canada. *The Holocene* **18**: 693–703.
- Andalo, C., J. Beaulieu and J. Bousquet. 2005. The impact of climate change on growth of local white spruce populations in Québec, Canada. *Forest Ecology Management* **205**: 169–182.
- Apple, M.E., M.S. Lucash, D.M. Olszyk, and D.T. Tingey. 1998. Morphogenesis of Douglas fir buds is altered at elevated temperature but not at elevated CO₂. *Environmental and Experimental Botany* **40**: 159–172.
- Asshoff, R., G. Zotz, and C. Körner. 2006. Growth and phenology of mature temperate forest trees in elevated CO₂. *Global Change Biology* **12**: 848–861.
- Ayres, M.P. and M.J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* **262**: 263–286.
- Bachelet, D., J.M. Lenihan, C. Daly, R.P. Neilson, D.S. Ojima and W.J. Parton. 2001. MC1: a dynamic vegetation model for estimating the distribution of vegetation and associated carbon, nutrients, and water—technical documentation. Version 1.0. General Technical Report PNW-GTR-508, Portland OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 95 p.

- Bale, J.S., G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse, J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press, I. Symrnioudis, A.D. Watt and J.B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**: 1-16.
- Balshi, M. S., A. D. McGuire, P. Duffy, M. D. Flannigan, J. Walsh and J. Melillo. 2009. Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology* **15**: 578-600.
- Barber, V. A., G.P. Juday and B.P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* **405**: 668-673.
- Barnes, B. V. 2009. Tree response to the ecosystem change at landscape level in eastern North America. *Forstarchiv* **80**: 76-89.
- Barrow, E., B. Maxwell and P. Gachon. 2004. Climate variability and change in Canada: past, present and future. ACSD Science Assessment Series No. 2, Meteorological Service of Canada, Environment Canada, Ottawa, ON.
- BassiriRad, H., K.L. Griffin, J.F. Reynolds and B.R. Strain. 1997. Changes in root NH_4^+ and NO_3^- absorption rates of loblolly and ponderosa pine in response to CO_2 enrichment. *Plant and Soil* **190**: 1-9.
- Beaubien, E. G. and M. Hall-Beyer. 2003. Plant phenology in western Canada: trends and links to the view from space. *Environmental Monitoring and Assessment* **88**: 419-429.
- Beaulieu, J., M. Perron and J. Bousquet. 2004. Multivariate patterns of adaptive genetic variation and seed source transfer in *Picea mariana*. *Canadian Journal of Forest Research* **34**: 531-545.
- Beaulieu, J. and A. Rainville. 2005. Adaptation to climate change: Genetic variation is both a short- and a long-term solution. *The Forestry Chronicle* **81**: 704-709.
- Beedlow, P. A. and D.T. Tingey. 2007. A summary of NHEERL ecological research on global climate change. Report EPA/600/R-05/007, Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Corvallis, OR. 114 pp.
- Beerling, D. J. and C.K. Kelly. 1997. Stomatal density responses of temperate woodland plants over the past seven decades of CO_2 increase: A comparison of Salisbury (1927) with contemporary data. *American Journal of Botany* **84**: 1572-1583.

- Beier, C. M., S.E. Sink, P.E. Hennon, D.V. D'Amore and G.P. Juday. 2008. Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research* **38**: 1319-1334.
- Bentz, B. J., J. A. Logan and J. C. Vandygriff. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. *Canadian Entomologist* **133**: 375–387.
- Besnard, G., V. Acheré, S. Jeandroz, Ø. Johnsen, P.F. Rampant, R. Baumann, G. Müller-Starck, T. Skrøppa, and J.-M. Favre. 2008. Does maternal environmental condition during reproductive development induce genotypic selection in *Picea abies*? *Annals of Forestry Science* **65**: 109.
- Bezemer, T.M. and T.H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos* **82**: 212-222.
- Bigras, F.J. 2000. Selection of white spruce families in the context of climate change: heat tolerance. *Tree Physiology* **20**: 1227-1234.
- Bigras, F.J. 2005. Photosynthetic response of white spruce families to drought stress. *New Forests* **29**: 135-148.
- Bigras, F.J. and A. Bertrand. 2006. Responses of *Picea mariana* to elevated CO₂ concentration during growth, cold hardening and dehardening: phenology, cold tolerance, photosynthesis and growth. *Tree Physiology* **26**: 875-888.
- Boisvenue, C. and S.W. Running. 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology* **12**: 1-21.
- Boland, G. J., V. Higgins, A. Hopkin, A. Nasuth and M. S. Melzer. 2003. Climate change and plant disease in Ontario. Ontario Forest Research Institute, Sault Ste. Marie, ON.
- Bonan, G.B. 1990. Carbon and nitrogen cycling in North American boreal forests. II Biogeographic patterns. *Canadian Journal of Forest Research* **20**: 1077–1088.
- Bonan, G.B. 1992. A simulation analysis of environmental factors and ecological processes in North American boreal forests. Pages 404–427 in Shugart, H.H., R. Leemans and G.B. Bonan. Editors. *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge, UK.
- Bonan, G.B. and K. Van Cleve. 1992. Soil temperature, nitrogen mineralization and carbon source-sink relationships in boreal forests. *Canadian Journal of Forest Research* **22**: 629–639.

- Bonello, P., T.R. Gordon, D.A. Herms, D.L. Wood and N. Erbilgin. 2006. Nature and ecological implications of pathogen-induced systemic resistance in conifers: A novel hypothesis. *Physiological and Molecular Plant Pathology* **68**: 95-104.
- Borsos-Matovina, V. and T.J. Blake. 2001. Seed treatment with the antioxidant Ambiol enhances membrane protection in seedlings exposed to drought and low temperature. *Trees - Structure and Function* **15**: 163-167.
- Bossdorf, O., C.L. Richards and M. Pigliucci. 2008. Epigenetics for ecologists. *Ecology Letters* **11**: 106–115.
- Bouchard, M. and D. Pothier. 2008. Simulations of the effects of changes in mean fire return intervals on balsam fir abundance, and implications for spruce budworm outbreaks. *Ecological Modelling* **218**: 207-218.
- Botkin, D.B., J.F. Janak and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* **60**: 849–872.
- Brandt, J. P., Y. Hiratsuka and D. J. Pluth. 2004. Extreme cold temperatures and survival of overwintering and germinated *Arceuthobium americanum* seeds. *Canadian Journal of Forest Research* **34**: 174-183.
- Brodribb, T. J., S.A.M. McAdam, G.J. Jordan and T.S. Feild. 2009. Evolution of stomatal responsiveness to CO₂ and optimization of water-use efficiency among land plants. *The New Phytologist* **183**: 839 - 847.
- Brown, K. and K.O. Higginbotham. 1986. Effects of carbon dioxide enrichment and nitrogen supply on growth of boreal tree seedlings. *Tree Physiology* **2**: 223-232.
- Bruhn, D., T.N. Mikkelsen, K. Pilegaard, M.E. Gavito and H. Saxe. 2001. Climate change in a plant ecophysiological perspective. Pages 167-190 in Jørgensen, A. M. K., J. Fenger, and K. Halsnæs. Editors. *Climate Change Research. Danish Contributions*. Gads Forlag, Copenhagen.
- Buchmann, N. 2002. Plant ecophysiology and forest response to global change. *Tree Physiology* **22**: 1177-1184.
- Bugmann, H. 2001. A review of forest gap models. *Climatic Change* **51**: 259–305.
- Bugmann, H.K., S.D. Wullschleger, D.T. Price, K. Ogle, D.F. Clark and A.M. Solomon. 2001. Comparing the performance of forest gap models in North America. *Climatic Change* **51**: 349–388.

- Burleigh, J.S., R.I. Alfaro, J.H. Borden and S. Taylor. 2002. Historical and spatial characteristics of spruce budworm *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) outbreaks in northeastern British Columbia. *Forest Ecology and Management* **168**: 301-309.
- Burton, P.J. and S.G. Cumming. 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. *Water, Air and Soil Pollution* **82**: 401–414.
- Busch, F., N.P.A. Hüner and I. Ensminger. 2007. Increased air temperature during simulated autumn conditions does not increase photosynthetic carbon gain but affects the dissipation of excess energy in seedlings of the evergreen conifer jack pine. *Plant Physiology* **143**: 1242-1251.
- Buse, A. and J.E.G. Good. 1996. Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. *Ecological Entomology* **21**: 335–343.
- Butin, E., A.H. Porter and J. Elkinton. 2005. Adaptation during biological invasions and the case of *Adelges tsugae*. *Evolutionary Ecology Research* **7**: 887–900.
- Caccianiga, M. and S. Payette. 2006. Recent advance of white spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). *Journal of Biogeography* **33**: 2120-2135.
- Campagna, M.A. and H.A. Margolis. 1989. Influence of short-term atmospheric CO₂ enrichment on growth, allocation patterns, and biochemistry of black spruce seedlings at different stages of development. *Canadian Journal of Forest Research* **19**: 773-782.
- CCFM (Canadian Council of Forest Ministers). 2003. *Defining Sustainable Forest Management In Canada: Criteria and Indicators*. Canadian Council of Forest Ministers, Ottawa, ON.
- CFIA (Canadian Food Inspection Agency). 2009. *Forestry surveys. 2008 Plant Protection Survey Report*. Canadian Food Inspection Agency, Ottawa.
- CSA (Canadian Standards Association). 2008. *Sustainable Forest Management. CSA Standard Z809-08*. Canadian Standards Association, Ottawa ON. 98pp.
- Candau, J.-N. and R.A. Fleming. 2008. *Forecasting the response to climate change of the major biotic disturbance regime in Ontario's forests: the spruce budworm*. Ontario Ministry of Natural Resources, Applied Research and Development Branch, Sault Ste. Marie, ON. Climate Change Research Report CCRR-13. 14p.
- Candau J.-N., R.A. Fleming and A.A. Hopkin. 1998. Spatio-temporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Canadian Journal of Forest Research* **28**: 1-9.

- Canham, C.D., P.T. LePage and K.D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* **34**: 778–787.
- Cannell, M.G.R. and R.I. Smith. 1986. Climatic warming, spring budburst and frost damage on trees. *Journal of Applied Ecology* **23**: 177-191.
- Cao, B., Q.-L. Dang, X. Yü and S. Zhang. 2008. Effects of [CO₂] and nitrogen on morphological and biomass traits of white birch (*Betula papyrifera*) seedlings. *Forest Ecology and Management* **254**: 217-224.
- Carroll, A.L., S.W. Taylor, J. Régnière and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223–232 in Shore, T.L., J. E. Brooks, and J. E. Stone. Editors. *Mountain Pine Beetle Symposium: Challenges and Solutions*. Information Report BC-X-399. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, BC.
- Catovsky, S. and F.A. Bazzaz. 1999. Elevated CO₂ influences the responses of two birch species to soil moisture: implications for forest community structure. *Global Change Biology* **5**: 507-518.
- Centritto, M. and P.G. Jarvis. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology* **19**: 807-814.
- Centritto, M., H.S.J. Lee and P.G. Jarvis. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). I. Plant growth, allocation and ontogeny. *Tree Physiology* **19**: 799-806.
- Chapin III, F.S. and A.M. Starfield. 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change* **35**: 1573–1480.
- Chiang J-M, L.R. Iverson, A. Prasad and K.J. Brown. 2008. Effects of climate change and shifts in forest composition on forest net primary production. *Journal of Integrative Plant Biology* **50**: 1426–1439.
- Chhin, S., E.H. Hogg, V.J. Lieffers and S. Huang. 2008. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. *Forest Ecology and Management* **256**: 1692-1703.
- Chourmouzis, C., A.D. Yanchuk, A. Hamann, P. Smets and S. N. Aitken. 2009. Forest Tree Genetic Conservation Status Report 1: *In Situ* Conservation Status of All Indigenous British Columbia Species. Technical Report 053, BC Ministry of Forests and Range, Victoria, BC.

- 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.
- Cohen, S., K. Miller, K. Duncan, E. Gregorich, P. Groffman, P. Kovacs, V. Magaña, D. McKnight, E. Mills, D. Schimel, G. Chichilnisky, D. Etkin, R. Fleming, K. Hall, S. Meyn, J. Patz, R. Pulwarty, D. Scott and G. Wall. 2001. North America. Pages 735-799 in McCarthy, J.J., O.F. Canziani, N.A. Leary, D.J. Dokken, and K.S. White. Editors. *Climate Change 2001: Impacts, Adaptation and Vulnerability. Working Group II, Intergovernmental Panel on Climate Change Third Assessment Report*. Cambridge University Press, Cambridge, UK. 1042p.
- Colombo, S.J. 1998. Climatic warming and its effect on bud burst and risk of frost damage to white spruce in Canada. *The Forestry Chronicle* **74**: 567-577.
- Cooke, B.J. 2009. Forecasting mountain pine beetle-overwintering mortality in a variable environment. Mountain Pine Beetle Working Paper 2009-03. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. 31p. Available on-line at: <http://warehouse.pfc.forestry.ca/pfc/29920.pdf>
- Constable, J.V.H., G.E.J. Taylor, J.A. Laurence and J.A. Weber. 1996. Climatic change effects on the physiology and growth of *Pinus ponderosa*: expectations from simulation modeling. *Canadian Journal of Forest Research* **26**: 1315-1325.
- Coursolle, C., H.A. Margolis, A.G. Barr, T.A. Black, B.D. Amiro, J.H. McCaughey, L.B. Flanagan, P.M. Lafleur, N.T. Roulet, C.P.-A. Bourque, M.A. Arain, S.C. Wofsy, A. Dunn, K. Morgenstern, A.L. Orchansky, P.Y. Bernier, J.M. Chen, J. Kidston, N. Saigusa and N. Hedstrom. 2006. Late-summer carbon fluxes from Canadian forests and peatlands along an east-west continental transect. *Canadian Journal of Forest Research* **36**: 783–800.
- Cowling, S.A. 1999. Plants and temperature-CO₂ uncoupling. *Science* **285**: 1500-1501.
- Cumming, S.G. and P.J. Burton. 1996. Phenology-mediated effects of climatic change on some simulated British Columbia forests. *Climatic Change* **34**: 213–222.
- Curtis, P.S. and X. Wang. 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* **113**: 299-313.
- 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**: 723–734.
- Danby, R.K. and D.S. Hik. 2007. Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Global Change Biology* **13**: 437–451.

- Davey, P.A., S. Hunt, G.J. Hymus, E.H. DeLucia, B.G. Drake, D.F. Karnosky and S.P. Long. 2004. Respiratory oxygen uptake is not decreased by an instantaneous elevation of [CO₂], but is increased with long-term growth in the field at elevated [CO₂]. *Plant Physiology* **134**: 520–527.
- Davis, A.J., L.S. Jenkinson, J.H. Lawton, B. Shorrocks and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**: 783–786.
- Davis, M.B., R.G. Shaw and J.R. Etterson. 2005. Evolutionary responses to changing climate. *Ecology* **86**: 1704–1714.
- Davis, M.B. 1981. Quaternary history and the stability of forest communities. Pages 132–153 in West, D.C., H.H. Shugart and D.B. Botkin. Editors. *Forest succession: Concepts and Application*. Springer-Verlag, New York, New York, USA.
- de Groot, W. J., P. M. Bothwell, D. H. Carlsson and K. A. Logan. 2003. Simulating the effects of future fire regimes on western Canadian boreal forests. *Journal of Vegetation Science* **14**: 355-364.
- Delcourt, P.A. and H.R. Delcourt. 1987. *Long Term Forest Dynamics of the Temperate Zone: A Case Study of Late-Quaternary Forests in Eastern North America*. Springer-Verlag, New York, New York, USA.
- Dormling, I. and Ø. Johnsen. 1992. Effects of the parental environment on full-sib families of *Pinus sylvestris*. *Canadian Journal of Forest Research* **22**: 88-100.
- Dukes, J.S., J. Pontius, D. Orwig, J.R. Garnas, V.L. Rodgers, N. Brazee, B. Cooke, K.A. Theoharides, E.E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerda, K. Stinson, R. Wick and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research* **39**: 231-248.
- Dullinger, S., T. Dirnböck and G. Grabherr. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invisibility. *Journal of Ecology* **92**: 241–252.
- Ellsworth, D. S., P.B. Reich, E.S. Naumburg, G.W. Koch, M.E. Kubiske and S.D. Smith. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO₂ across four free-air CO₂ enrichment experiments in forest, grassland and desert. *Global Change Biology* **10**: 1-18.
- Ettl, G.J. and D.L. Peterson. 1995. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. *Global Change Biology* **1**: 213 - 230.

- Farrar, C.D., M.L. Sorey, W.C. Evans, J.F. Howle, B.D. Kerr, B.M. Kennedy, C.-Y. King and J.R. Southon. 1995. Forest-killing diffuse CO₂ emission at Mammoth Mountain as a sign of magmatic unrest. *Nature* **376**: 675-678.
- Feng, X. 1999. Trends in intrinsic water-use efficiency of natural trees for the past 100-200 years: A response to atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta* **63**: 1891-1903.
- Field, C. B., L. D. Mortsch, M. Brklacich, D. Forbes, P. Kovacs, J. Patz, S. Running and M. Scott. 2007. North America. Pages 617-652 in Parry, M. L., O. F. Canziani, J. P. Palutikof, P. J. v. d. Linden, and C. E. Hanson. Editors. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Flannigan, M.D. and F. I. Woodward. 1994. Red pine abundance: current climatic control and responses to future warming. *Canadian Journal of Forest Research* **24**: 1166-1175.
- Flannigan, M.D., I. Campbell, M. Wotton, C. Carcaillet, P. Richard and Y. Bergeron. 2001. Future fire in Canada's boreal forest: paleoecology results and general circulation model - regional climate model simulations. *Canadian Journal of Forest Research* **31**: 854-864.
- Flannigan, M.D., K. A. Logan, B. D. Amiro, W. R. Skinner and B. J. Stocks. 2005. Future area burned in Canada. *Climatic Change* **72**: 1-16.
- Fleming, R.A. 2000. Climate change and insect disturbance regimes in Canada's boreal forests. *World Resources Review* **12**: 520-554.
- Fleming R.A. and Volney W.J.A. 1995. Effects of climate change on insect defoliator population processes in Canada's boreal forest: some plausible scenarios. *Water, Air and Soil Pollution* **8**: 445-454.
- Fleming, R.A. and J.-N. Candau. 1998. Influences of climatic change on some ecological processes of an insect outbreak system in Canada's boreal forests and the implications for biodiversity. *Environmental Monitoring and Assessment* **49**: 235-249.
- Fleming, R.A., J.-N. Candau and R.S. McAlpine. 2002. Landscape-scale analysis of interactions between insect defoliation and forest fire in central Canada. *Climatic Change* **55**: 251-272.
- Flower, A. and T.Q. Murdock. 2009. Modeling the future impacts of climate change on Douglas fir and spruce forests in British Columbia. B.C. Ministry of Forests and Range Climate Change Seminar, 22 April 2009. Victoria, B.C. See also <http://www.pacificclimate.org/resources/climateimpacts/forests/>

- Foley, J.A., I.C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch and A. Haxeltine. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles* **10**: 603–623.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson and C.S. Holling. 2004. Regime shifts, resilience and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution and Systematics* **35**: 557-581.
- Frey, B.R., V.J. Lieffers, E.H. Hogg and S.M. Landhausser. 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Canadian Journal of Forest Research* **34**: 1379-1390.
- Gamache, I., Payette, S. 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. *Journal of Biogeography* **32**: 849-862.
- Girardin, M.P., F. Raulier, P.Y. Bernier and J.C. Tardif. 2008. Response of tree growth to a changing climate in boreal central Canada: a comparison of empirical, process-based, and hybrid modelling approaches. *Ecological Modelling* **213**: 209-228.
- Gitay H., S. Brown, W. Easterling, B. Jallow, J. Antle, M. Apps, R. Beamish, T. Chapin, W. Cramer, J. Frangi, J. Laine, Lin Erda, J. Magnuson, I. Noble, J. Price, T. Prowse, T. Root, E. Schulze, O. Sirotenko, B. Sohngen, J. Soussana, H. Bugmann, C. Egorov, M. Finlayson, R. Fleming, W. Fraser, L. Hahn, K. Hall, M. Howden, M. Hutchins, J. Ingram, J. Hui, G. Masters, P. Megonigal, J. Morgan, N. Myers, R. Neilson, S. Page, C. Parmesan, J. Rieley, N. Roulet, G. Takle, J. van Minnen, D. Williams, T. Williamson, K. Wilson. 2001. Ecosystems and their goods and services. Pages 235-342 in McCarthy, J.J., O.F. Canziani, N.A. Leary, D.J. Dokken, and K.S. White. Editors. *Climate Change 2001: Impacts, Adaptation and Vulnerability. Working Group II, Intergovernmental Panel on Climate Change Third Assessment Report*. Cambridge University Press, Cambridge, UK.
- Gray, D.R. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. *Climatic Change* **87**: 361–383.
- Greene, D.F., C.D. Canham, K.D. Coates and P.T. LePage. 2004. An evaluation of alternative dispersal functions for trees. *Journal of Ecology* **92**: 758–766.
- Greenwood, D.R. and J.F. Basinger. 1994. The paleoecology of high-latitude Eocene swamp forests from Axel Heiberg Island, Canadian High Arctic. *Review of Palaeobotany and Palynology* **81**: 83-97.
- Greenwood, M.S. and K.W. Hutchinson. 1996. Genetic aftereffects of increased temperature in *Larix*. Pages 56-62 in Hom, J., R. Birdsey, and K. O'Brian. Editors. 1995 meeting of the Northern Global Change Program. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA.

- Guak, S., D.M. Olszyk, L.H. Fuchigami, and D.T. Tingey. 1998. Effects of elevated CO₂ and temperature on cold hardiness and spring bud burst and growth of Douglas-fir (*Pseudotsuga menziesii*). *Tree Physiology* **18**: 671-679.
- Gunderson, L.H. and C.S. Holling, editors. 2002. *Panarchy: Understanding transformations in human and natural systems*. Island Press, Washington, DC, USA.
- Hall, J.P. and B.H. Moody. 1994. Forest depletions caused by insects and diseases in Canada 1982–1987. Natural Resources Canada, Canadian Forest Service, Hull, Québec.
- Hamann, A. and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* **87**: 2773–2786.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management* **197**: 323-335.
- Hänninen, H. 2006. Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. *Tree Physiology* **26**: 889–898.
- Harrington, R., R. Fleming and P. Woiwod. 2001. Climate change impacts on insect management and conservation in temperate regions: Can they be predicted? *Agricultural and Forest Entomology* **3**: 233–240.
- Harrison, K J., J E. Hurley and M.E. Ostry. 1998. Disease Notes: First report of butternut canker caused by *Sirococcus clavigignenti-juglandacearum* in New Brunswick, Canada. *Plant Disease* **82**: 1282.
- Harvey, B.D., T. Nguyen-xuan, Y. Bergeron, S. Gautier and A. Leduc. 2003. Forest management planning based on natural disturbance and forest dynamics. Pages 395–432 in Burton, P.J., C. Messier, D.W. Smith, and W.L. Adamowicz. Editors. *Towards Sustainable Management of the Boreal Forest*. National Research Council Research Press, Ottawa, Ontario.
- Hawkins, C.D.B. and K.B. Shewan. 2000. Frost hardiness, height, and dormancy of 15 short-day, nursery-treated interior spruce seed lots. *Canadian Journal of Forest Research* **30**: 1096-1105.
- Heath, R. and R.I. Alfaro. 1990. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle. *Journal of the Entomological Society of British Columbia* **87**: 16-21.
- Heinrichs, M.L., J.A. Antos, R.J. Hebda, and G.B. Allen. 2002. *Abies lasiocarpa* (Hook.) Nutt. in the late-glacial and early-Holocene vegetation of British Columbia, Canada, and adjacent regions in Washington, USA. *Review of Palaeobotany and Palynology* **120**: 107-122.

- Henderson, N., E. Hogg, E. Barrow and B. Dolter. 2002. Climate change impacts on the Island Forests of the Great Plains and the implications for nature conservation policy. Prairie Adpatation Research Collaborative, University of Regina, Regina SK.
- Hennon, P., D. D'Amore, D. Wittwer, A. Johnson, P. Schaberg, G. Hawley, C. Beier, S. Sink and G. Juday. 2006. Climate warming, reduced snow, and freezing injury could explain the demise of yellow-cedar in southeast Alaska, USA. *World Resources Review* **18**: 427–450.
- Herrick, J.D. and R.B. Thomas. 1999. Effects of CO₂ enrichment on the photosynthetic light response of sun and shade leaves of canopy sweetgum trees (*Liquidambar styraciflua*) in a forest ecosystem. *Tree Physiology* **19**: 779-786.
- Hetherington, A.M. and F.I. Woodward. 2003. The role of stomata in sensing and driving environmental change. *Nature* **424**: 901-908.
- Higginbotham, K.O., J.M. Mayo, S. L'Hirondelle and D.K. Krystofiak. 1985. Physiological ecology of lodgepole pine (*Pinus contorta*) in an enriched CO₂ environment. *Canadian Journal of Forest Research* **15**: 417-421.
- Higgins, S.I., J. S. Clark, R. Nathan, T. Hovestadt, F. Schurr, J. M. V. Fragoso, M. R. Aguiar, E. Ribbens and S. Lavorel. 2003. Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology* **91**: 341-347.
- Hoddinott, J. and R. Scott. 1996. The influence of light quality and carbon dioxide enrichment on the cold hardiness of three conifer species seedlings. *Biotronics* **25**: 33-44.
- Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham and C. D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* **321**: 345-346.
- Hogg, E.H and P.A. Hurdle. 1995. The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? *Water, Air and Soil Pollution* **82**: 391-400.
- Hogg, E.H. and P. Y. Bernier. 2005. Climate change impacts on drought-prone forests in western Canada. *The Forestry Chronicle* **81**: 675-682.
- Hogg, E.H., J.P. Brandt and B. Kochtubajda. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research* **32**: 823–832.
- Hogg, E.H., J. Brandt and M. Michaelian. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research* **38**: 1373-1384.

- Iverson, L.R. and A.M. Prasad. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. *Forest Ecology and Management* **155**: 205–222.
- Iverson, L.R., M.W. Schwartz and A.M. Prasad. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography*. **13**: 209–219.
- Iverson, L.R., A.M. Prasad and S. Matthews. 2008a. Modeling potential climate change impacts on the trees of the northeastern United States. *Mitigation and Adaptation Strategies for Global Change* **13**: 487–516.
- Iverson, L.R., A.M. Prasad, B.J. Hale and E. K. Sutherland. 1999. Atlas of Current and Potential Future Distributions of Common Trees of the Eastern United States. General Technical Report NE-265, Radnor PA. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, 245 p.
- Iverson, L.R., A.M. Prasad, S.N. Matthews and M. Peters. 2008b. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* **254**: 390–406. See also <http://www.nrs.fs.fed.us/atlas>
- Jablonka, E. and G. Raz. 2009. Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *The Quarterly Review of Biology* **84**: 131-176.
- Jacoby, G. C. and R.D. D'Arrigo. 1997. Tree rings, carbon dioxide, and climatic change. *Proceedings of the National Academy of Sciences USA* **94**: 8350-8353.
- Johnsen, K.H. 1993. Growth and ecophysiological responses of black spruce seedlings to elevated CO₂ under varied water and nutrient additions. *Canadian Journal of Forest Research* **23**: 1033-1042.
- Johnsen, K.H. and J.E. Major. 1998. Black spruce family growth performance under ambient and elevated atmospheric CO₂. *New Forests* **15**: 271-281.
- Johnsen, K.H. and J.R. Seiler. 1996. Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO₂ concentrations and photoperiods. *Tree Physiology* **16**: 367-373.
- Johnsen, Ø. 1989. Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard. I. Frost hardiness in a phytotron experiment. *Scandinavian Journal of Forest Research* **4**: 317-330.
- Johnsen, Ø., C.G. Fossdal, N. Nagy, J. Mølmann, O.G. Dæhlen and T. Skrøppa. 2005. Climatic adaptation in *Picea abies* progenies is affected by the temperature during zygotic embryogenesis and seed maturation. *Plant, Cell & Environment* **28**: 1090–1102.

- Johnson, D. W., J.T. Ball and R.F. Walker. 1997. Effects of CO₂ and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. *Plant and Soil* **190**: 29-40.
- Johnson, E.A. and K. Miyanishi, editors. 2007. *Plant Disturbance Ecology - The Process And The Response*. Elsevier, London, UK.
- Johnston, M. and T. Williamson. 2005. Climate change implications for stand yields and soil expectation values: A northern Saskatchewan case study. *The Forestry Chronicle* **81**: 683-690.
- Johnston, M. and T. Williamson. 2007. A framework for assessing climate change vulnerability of the Canadian forest sector. *The Forestry Chronicle* **83**: 358-361.
- Johnston, M., J. Thorpe and B. Godwin. 2008. *Impacts of Climate Change on the Island Forests of Saskatchewan*. Publication Number 12168-1E08, Saskatchewan Research Council, Saskatoon, SK.
- Johnston, M., M. Campagna, P. Gray, H. Kope, J. Loo, A. Ogden, G. A. O'Neill, D. Price and T. Williamson. 2009. *Vulnerability of Canada's Tree Species to Climate Change and Management Options for Adaptation: An Overview for Policy Makers and Practitioners*. Canadian Council of Forest Ministers, Ottawa, ON.
- Johnston, M., T. Williamson, A. Munson, A. Ogden, M. Moroni, R. Parsons, D. Price and J. Stadt. 2010. *Climate Change and Forest Management in Canada: Impacts, Adaptive Capacity and Adaptation Options*. Sustainable Forest Management Network, Edmonton AB.
- Johnstone, J.F., T.N. Hollingsworth, F.S. Chapin and M.C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* **16**: 1281-1295.
- Karnosky, D.F., K.S. Pregitzer, D.R. Zak, M.E. Kubiske, G.R. Hendrey, D.A. Weinstein, M. Nosal and K.E. Percy. 2005. Scaling ozone responses of forest trees to the ecosystem level in a changing climate. *Plant, Cell & Environment* **28**: 965-981.
- Kawecki, T.J. and D. Ebert. 2004. Conceptual issues in local adaptation. *Ecology Letters* **7**: 1225-1241.
- Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO₂ in trees. *Plant Physiology* **102**: 472-480.
- King, G.A. and A.A. Herstrom. 1997. Holocene tree migration rates objectively determined from fossil pollen data. Pages 91-101 in Huntley, B., W. Cramer, A. Morgan, H.C. Prentice and J.R.M. Allen. Editors. *Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*. Springer Verlag, Berlin.

- King, J.S., R.B. Thomas and B.R. Strain. 1996. Growth and carbon accumulation in root systems of *Pinus taeda* and *Pinus ponderosa* seedlings as affected by varying CO₂, temperature and nitrogen. *Tree Physiology* **16**: 635-642.
- King, J.S., R.B. Thomas and B.R. Strain. 1997. Morphology and tissue quality of seedling root systems of *Pinus taeda* and *Pinus ponderosa* as affected by varying CO₂, temperature, and nitrogen. *Plant and Soil* **195**: 107-119.
- King, J.S., K.S. Pregitzer and D.R. Zak. 1999. Clonal variation in above- and below-ground growth responses of *Populus tremuloides* Michaux: influence of soil warming and nutrient availability. *Plant and Soil* **217**: 119-130.
- Kirschbaum, M.U.F. 2000. Forest growth and species distribution in a changing climate. *Tree Physiology* **20**: 309-322.
- Kirschbaum, M.U.F. 2005. A modeling analysis of the interaction between forest age and forest responsiveness to increasing CO₂ concentration. *Tree Physiology* **25**: 953-963.
- Kliejunas, J. T., B. W. Geils, J. M. Glaeser, E. M. Goheen, P. Hennon, M.-S. Kim, H. Kope, J. Stone, R. Sturrock and S. J. Frankel. 2009. Review of Literature on Climate Change and Forest Diseases of Western North America. General Technical Report PSW-GTR-225, USDA Forest Service, Albany, CA.
- Körner, C., R. Asshoff, O. Bignucolo, S. Hättenschwiler, S.G. Keel, S. Peláez-Riedl, S. Pepin, R.T.W. Siegwolf and G. Zotz. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. *Science* **309**: 1360-1362.
- Kotyk, M. E. A., J.F. Basinger and E.E. McIver. 2003. Early Tertiary *Chamaecyparis* Spach from Axel Heiberg Island, Canadian High Arctic. *Canadian Journal of Botany* **81**: 113-130.
- Kouwenberg, L., R. Wagner, W. Kürschner and H. Visscher. 2005. Atmospheric CO₂ fluctuations during the last millennium reconstructed by stomatal frequency analysis of *Tsuga heterophylla* needles. *Geology* **33**: 33-36.
- Kramer, P.J. 1986. The role of physiology in forestry. *Tree Physiology* **2**: 1-16.
- Kremer, A. 2007. How well can existing forests withstand climate change? Pages 3–17 in Koskela, J., A. Buck, and E. Teissier du Cros. Editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy.
- Kubiske, M. E. and K.S. Pregitzer. 1996. Effects of elevated CO₂ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology* **16**: 351-358.

- Kubiske, M.E., K.S. Pregitzer, D.R. Zak and C.J. Mikan. 1998. Growth and C allocation of *Populus tremuloides* genotypes in response to atmospheric CO₂ and soil N availability. *The New Phytologist* **140**: 251-260.
- Kubiske, M.E., V.S. Quinn, W.E. Heilman, E.P. McDonald, P.E. Marquardt, R.M. Teclaw, A.L. Friend and D.F. Karnosky. 2006. Interannual climatic variation mediates elevated CO₂ and O₃ effects on forest growth. *Global Change Biology* **12**: 1054 - 1068.
- Kulakowski, D., T.T. Veblen and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *Journal of Biogeography* **30**: 1445-1456.
- Kurz, W.A., S.J. Beukema and M.J. Apps. 1998. Carbon budget implications of the transition from natural to managed disturbance regimes in forest landscapes. *Mitigation and Adaptation Strategies for Global Change* **2**: 405-421.
- Kurz, W.A., C.C. Dymond, G. Stinson, G.J. Rampley, E.T. Neilson, A.L. Carroll, T. Ebata and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**: 987-990.
- Kvaalen, H. and Ø. Johnsen. 2008. Timing of bud set in *Picea abies* is regulated by a memory of temperature during zygotic and somatic embryogenesis. *The New Phytologist* **177**: 49-59.
- Ladeau, S.L. and J.S. Clark. 2006. Elevated CO₂ and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. *Global Change Biology* **12**: 822-833.
- Ladjal, M., D. Epron and M. Ducrey. 2000. Effects of drought preconditioning on thermotolerance of photosystem II and susceptibility of photosynthesis to heat stress in cedar seedlings. *Tree Physiology* **20**: 1235-1241.
- Landhäusser, S.M., A. DesRochers and V.J. Lieffers. 2001. A comparison of growth and physiology in *Picea glauca* and *Populus tremuloides* at different soil temperatures. *Canadian Journal of Forest Research* **31**: 1922-1929.
- Lau, J.A., J. Peiffer, P.B. Reich and P. Tiffin. 2008. Transgenerational effects of global environmental change: long-term CO₂ and nitrogen treatments influence offspring growth response to elevated CO₂. *Oecologia* **158**: 141-150.
- Lemmen, D.S., F.J. Warren, J. Lacroix and E. Bush, editors. 2008. *From Impacts to Adaptation: Canada in a Changing Climate 2007*. Government of Canada.
- Lempriere, T.C., P.Y. Bernier, A.L. Carroll, M.D. Flannigan, R.P. Gilson, D.W. McKenney, E.H. Hogg, J.H. Pedlar and D. Blain. 2008. *The Importance of Forest Sector Adaptation*

- to Climate Change. Information Report NOR-X-416E, Natural Resources Canada, Ottawa, Ont.
- Lenihan, J.M. and R.P. Neilson. 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. *Climatic Change* **30**: 27–56.
- LePage, B.A. 2003. A new species of *Tsuga* (Pinaceae) from the middle Eocene of Axel Heiberg Island, Canada, and an assessment of the evolution and biogeographical history of the genus. *Botanical Journal of the Linnean Society* **141**: 257-296.
- Lewis, J.D., D. Olszyk and D.T. Tingey. 1999. Seasonal patterns of photosynthetic light response in Douglas-fir seedlings subjected to elevated atmospheric CO₂ and temperature. *Tree Physiology* **19**: 243-252.
- Lewis, J.D., M. Lucash, D. Olszyk and D.T. Tingey. 2001. Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO₂ and temperature. *Plant, Cell & Environment* **24**: 539-548.
- Lewis, J.D., Lucash, M., Olszyk, D. M., and Tingey, D. T. 2002. Stomatal responses of Douglas-fir seedlings to elevated carbon dioxide and temperature during the third and fourth years of exposure. *Plant, Cell & Environment* **25**: 1411-1421.
- Li, P., J. Beaulieu, A. Corriveau and F. Bousquet. 1997. Genetic structure and patterns of genetic variation among populations in eastern white spruce (*Picea glauca*). *Canadian Journal of Forest Research* **27**: 189-198.
- Lippert, M., K.-H. Häberle, K. Steiner, H.-D. Payer and K.-E. Rehfuss. 1996. Interactive effects of elevated CO₂ and O₃ on photosynthesis and biomass production of clonal 5-year-old Norway spruce [*Picea abies* (L.) Karst.] under different nitrogen nutrition and irrigation treatments. *Trees – Structure and Function* **10**: 382-392.
- Llorens, L. J., J. Llusà, E.H. Murchie, J. Peñuelas and D.J. Beerling. 2009a. Monoterpene emissions and photoinhibition of “living fossil” trees grown under CO₂ enrichment in a simulated Cretaceous polar environment. *Journal of Geophysical Research* **114**: G01005 1-15.
- Llorens, L., C.P. Osborne and D.J. Beerling. 2009b. Water-use responses of ‘living fossil’ conifers to CO₂ enrichment in a simulated Cretaceous polar environment. *Annals of Botany* **104**: 179-188.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field and D. D. Ackerly. 2009. The velocity of climate change. *Nature* **462**: 1052-1057.
- Logan, B. A., A. Combs, K. Myers, R. Kent, L. Stanley and D.T. Tissue. 2009. Seasonal response of photosynthetic electron transport and energy dissipation in the eighth year of exposure to elevated atmospheric CO₂ (FACE) in *Pinus taeda* (loblolly pine). *Tree Physiology* **29**: 789-798.

- Logan, J.A., J. Regniere and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* **1**: 130–137.
- Loo, J. and K. O'Leary. 2009. Vulnerability of Forest Tree Genetic Resources to Climate Change. Pages 1-11. Unpublished manuscript, Canadian Forest Service, Fredericton, NB.
- Luckman, B. and T. Kavanagh. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* **29**: 371-380.
- MacDonald, G.M., T.W.D. Edwards, K.A. Moser, R. Pienitz and J.A. Smol. 1993. Rapid responses of treeline vegetation to past climate warming. *Nature* **361**: 243–256.
- Malcolm, J.R., D. Puric-Mladenovic and H. Shi. 2005a. Projected tree distributions, tree migration rates, and forest types in Ontario under a 2°C global temperature rise. , Pages 51–99 in: Malcolm, J.R. Editor. Implications of a 2°C global temperature rise for Canada's natural resources. Report to World Wildlife Fund, 30 November 2005, Toronto, Ontario.
- Malcolm, J.R., H. Shi and D. Puric-Mladenovic. 2005b. Implications of climate change on disturbance regimes, carbon stocks, management and biodiversity of Canada's boreal forests. Pages 100–109 in Malcolm, J.R. Editor. Implications of a 2°C global temperature rise for Canada's natural resources. Report to World Wildlife Fund, 30 November 2005, University of Toronto, Toronto, Ontario.
- Mallett, K.I. and W.J.A. Volney. 1990. Relationships among jack pine budworm damage, selected tree characteristics, and *Armillaria* root rot in jack pine. *Canadian Journal of Forest Research* **20**: 1791-1795.
- Marfo, J. and Q.-L. Dang. 2009. Interactive effects of carbon dioxide concentration and light on the morphological and biomass characteristics of black spruce and white spruce seedlings. *Botany* **87**: 67-77.
- Margolis, H. A. and L.-P. Vézina. 1990. Atmospheric CO₂ enrichment and the development of frost hardiness in containerized black spruce seedlings. *Canadian Journal of Forest Research* **20**: 1392-1398.
- Mattson, W. J. and R. A. Hack. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* **37**: 110-118.
- Mátyás, C. 2006. Migratory, genetic and phenetic response potential of forest tree populations facing climate change. *Acta Silvatica and Lignaria Hungarica* **2**: 33-46.
- Mátyás, C. 2007. What do field trials tell about the future use of forest reproductive material? Pages 53-68 in Koskela, J., A. Buck, and E. Tessier du Cros. Editors. Climate change and

- forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, IT.
- Mátyás, C. 2010. Forecasts needed for retreating forests. *Nature* **464**: 1271.
- Mátyás, C., G. G. Vendramin and B. Fady. 2009. Forests at the limit: evolutionary - genetic consequences of environmental changes at the receding (xeric) edge of distribution. Report from a research workshop. *Annals of Forest Science* **66**: 800-803.
- McCreary, D.D., D.P. Lavender and R.K. Hermann. 1990. Predicted global warming and Douglas-fir chilling requirements. *Annals of Forest Science* **47**: 325–330.
- McDowell, N., W.T. Pockman, C.D. Allen, D.D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D.G. Williams and E.A. Yezzer. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *The New Phytologist* **178**: 719-739.
- McKenney, D., B. G. Mackey and D. Joyce. 1999. Seedwhere: a computer tool to support seed transfer and ecological restoration decisions. *Environmental Modelling & Software* **47**: 589-595.
- McKenney, D., J. Pedlar and G. O'Neill. 2009. Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *The Forestry Chronicle* **85**: 258–266.
- McKenney, D., J.H. Pedlar, K. Lawrence, K. Campbell and M.F. Hutchinson. 2007. Potential impacts of climate change on the distribution of North American trees. *BioScience* **57**: 939–948.
- McLachlan, J.S., J.S. Clark and P.S. Manos. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* **86**: 2088–2098.
- McLachlan, J.S., J.J. Hellmann and M.W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* **21**: 297–302.
- Medlyn, B. E., C.V.M. Barton, M.S.J. Broadmeadow, R. Ceulemans, P. de Angelis, M. Forstreuter, M. Freeman, S.B. Jackson, S. Kellomäki, E. Laitat, A. Rey, P. Roberntz, B.D. Sigurdsson, J. Strassemeier, K. Wang, P.S. Curtis and P.G. Jarvis. 2001. Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *The New Phytologist* **149**: 247-264.
- Messaoud, Y., Y. Bergeron and H. Asselin. 2007. Reproductive potential of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Québec. *American Journal of Botany* **94**: 746-754.

- Meunier, C., L. Sirois and Y. Bégin. 2007. Climate and *Picea mariana* seed maturation relationships: A multi-scale perspective. *Ecological Monographs* **77**: 361-376.
- Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* **20**: 685-692.
- Monserud, R.A., Y. Yang, S. Huang and N. Tchebakova. 2008. Potential change in lodgepole pine site index and distribution under climatic change in Alberta. *Canadian Journal of Forest Research* **38**: 343–352.
- Montréal Process. 2009. Criteria and indicators for the conservation and sustainable management of temperate and boreal forests: Fourth Ed. (October 2009). ISBN: 978-0-9825274-0-3. Available on-line at: <http://www.mpci.org>.
- Morse, A.M., D.G. Peterson, M.N. Islam-Faridi, K.E. Smith, Z. Magbanua, S.A. Garcia, T.L. Kubisiak, H.V. Amerson, J.E. Carlson, C.D. Nelson and J.M. Davis. 2009. Evolution of genome size and complexity in *Pinus*. *PLoS ONE* **4**: e4332.
- Moser, S.C., R. E. Kasperson, G. Yohe and J. Agyeman. 2008. Adaptation to climate change in the Northeast United States: opportunities, processes, constraints. *Mitigation and Adaptation Strategies for Global Change* **13**: 643-659.
- Murray, M.B., I.D. Leith and P.G. Jarvis. 1996. The effect of long term CO₂ enrichment on the growth, biomass partitioning and mineral nutrition of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Trees - Structure and Function* **10**: 393-402.
- Murray, M.B., R.I. Smith, A. Friend and P.G. Jarvis. 2000. Effect of elevated [CO₂] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). *Tree Physiology* **20**: 421-434.
- Murray, M.B., R.I. Smith, I.D. Leith, D. Fowler, H.S.J. Lee, A.D. Friend and P.G. Jarvis. 1994. Effects of elevated CO₂, nutrition and climatic warming on bud phenology in Sitka spruce (*Picea sitchensis*) and their impact on the risk of frost damage. *Tree Physiology* **14**: 691-706.
- Nalder, I.A. 2002. Can patch models replicate observed stand dynamics? A test of BORFOR and FORSKA2V in the boreal forests of western Canada. Pp. 119–150 in: Nalder, I.A. Post-fire dynamics of the boreal forest floor: measurement and modelling of long-term carbon accumulation in boreal forests. Ph.D. Thesis, University of Alberta, Edmonton, Alberta.
- Nalder, I.A. and H.G. Merriam. 1995. Simulating carbon dynamics of the boreal forest in Pukaskwa National Park. *Water, Air and Soil Pollution* **82**: 283-298.
- Nielsen, C.C.N. and H.N. Rasmussen. 2009. Frost hardening and dehardening in *Abies procera* and other conifers under differing temperature regimes and warm-spell treatments. *Forestry* **82**: 43-59.

- Niemela, P. and W.J. Mattson. 1996. Invasion of North American forests by European phytophagous insects. *BioScience* **46**: 741-753.
- Nitschke, C. R. and J. L. Innes. 2008. Integrating climate change into forest management in South-Central British Columbia: An assessment of landscape vulnerability and development of a climate-smart framework. *Forest Ecology and Management* **256**: 313-327.
- Noble, I. R. and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**: 5-21.
- Norby, R.J., E.H. DeLucia, B. Gielen, C. Calfapietra, C.P. Giardina, J.S. King, J. Ledford, H.R. McCarthy, D.J.P. Moore, R. Ceulemans, P. De Angelis, A.C. Finzi, D.F. Karnosky, M.E. Kubiske, M. Lukac, K.S. Pregitzer, G.E. Scarascia-Mugnozza, W.H. Schlesinger and R. Oren. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* **162**: 18052–18056.
- Ogden, A. E. and J. Innes. 2007. Incorporating climate change adaptation considerations into forest management planning in the boreal forest. *International Forestry Review* **9**: 713-733.
- Ögren, E. 2001. Effects of climatic warming on cold hardiness of some northern woody plants assessed from simulation experiments. *Plant Physiology* **112**: 71-77.
- Oleksyn, J., M.G. Tjoelker and P.B. Reich. 1998. Adaptation to changing environment in Scots pine populations across a latitudinal gradient. *Silva Fennica* **32**: 129-40.
- Olszyk, D. M., C. Wise, E. VanEss, M. Apple and D.T. Tingey. 1998. Phenology and growth of shoots, needles, and buds of Douglas-fir seedlings with elevated CO₂ and (or) temperature. *Canadian Journal of Botany* **76**: 1991-2001.
- Olszyk, D. M., M.G. Johnson, D.T. Tingey, P.T. Rygielwicz, C. Wise, E. VanEss, A. Benson, M.J. Storm and R. King. 2003. Whole-seedling biomass allocation, leaf area, and tissue chemistry for Douglas-fir exposed to elevated CO₂ and temperature for 4 years. *Canadian Journal of Forestry Research* **33**: 269-278.
- O'Neill, G. and A. Yanchuk. 2005. A Primer on Seed Transfer for Compliance and Enforcement in B.C. Pages 1-6. BC Ministry of Forests and Range, Victoria, BC.
- O'Neill, G., N. Ukrainetz, M. Carlson, C. Cartwright, B. Jaquish, J. King, J. Krakowski, J. H. Russell, M. Stoehr, C. Y. Xie and A. Yanchuk. 2008a. Assisted Migration to Address Climate Change in British Columbia: Recommendations for Interim Seed Transfer Standards. Technical Report 048, BC Ministry of Forests and Range, Victoria, BC.

- O'Neill, G., A. Hamann and T. Wang. 2008b. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology* **45**: 1040-1049.
- O'Neill, G., G. Nigh, T. Wang and P. K. Ott. 2007. Growth response functions improved by accounting for nonclimatic site effects. *Canadian Journal of Forest Research* **37**: 2724-2730.
- Ono, H. 2003. The Mountain Pine Beetle: Scope of the Problem and Key Issues in Alberta. In: Shore, T.L., J.E. Brooks and J.E. Stone, editors. *Natural Resources Canada, Canadian Forest Service, Information Report BC-X-339*, Victoria, BC. 298 p.
- Oren, R., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maler, K. V. R. Schäfer, H. McCarthy, G. Hendrey, S. G. McNulty and G. G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* **411**: 469-472.
- Osborne, C. P. and D.J. Beerling. 2003. The penalty of a long, hot summer. photosynthetic acclimation to high CO₂ and continuous light in "living fossil" conifers. *Plant Physiology* **133**: 803-812.
- Overdieck, D. and K. Fenselau. 2009. Elevated CO₂ concentration and temperature effects on the partitioning of chemical components along juvenile Scots pine stems (*Pinus sylvestris* L.). *Trees – Structure and Function* **23**: 771-786.
- Overpeck, J.T., D. Rind and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* **343**: 51–53.
- Owens, J. N., Ø. Johnsen, O.G. Dæhlen and T. Skråppa. 2001. Potential effects of temperature on early reproductive development and progeny performance in *Picea abies* (L.) Karst. *Scandinavian Journal of Forest Research* **16**: 221-237.
- Papadopol, C. 2001. Adapting Existing Forests to Climate Change. Green Pages Directory for Environmental Technology (on-line journal <http://www.eco-web.com/edi/05934-02.html>). ECO Services International, Zurich CH.
- Paradis, A., J. Elkinton, K. Hayhoe and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change* **13**: 541–554.
- Parker, T. J., K.M. Clancy and R.L. Mathiasen. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology* **8**: 167–189.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*. **37**: 637-669.

- Pastor, J. and W.M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature* **334**: 55–58.
- Payette, S., M.-J. Fortin and I. Gamache. 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. *BioScience* **51**: 709–718.
- Pearson, R.G. and T.P. 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.
- Peterken, G. F. 2001. Ecological effects of introduced tree species in Britain. *Forest Ecology and Management* **141**: 31–42.
- Phillips, N. G., T.N. Buckley and D. Tissue. 2008. Capacity of old trees to respond to environmental change. *Journal of Integrative Plant Biology* **50**: 1355–1364.
- Poncet, B. N., P. Garat, S. Manel, N. Bru, J.-M. Sachet, A. Roques and L. Despres. 2009. The effect of climate on masting in the European larch and on its specific seed predators. *Oecologia* **159**: 527–537.
- Pontius, J.A., R.A. Hallett and J.C. Jenkins. 2006. Foliar chemistry linked to infestation and susceptibility to hemlock woolly adelgid (Homoptera: Adelgidae). *Environmental Entomology* **35**: 112–120.
- Poulson, M. E., R.A. Donahue, J. Konvalinka and M.R.T. Boeger. 2002. Enhanced tolerance of photosynthesis to high-light and drought stress in *Pseudotsuga menziesii* seedlings grown in ultraviolet-B radiation. *Tree Physiology* **22**: 829–838.
- Post, E. S., C. Pedersen, C.C. Wilmsers and M.C. Forchhammer. 2008. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* **89**: 363–370.
- Prasad, A.M., L.R. Iverson and A. Liaw. 2006. Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. *Ecosystems* **9**: 181–199.
- Prentice, I.C., M.T. Sykes and W. Cramer. 1993. A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* **65**: 51–70.
- Prentice, I.C., W.P. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud and A.M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* **19**: 117–134.
- Price, D.T. and M.J. Apps. 1996. Boreal forest responses to climate-change scenarios along an ecoclimatic transect in central Canada. *Climatic Change* **34**: 179–190.

- Price, D.T. and D. Scott. 2006. Large scale modelling of Canada's forest ecosystem responses to climate change. Final Report on Climate Change Action Fund Project A636. Climate Change Impacts and Adaptation Program, Natural Resources Canada, Ottawa, ON.
- Price, D.T., D.H. Halliwell, M.J. Apps and C.H. Peng. 1999a. Adapting a patch model to simulate the sensitivity of central-Canadian boreal ecosystems to climate variability. *Journal of Biogeography* **26**: 1101–1113.
- Price, D.T., C.H. Peng, M.J. Apps and D.H. Halliwell. 1999b. Simulating effects of climate change on boreal ecosystem carbon pools in central Canada. *Journal of Biogeography* **26**: 1237–1248.
- Price, D.T., R.J. Hall, B.S. Case, F. Raulier and M. Lindner. 2005. Exploring the impacts of climate change and adaptation options for boreal forest ecosystems. Summary Document No. 05-02. PARC (Prairie Adaptation Research Collaborative), University of Regina, Regina, SK. 12 p.
- Price, D.T., D.H. Halliwell, M.J. Apps, W.A. Kurz and S.R. Curry. 1997. Comprehensive assessment of carbon stocks and fluxes in a Boreal-Cordilleran forest management unit. *Canadian Journal of Forest Research* **27**: 2005-2016.
- Price, D.T., N.E. Zimmermann, P.J. van der Meer, M.J. Lexer, P. Leadley, I.T.M. Jorritsma, J. Schaber, D.F. Clark, P. Lasch, S. McNulty, J. Wu and B. Smith. 2001. Pattern and process of regeneration in gap models: Priority issues for studying forest responses to climate change. *Climatic Change* **51**: 475–508.
- Radeloff, V.C., D.J. Mladenoff and M.S. Boyce. 2000. Effects of interacting disturbances on landscape patterns: Budworm defoliation and salvage logging. *Ecological Applications* **10**: 233-247.
- Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner and W.H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* **58**: 501–517.
- Regniere, J., V. Nealis and K. Porter. 2009. Climate suitability and management of the gypsy moth invasion into Canada. *Biological Invasions* **11**: 135-148.
- Rehfeldt, G.E. 1994. Adaptation of *Picea engelmannii* populations to the heterogeneous environments of the Intermountain West. *Canadian Journal of Botany* **72**: 1197-1208.
- Rehfeldt, G.E. 2005. Geographic clines in genetic variation. Pages 223-262 in M. Marsden, M. Downing, and M. Riffe, eds. Quantitative Techniques for Deriving National Scale Data. Forest Health Technology Enterprise Team, USDA Forest Service, Fort Collins, CO, FHTET-05-12, Westminster, CO.

- Rehfeldt, G.E. and L.A. Gallo. 2001. Introduction of ponderosa pine and Douglas-fir to Argentina. *New Forests* **21**: 35-44.
- Rehfeldt, G. and B. Jaquish. 2010. Ecological impacts and management strategies for western larch in the face of climate change. *Mitigation and Adaptation Strategies for Global Change* **15**: 283–306.
- Rehfeldt, G.E., W.R. Wykoff and C.C. Ying. 2001. Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. *Climatic Change* **50**: 355-376.
- Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A.J. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs* **69**: 375-407.
- Rehfeldt, G.E., N.L. Crookston, M.V. Warwell and J.S. Evans. 2006. Empirical analyses of plant climate relationships for the western United States. *International Journal of Plant Science* **167**: 1123–1150.
- Rempel, R. S., J. Baker, P. C. Elkie, M. J. Gluck, J. Jackson, R. S. Kushneriuk, T. Moore and A. H. Perera. 2007. Forest policy scenario analysis: sensitivity of songbird community to changes in forest cover amount and configuration. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* [online] URL: <http://www.ace-eco.org/vol2/iss1/art5/> **2**: 1-32.
- Retallack, G. J. 2001. A 300-million-year record of atmospheric carbon dioxide from fossil plant cuticles. *Nature* **411**: 287-290.
- Ricciardi, A. and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. *Trends in Ecology and Evolution* **24**: 248-253.
- Richardson, D. M., J. J. Hellmann, J. S. McLachlan, D. F. Sax, M. W. Schwartz, P. Gonzalez, E. J. Brennen, A. Camacho, T. L. Root, O. E. Sala, S. H. Schneider, D. M. Ashe, J. R. Clark, R. Early, J. R. Etterson, E. D. Fielder, J. L. Gill, B. A. Minteer, S. Polasky, H. D. Safford, A. R. Thompson and M. Vellend. 2009. Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences* **106**: 9721-9724.
- Robinson, D., S. Beukema and L. Greig. 2008. *Vegetation Models and Climate Change: Workshop Results*. Prepared for Western Wildlands Environmental Threat Assessment Center, USDA Forest Service. Essa Technologies Ltd., Vancouver BC.
- Rohde, A. and O. Junttila. 2008. Remembrances of an embryo: long-term effects on phenology traits in spruce. *The New Phytologist* **177**: 2–5.
- Rossi, S., A. Deslauriers, T. Anfodillo, H. Morin, A. Saracino, R. Motta and M. Borghetti. 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *The New Phytologist* **170**: 301–310.

- Rossi, S., S. Simard, C. Rathgeber, A. Deslauriers and C. De Zan. 2009. Effects of a 20-day-long dry period on cambial and apical meristem growth in *Abies balsamea* seedlings. *Trees – Structure and Function* **23**: 85-93.
- Rothstein, D. E., D.R. Zak, K.S. Pregitzer and P.S. Curtis. 2000. Kinetics of nitrogen uptake by *Populus tremuloides* in relation to atmospheric CO₂ and soil nitrogen availability. *Tree Physiology* **20**: 265-270.
- Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. Pages 135-154 in Wein, R.W., and D.A. MacLean. Editors. *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley & Sons, Chichester, UK.
- Ruel, J. J. and M.P. Ayres. 1996. Variation in temperature responses among populations of *Betula papyrifera*. *Silva Fennica* **30**: 145-158.
- Rupp, T.S., F.S. Chapin III and A.M. Starfield. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. *Climatic Change* **48**: 399–416.
- Rweyongeza, D. M., N. K. Dhir, L. K. Bernhardt, C. Hansen and R. C. Yang. 2007a. Population differentiation of the lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) complex in Alberta: Growth, survival, and responses to climate. *Canadian Journal of Botany* **85**: 545-556.
- Rweyongeza, D. M., R. C. Yang, N. K. Dhir, L. K. Barnhardt and C. Hansen. 2007b. Genetic variation and climatic impacts on survival and growth of white spruce in Alberta, Canada. *Silvae Genetica* **56**: 117-127.
- Rygiewicz, P. T., M.G. Johnson, L.M. Ganio, D.T. Tingey and M.J. Storm. 1997. Lifetime and temporal occurrence of ectomycorrhizae on ponderosa pine (*Pinus ponderosa* Laws.) seedlings grown under varied atmospheric CO₂ and nitrogen levels. *Plant and Soil* **189**: 275-287.
- Sallas, L., E.-M. Luomala, J. Ultriainen, P. Kainulainen and J.K. Holopainen. 2003. Contrasting effects of elevated carbon dioxide concentration and temperature on Rubisco activity, chlorophyll fluorescence, needle ultrastructure and secondary metabolites in conifer seedlings. *Tree Physiology* **23**: 97-108.
- Savolainen, O., T. Pyhäjärvi and T. Knürr. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution and Systematics* **38**: 595-619.
- Savva, Y., B. Denneler, A. Koubaa, F. Tremblay, Y. Bergeron and M. G. Tjoelker. 2007. Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada. *Forest Ecology and Management* **242**: 636–647.

- Saxe, H., D.S. Ellsworth and J. Heath. 1998. Tree and forest functioning in an enriched CO₂ atmosphere. Tansley Review No. 98. *The New Phytologist* **139**: 395-436.
- Saxe, H., M.G.R. Cannell, Ø. Johnsen, M.G. Ryan and G. Vourlitis. 2001. Tree and forest functioning in response to global warming. Tansley Review No. 123. *The New Phytologist* **149**: 369–400.
- Schneider, R.R., A. Hamann, D. Farr, X. Wang and S. Boutin. 2009. Potential effects of climate change on ecosystem distribution in Alberta. *Canadian Journal of Forest Research* **39**: 1001–1010.
- Schwartz, M. D., R. Ahas, and A. Aasa. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* **12**: 343 - 351.
- Seppälä, R., A. Buck and P. Katila, eds. 2009. Adaptation of forests and people to climate change: A global assessment report. IUFRO, Helsinki, Finland. 224 pp.
- Sherry, R. A., X. Zhou, S. Gu, J.A.I. Arnone, D.S. Schimel, P.S. Verburg, L.L. Wallace and Y. Luo. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences USA* **104**: 198-202.
- Shugart, H.H. 1984. *A Theory of Forest Dynamics*. Springer-Verlag, New York, NY, USA.
- Slaney, M. 2006. Impact of elevated temperature and [CO₂] on spring phenology and photosynthetic recovery of boreal Norway spruce. Ph.D. Thesis, Forest Sciences. Swedish University of Agricultural Sciences, Alnarp, Sweden, 47 pp.
- Smit, B. and J. Wandel. 2006. Adaptation, adaptive capacity and vulnerability. *Global Environmental Change* **16**: 282-292.
- Soulé, P. T. and P.A. Knapp. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO₂ fertilization effect? *The New Phytologist* **171**: 379–390.
- Spittlehouse, D. 2005. Integrating climate change adaptation into forest management. *The Forestry Chronicle* **81**: 691-695.
- Spittlehouse, D.L. and R.B. Stewart. 2003. Adaptation to climate change in forest management. *BC Journal of Ecosystems and Management* **4**: 1-11.
- Starfield, A.M. and F.S. Chapin III. 1996 Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecological Applications* **6**: 842–864.

- St. Clair, J. B. and G. T. Howe. 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biology* **13**: 1441 - 1454.
- Stoehr, M.U., S.J. L'Hirondelle, W.D. Binder and J.E. Webber. 1998. Parental environment aftereffects on germination, growth, and adaptive traits in white spruce seedlings. *Canadian Journal of Forest Research* **28**: 418-426.
- Stratton, T. 2008. Modeling boreal forest response to climate variability in central Canada. M.Sc. Thesis, University of Ottawa, Ottawa ON. 178 p.
- Strimbeck, G. R., T.D. Kjellsen, P.G. Schaberg and P.F. Murakami. 2008. Dynamics of low-temperature acclimation in temperate and boreal conifer foliage in a mild winter climate. *Tree Physiology* **28**: 1365–1374.
- SFI (Sustainable Forestry Initiative). 2010. SFI 2010-2014 STANDARD. Sustainable Forestry Initiative, Washington DC, 14 pp. Available on-line at: [http:// www.sfiprogram.org](http://www.sfiprogram.org)
- Taylor, G., M.J. Tallis, C.P. Giardina, K.E. Percy, F. Miglietta, P.S. Gupta, B. Gioli, C. Calfapietra, B. Gielen, M.E. Kubiske, G.E. Scarascia-Mugnozza, K. Kets, S.P. Long and D.F. Karnosky. 2008. Future atmospheric CO₂ leads to delayed autumnal senescence. *Global Change Biology* **14**: 264–275.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips and S.E. Williams. 2004. Extinction risk from climate change. *Nature* **427**: 145-148.
- Thomas, S.C. and W.E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology* **22**: 117-127.
- Thomson, A.M. and W.H. Parker. 2008. Boreal forest provenance tests used to predict optimal growth and response to climate change. 1. Jack pine. *Canadian Journal of Forest Research* **38**: 157-170.
- Thomson, A.M., C.L. Riddell and W.H. Parker. 2009. Boreal forest provenance tests used to predict optimal growth and response to climate change: 2. Black spruce. *Canadian Journal of Forest Research* **39**: 143 - 153.
- Thorpe, J., N. Henderson and J. Vandall. 2006. Ecological and Policy Implications of Introducing Exotic Trees for Adaptation to Climate Change in the Western Boreal Forest. Publication Number 11776-1E06, Saskatchewan Research Council, Saskatoon, SK.
- Tissue, D., K.L. Griffin and J.T. Ball. 1999. Photosynthetic adjustment in field-grown ponderosa pine trees after six years of exposure to elevated CO₂. *Tree Physiology* **19**: 221-228.

- Tjoelker, M. G., J. Oleksyn and P.B. Reich. 1998a. Seedlings of five boreal species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology* **18**: 715-726.
- Tjoelker, M. G., Oleksyn, J., and Reich, P. B. 1998b. Temperature and ontogeny mediate growth response to elevated CO₂ in seedlings of five boreal tree species. *The New Phytologist* **140**: 197-210.
- Tjoelker, M. G., J. Oleksyn and P.B. Reich. 1999. Acclimation of respiration to temperature and CO₂ in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology* **5**: 679-691.
- Townend, J. 1993. Effects of elevated carbon dioxide and drought on the growth and physiology of clonal Sitka spruce plants (*Picea sitchensis* (Bong.) Carr.). *Tree Physiology* **13**: 389-399.
- Townend, J. 1995. Effects of elevated CO₂, water and nutrients on (*Picea sitchensis* (Bong.) Carr.) seedlings. *The New Phytologist* **130**: 193-206.
- Urban, D.L., M.R. Harmon and C.B. Halpern. 1993. Potential response of Pacific Northwestern forests to climatic change, effects of stand age and initial composition. *Climatic Change* **23**: 247-266.
- Utriainen, J. 2003. Global climate change: Threat for the vitality of northern conifers? *Eurasian Journal of Forest Research* **6**: 145-153.
- van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the Western United States. *Science* **323**: 521-524.
- Vitasse, Y., A.J. Porté, A. Kremer, R. Michalet and S. Delzon. 2009. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia* **161**: 187-198.
- Voelker, S. L., R.-M. Muzika, R.P. Guyette and M.C. Stambaugh. 2006. Historical CO₂ growth enhancement declines with age in *Quercus* and *Pinus*. *Ecological Monographs* **76**: 549-564.
- Volney, W.J.A. and R.A. Fleming. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment* **82**: 283-294.
- Volney, W.J.A. and R.A. Fleming. 2007. Spruce budworm (*Choristoneura spp.*) biotype reactions to forest and climate characteristics. *Global Change Biology* **13**: 1630-1643.

- Volney, W.J.A. and K.G. Hirsch. 2005. Disturbing forest disturbances. *The Forestry Chronicle* **81**: 662-668.
- Walker, R. F., D.R. Geisinger, D.W. Johnson and J.T. Ball. 1998. Atmospheric CO₂ enrichment and soil N fertility effects on juvenile ponderosa pine: Growth, ectomycorrhizal development, and xylem water potential. *Forest Ecology and Management* **102**: 33-43.
- Wang, K.-Y., S. Kellomäki, C. Li and T. Zha. 2003. Light and water-use efficiencies of pine shoots exposed to elevated carbon dioxide and temperature. *Annals of Botany* **92**: 53-64.
- Wang, T., A. Hamann, A. Yanchuk, 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.
- Wang, X. 2007. Effects of species richness and elevated carbon dioxide on biomass accumulation: a synthesis using meta-analysis. *Oecologia* **152**: 595-605.
- Wang, X., P.S. Curtis, K.S. Pregitzer and D.R. Zak. 2000. Genotypic variation in physiological and growth responses of *Populus tremuloides* to elevated CO₂ concentration. *Tree Physiology* **20**: 1019-1028.
- Wang, Z. M., M.J. Lechowicz and C. Potvin. 1994. Early selection of black spruce seedlings and global change: Which genotypes should we favor? *Ecological Applications* **4**: 604-616.
- Ward, J. K. and B.R. Strain. 1999. Elevated CO₂ studies: past, present and future. *Tree Physiology* **19**: 211-220.
- Way, D. A. and R.F. Sage. 2008. Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) B.S.P.]. *Global Change Biology* **14**: 624-636.
- Way, D. A., S.D. Seegobin and R.F. Sage. 2007. The effect of carbon and nutrient loading during nursery culture on the growth of black spruce seedlings: a six-year field study. *New Forests* **34**: 307-312.
- Webber, J. E., P. Ott, J.N. Owens and W. Binder. 2005. Elevated temperature during reproductive development affects cone traits and progeny performance in *Picea glauca* x *engelmannii* complex. *Tree Physiology* **25**: 1219-1227.
- Wiken, E.B. (compiler). 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series No. 19. Environment Canada, Hull, Québec. 26 p. + map.
- Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* **6**: 2621-2626.

- Williamson, T., S. J. Colombo, P. Duinker, P. Gray, R. Hennessey, D. Houle, M. Johnston, A. Ogden and D. L. Spittlehouse. 2009. Climate change and Canada's forests. Sustainable Forest Management Network and Natural Resources Canada.
- Woods, A. 2009. Free growing and climate change. Climate Change Seminar, B.C. Ministry of Forests and Range, available on-line at:
http://www.for.gov.bc.ca/ftp/HFP/external/!publish/ClimateChange/Seminar_Series/
- Woodward, F.I., M.R. Lomas and R.A. Betts. 1998. Vegetation–climate feedbacks in a greenhouse world. 1998. Philosophical Transactions of the Royal Society of London B. **353**: 29–39.
- Woodward, F.I., T.M. Smith and W.R. Emmanuel. 1995. A global primary productivity and phytogeography model. *Global Biogeochemical Cycles* **9**: 471–490.
- Wustman, B. A., E. Oksanen, D.F. Karnosky, A. Noormets, J.G. Isebrands, K.S. Pregitzer, G.R. Hendrey, J. Sober and G.K. Podila. 2001. Effects of elevated CO₂ and O₃ on aspen clones varying in O₃ sensitivity: can CO₂ ameliorate the harmful effects of O₃? *Environmental Pollution* **115**: 473-481.
- Yakimchuk, R. and J. Hoddinott. 1994. The influence of ultraviolet-B light and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species. *Canadian Journal of Forest Research* **24**: 1-8.
- Yamamura, K. and K. Kiritani. 1998. A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Applied Entomology and Zoology* **33**: 289-298.
- Yin, H. J., Q. Liu and T. Lai. 2008. Warming effects on growth and physiology in the seedlings of the two conifers *Picea asperata* and *Abies faxoniana* under two contrasting light conditions. *Ecological Research* **23**: 459-469.
- Ying, C. C., C. Thompson and L. Herring. 1989. Geographic variation, nursery effects, and early selection in lodgepole pine. *Canadian Journal of Forest Research* **19**: 832-841.
- Zhang, S. and Q.-L. Dang. 2005. Effects of soil temperature and elevated atmospheric CO₂ concentration on gas exchange, in vivo carboxylation and chlorophyll fluorescence in jack pine and white birch seedlings. *Tree Physiology* **25**: 523-531.
- Zhang, S. and Q.-L. Dang. 2007. Interactive effects of soil temperature and [CO₂] on morphological and biomass traits in seedlings of four boreal tree species. *Forest Science* **53**: 453-460.

Zobel, B. and J. Talbert. 1984. Applied forest tree improvement. John Wiley & Sons, NY.
505 pp.