The Role of Adaptation in Forest Management

Contents

Genetic resource management of forest trees traditionally covers three main topics: selection and breeding for genetic gain, regulating transfer of planting stock through seed transfer guidelines and seed zones, and maintaining adequate genetic diversity in breeding stock, plantations, and natural populations. The concept of adaptation is central to all three themes. On the following pages you can find information why adaptation is important for forest health and productivity, how we study adaptation in trees, how this knowledge translates into policies, and how you can implement effective management practices by understanding concepts and issues related to adaptation of trees.

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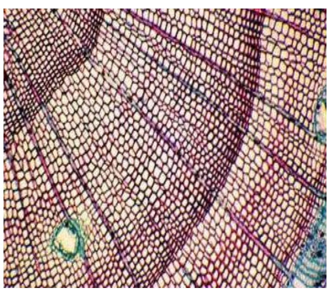
Dr. Hamann began his career working on tropical ecology topics in Kenya and the Philippines. He has also worked in South Carolina for Westvaco Corp. in tree improvement, and has been Assistant Director for the Centre for Forest Conservation Genetics at UBC. Since 2005 he is Assistant Professor at the University of Alberta, Dept. of Renewable Resources, where he developed a program in forest genetics and climate change research.

1. What is Adaptation?

Adaptation has been defined by evolutionary biologists as both a process and a product. The process of adaptation is driven by natural selection resulting in a characteristic that is essential for survival, also referred to as an adaptive trait. For example, conifers have evolved a number of characteristics that allow them to survive and thrive in cold and dry environments:

Buds are pre-formed embryonic shoots that can very quickly grow during favorable conditions in spring, so that the tree can make the most of a short growing season. During winter, buds protect the vulnerable growing tip of shoots. In evolutionary history, buds were a key adaptation that allowed plants to conquer cold environments at high latitudes and high elevations.

Needles are specially adapted compact leaves with a thick waxy layer that provides protection against UV radiation at high elevation, and prevents water loss in dry environments. The orientation of needles in all directions is also suited for incident sunlight at high latitudes to capture all available light (you may have noticed that it is very dark under conifer canopies).



The ***wood*** of conifers is also specially suited for cold and dry environments. Instead of a thin layer of large-diameter vessels responsible for active water transport in broadleaves, conifers have a wide sapwood column with narrow tracheids that transport water. This prevents freeze damage through air bubbles that develop when ice forms in winter, and the wide sapwood column also serves as water reservoir for dry periods.

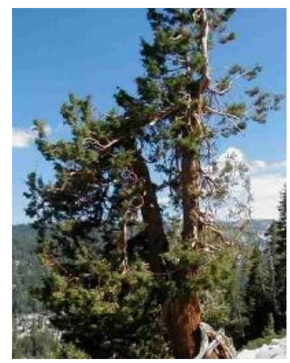
Many important adaptations are morphological characteristics, but there are also many important ***invisible adaptations***. For example, the biochemical process of photosynthesis that utilizes light energy to convert CO_2 into carbohydrates is optimized for cold temperatures in many conifers. In combination with evergreen needles, this allows conifers to always take advantage of suitable growing conditions including warm spells in early spring, fall, and sometimes even during winter.

Of course, there is ***more than one way to adapt*** to a particular environment. Aspen, for example, competes quite successfully with conifers in the boreal forest. Instead of leaves being capable to withstand harsh environmental conditions, aspen carefully times bud flush and leaf abscission with the best growing conditions. Aspen can also grow at elevations exceeding 3000m, where it uses phenolic glycosides in its leaves to absorb UV radiation (instead of having a protective wax layer).

2. Subspecies, Varieties, Ecotypes, and Clines

On the previous page, we have looked at adaptation as a characteristic of a species or a group of species. However, there is another important dimension to the concept: ***adaptation of populations*** within a species. Temperate tree species tend to be wide-ranging, experiencing a variety of different environments. The range of lodgepole pine, for example, stretches from Alaska to Mexico and populations can be found from sea level to well above 3000m elevation. It would be impossible for a lodgepole pine seedling collected from the Pacific coast to survive in Alberta because it is not adapted to the much colder winter conditions here. Adaptation of populations within a species to different environments can lead to the formation of subspecies, varieties, ecotypes, or populations of a cline. All these subdivisions can also be referred to as ***genotypes*** because they are genetically distinct.

The term ***subspecies*** is typically used for geographically isolated populations of a species (e.g. by oceans or mountain ranges). Subspecies show clearly visible differences in morphology, but they are still capable of interbreeding (i.e. the evolutionary speciation process is not quite complete).



Varieties also show visible differences in some traits, but the differences tend to be less pronounced than for subspecies. Varieties are also not always geographically isolated. Lodgepole pine, for example, is subdivided into four varieties: shorepine on the Pacific coast (right image), the rocky mountain variety of the interior (left image), as well as two other varieties in California and Nevada.

The term ***ecotype*** is used for at least somewhat geographically isolated (disjunct) populations of a species with limited genetic exchange through pollen and seed. The populations are not visibly different but there are physiological adaptations to different environments. In an evolutionary context, ecotypes can be thought of as an early stage of speciation, potentially leading to different subspecies, or even to different species under continued isolation and selection.

There is another type of genetic structure when adaptation occurs along an environmental gradient within the range of a species. This is called a ***cline***. Populations of a cline are not geographically isolated, and gene flow among populations prevents major differentiation or speciation. Clines can be found along elevational or latitudinal gradients. Populations of a cline are adapted to conditions along this environmental gradient.

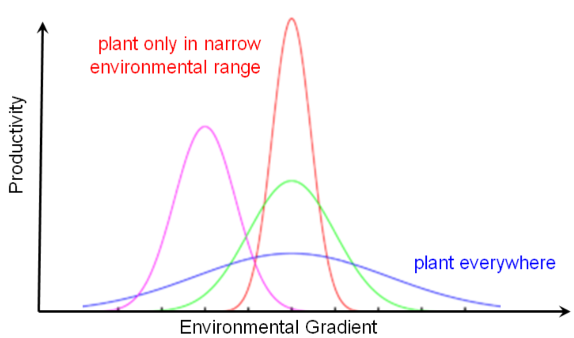
While populations of clines and ecotypes are not visibly different in natural populations, their adaptations can be investigated in ***provenance trials***, where seedlings from different locations are grown in a common environment to reveal genetic differences.

3. Adaptation and Forest Management

How is adaptation relevant for forest management? There are some obvious implications. If we choose planting stock that is well adapted to local growing conditions, our forests will be healthy and productive. The use of planting stock that lacks important adaptive traits may lead to immediate or long-term problems. Trees that are stressed because of mal-adaptation have ***suboptimal productivity*** and tend to be ***vulnerable to insect pests and diseases***. Sometimes these problems only become apparent after many years. For example, an exotic species from Norway that we plant in Alberta may grow very well for many years until an infrequent drought or cold event that never occurs in its home range causes major damage to trees or loss of the entire plantation.

If we want to optimize forest productivity and health, there are also more subtle considerations in choosing well adapted species, varieties, or genotypes. For this, we need to understand another concept: ***phenotypic plasticity***. Phenotypic plasticity is the ability of a tree to adapt to different environmental conditions by changing its morphological or physiological characteristics (without a genetic change through evolution). For example, if nutrient conditions are poor, a tree may adapt by allocating more resources to root growth. If trees are exposed to drought condition, they may adapt by changing leaf size and thickness or by altering physiological pathways that result in higher water use efficiency. This ability to adapt through phenotypic plasticity is more important for trees than any other organism, because they cannot move away from damaging environments and have to be able to handle environmental variability throughout a long lifetime.

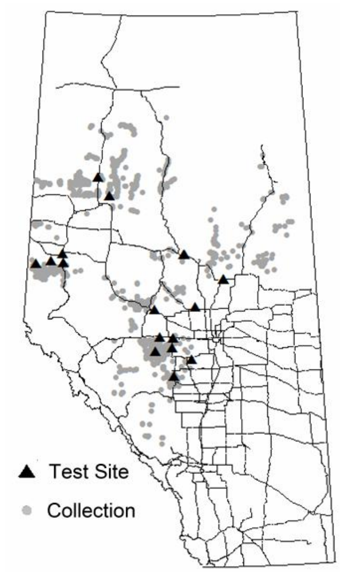
We can think of phenotypic plasticity as an adaptive trait itself. Species or populations that are subjected to strong environmental variability may evolve a high degree of phenotypic plasticity and become **generalists**. Species or populations that experience very stable environments may evolve very narrow environmental tolerances and become **specialists**. Often, there is a tradeoff between the ability to tolerate a wide range of environments and optimal fitness and productivity in a narrow environmental niche. The blue line represents a tree that is a "Jack of all trades, but master of none".



The red line represents a tree that is doing very well in one particular environment but is useless beyond its narrow range of specialization. In genetic resource management, we try to select genotypes that are **productive as well as widely adapted** for reforestation. Alternatively, we can optimize productivity of more narrowly adapted planting stock by **matching them to the environment** where they do best. The next section explains how.

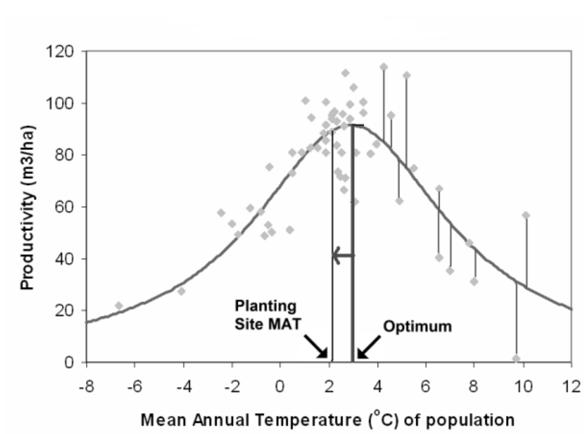
4. Genetic testing with provenance trials

Provenance trials are a special type of plantation experiment that helps us understand how trees are adapted to different environmental conditions through genetic adaptation or phenotypic plasticity. ***Provenance*** means "origin" and refers to a population of trees that come from a particular location. To establish a provenance trial series, seeds are collected throughout an area of interest. This can be the entire species range or an administrative region as on the figure to the right. Then, the seedlings from all collection locations are planted together in a systematic experimental design on one or preferably multiple sites.



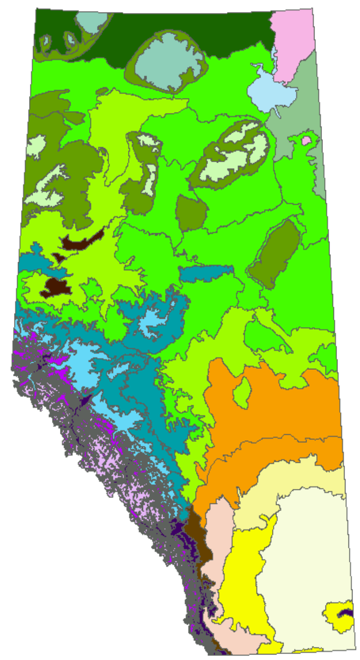
In the photo below, seedlings from the different source location were planted in row plots and you can quite easily see how they differ in performance. The sources that grow best can be considered best adapted to the planting site conditions, and those are the sources that we prefer for reforestation on sites that are similar to the test environment. As you can imagine, provenance testing is very expensive long-term research, and comprehensive trial series are only possible for the most valuable forest tree species in Alberta: white spruce, black spruce, lodgepole pine, tamarack, and aspen.

Data from provenance trials can be analyzed to understand how species adapt to environmental conditions in a general way: do we have a fine genetic subdivision with many different provenances that are specialists to their particular niche, or is the species genetically undifferentiated? Do provenances differ in their phenotypic plasticity? The data can further reveal non-optimal adaptation of natural populations. For example, the figure to the right suggests that provenances that come from slightly warmer locations (3°C) generally perform better than provenances that come from locations that match the planting site environment (2°C). This type of information can be used to develop general **seed transfer guidelines** for reforestation that help to improve productivity of our forests.

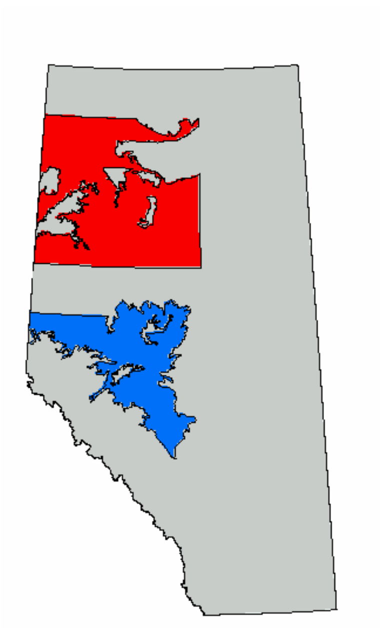


5. Seed zones and controlled parentage program regions

How do we accomplish the goal of ensuring adaptation of planting stock, and thereby optimum forest productivity and health? We have seen in the previous section that provenance testing can guide us in understanding to which environmental gradients tree populations are adapted, and how narrow their niche of optimum productivity is. However, even for commercially important forest trees we cannot afford to thoroughly test all provenances at all locations. We can, however, derive some general principles from provenance testing. One general result is ***local optimality***: provenances that originate near the test site often perform best. A second general result is the ***importance of climate*** as a selective force that has shaped adaptive traits in trees over the last few thousands of years. We often find differentiation in adaptive traits that are related to drought resistance, timing of the beginning and end of the growing season, frost hardiness, or growing season temperature.



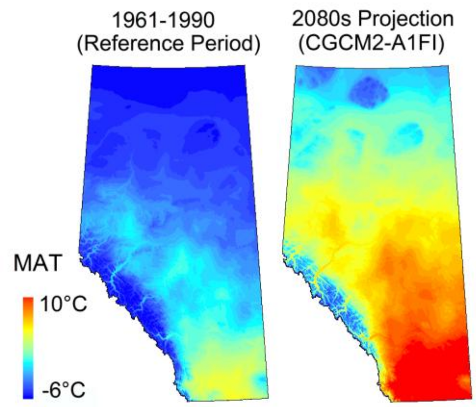
By delineating climatic or ecological regions and using only planting stock that originate within these regions, we can usually be sure that no loss of productivity or forest health occurs due to mal-adaptation. In Alberta, we have a framework of 90 ***seed zones*** shown on the image to the right. An alternative that is less sophisticated but is used in some other jurisdictions are ***seed transfer guidelines***. Before we adopted the seed zone system in Alberta, movement of seed was restricted by a transfer guideline that specified a maximum of 80 km distance and 500m elevation movement from source location to a planting site to avoid mal-adaptation.

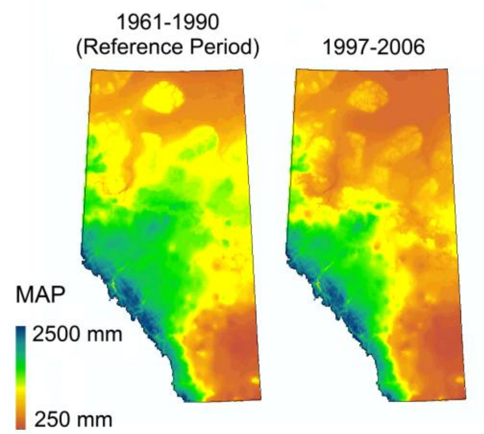


The above seed zone system applies to all collections from natural stands on public lands in Alberta. However, for white spruce, black spruce, lodgepole pine, and tamarack we also have material from controlled parentage programs that underwent extensive testing and selection. Because we know much more about the adaptability of this well tested planting material, there is an alternative delineation of ***controlled parentage program regions***, for deployment of planting stock that comes from tree improvement programs. Controlled parentage program regions tend to be larger than seed zones because the genotypes were tested over a wide range of environments and selected to be ***productive as well as widely adapted*** to various test site conditions. An example of for proposed aspen regions is shown on the left. You can find maps of controlled parentage program regions for other species on subsequent pages.

6. Adaptation and climate change

Given that climate conditions are a major selective force that results in physiological and morphological adaptation of tree population to local climate, global climate change is a major concern. If climate change projections are correct, we will see sub-optimal productivity and mal-adapted forests throughout Alberta in the near future. Over the past two decades, Alberta has experienced a warming trend of approximately 0.7°C in mean annual temperature (MAT) that matches or exceeds predictions from global circulation models. Those models also predict 3-5°C warming by the end of the century (figure top right). Over the past 20 years, we have also seen a pronounced trend towards drier condition with up to 25% less precipitation in central Alberta than two decades ago (figure bottom right).





On one hand, there may be reason for optimism. Forest productivity of boreal and sub-boreal ecosystems should increase considerably under moderate warming (1-2°C) due to an extended growing season, resulting in economic gains that match or exceed genetic gains from tree improvement efforts. On the other hand, temperature increases in the order of 3-5°C in combination with drier conditions will likely have negative consequences. Exceptional drought conditions in 2001 and 2002 have already caused dieback in aspen (photo below) and white spruce stands in central Alberta and generally reduced forest productivity during these years throughout the province.

Revising seed zones and controlled parentage program regions to match planting stock to new climate realities will become an important tool in the future to maintain forest healthy and productivity in the province. Data from our provenance trial programs that allow us to understand how species are adapted to various climatic factors will be crucial in meeting this challenge.

7. Research programs and publications

Scientific research and experimental field trials to study adaptation, effects of seed transfer, and climate change impacts are carried out cooperatively by provincial and federal government agencies, industry, and academia. The ***Alberta Tree Improvement and Seed Centre*** near Smoky Lake, operated by Alberta Sustainable Resource Development, establishes and maintains long-term field trials and studies environmental response of genotypes and populations to present and future climates. The ***Canadian Forest Service*** conducts research on climate change impacts and has a strong scientific program on forest pest and diseases. Industry initiatives and cooperatives (***HASOC, WBAC, FGAA, ALPAC***) maintain a large number of genetic trials to evaluate adaptation and field performance of aspen, poplar, white spruce and lodgepole pine. The ***University of Alberta*** has several research programs in forest genetics that study adaptation of forest trees and develop climate change adaptation strategies for the forestry sector.

Below is a selection of scientific studies and publications from these organizations that forms the basis of policies that guide forest genetic resource management in Alberta:

Li, B. 1995. Aspen improvement strategies for western Canada - Alberta and Saskatchewan. Forestry Chronicle 71: 720-724.

Morgenstern, E. K., and T. J. Mullin. 1990. Growth and survival of black spruce in the range-wide provenance study. Canadian Journal of Forest Research 20: 130-143.

Rajora, O., and B. P. Dancik. 2000. Population genetic variation, structure, and evolution in Engelmann spruce, white spruce, and their natural hybrid complex in Alberta. Canadian Journal of Botany 78: 768-780.

Rweyongeza, D. M., N. K. Dhir, L. K. Barnhardt, C. Hansen, and R. C. Yang. 2007. 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. 2007. Genetic variation and climatic impacts on survival and growth of white spruce in Alberta, Canada. Silvae Genetica 56: 117-127.

Wei, R. P., S. D. Han, N. K. Dhir, and F. C. Yeh. 2004. Population variation in growth and 15-year-old shoot elongation along geographic and climatic gradients in black spruce in Alberta. Canadian Journal of Forest Research 34: 1691-1702.

Wu, H. X., F. C. Yeh, N. K. Dhir, R. P. Pharis, and B. P. Dancik. 1997. Genotype by environment interaction and genetic correlation of greenhouse and field performance in Pinus contorta ssp. latifolia. Silvae Genetica 46: 170-175.

8. Policies, practices & what you can do

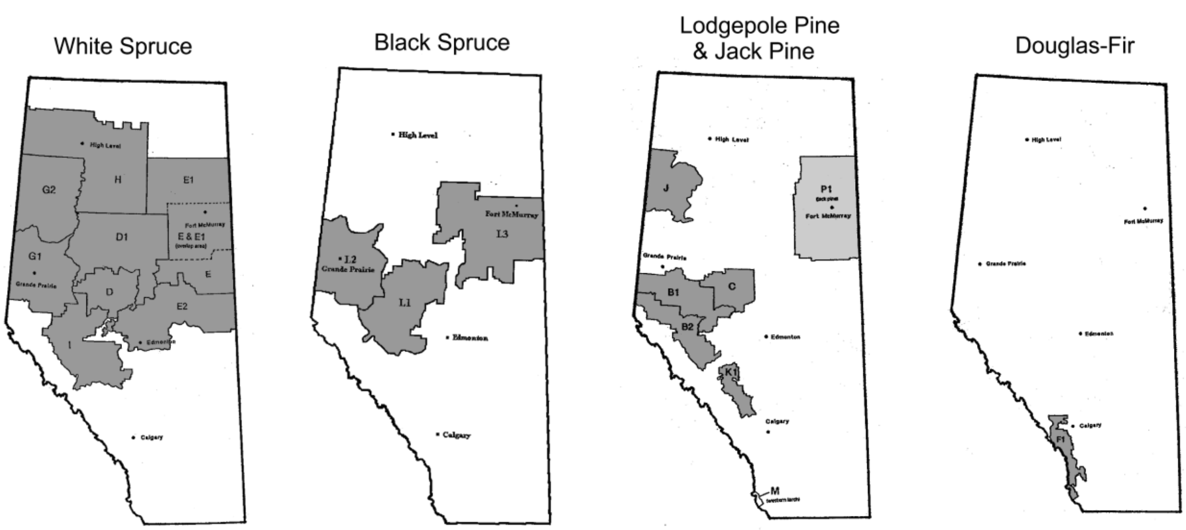
A comprehensive framework for collection, storage, handling, and deployment of seed and vegetative propagules were first released in 2003 as Standards for Tree Improvement in Alberta (STIA). This document has recently been updated and is now referred to as the **Alberta Forest Genetic Resource Management and Conservation Standards** (FGRMS). Understanding and following these guidelines will ensure that planting stock is well adapted to the planting site, resulting in optimum productivity and forest health.

As previously mentioned, there are two main sets of regulations governing collection, handling, and deployment of genetic materials for reforestation on public lands. Collections of seed or vegetative propagules from natural stands are referred to as **Stream 1 material**. The standards explain how this material needs to be registered, stored, propagated, and deployed. The Alberta seed zone system is used to ensure that planting stock is well adapted by planting Stream 1 material within the same seedzone from which it was collected.

- As a practitioner, you can ensure successful plantation establishment and release from reforestation obligations by making sure that appropriate collections of tree seed for your management unit are available.

As an alternative to collections from natural stands, Alberta Sustainable Resource Development recommends the use of genetically improved planting stock known as **Stream 2 material**. This material undergoes selection and/or breeding, with a known pedigree of individuals. In Alberta, this is called ***Controlled Parentage Program*** (CPP) and involves testing of selections or progeny for adaptation across multiple sites (3 test sites if provenances come from within the CPP region and 5 test sites if they were transferred from outside the CPP region boundaries). In addition to being well adapted, Stream 2 material is also selected for superior growth and/or disease resistance.

- Using Stream 2 material has many potential advantages not only with respect to productivity but also to maximize the adaptability of populations to changing climate. At the moment, there are 24 controlled parental programs, with approximately half of them operational as of 2009.



9. Reading materials and resources

Adaptation of forest trees

This short book explains in detail how trees are adapted to their environment and how this knowledge can be applied in forest management. This book comprehensively reviews scientific publications with an emphasis on research in Canada. The book can also be accessed via the ebrary on-line reader:

Morgenstern, E. K. 1996. Geographic Variation in Forest Trees. Genetic Basis and Application of Knowledge in Silviculture. University of British Columbia Press, Vancouver, BC, Canada.

Principles of seed zones and seed transfer guidelines

This review article explains the principles and science behind the development of seed zones and transfer guidelines. It comprehensively reviews the literature and provides a history of policies and practices in North America, with an emphasis on British Columbia:

Ying, C. C., and A. D. Yanchuk. 2006. The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. Forest Ecology and Management 227:1-13.

For additional information on the use of planting stock for reforestation in Alberta, read this the Alberta Forest Genetics Council fact sheet:

AFGRC 2008. Genetic resources and reforestation

Climate change adaptation strategies for forestry

This Nature news article explains what options we have in adapting forest management to climate change and discusses the risks involved in changing current policies and practices:

Marris, E. 2009. Planting the forest of the future. Nature 459: 906-908

For a background on climate change issues and a policy position advocated by the Alberta Forest Genetics Council, this fact sheet provides a good overview:

AFGRC 2008. Climate change and genetic resources

This web page by the University of Alberta, Department of Renewable Resources, provides up-to-date tools and publications for climate change related research in Alberta:

http://www.ales.ualberta.ca/rr/climate-change.cfm