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Old-growth forests: a science perspective - preliminary results of the conference

atural Resources Canada -Canadian Forest Service, in partnership with the Ontario Ministry of Natural Resources, Domtar, Tembec, Abitibi Consolidated, the Model Forest Network, and the Upper Lakes Environmental Research Network (ULERN), hosted a symposium on Canadian old-growth forests, in Sault Ste. Marie, Ontario, from October 15-19, 2001.

The purpose of the meeting was to showcase science specifically dealing with old forests conducted over the past decade in Canada. Another objective was to produce a book that could relate the state-of-theart knowledge about old forests to scientists, and provide information for managers and policy-makers. About 200 delegates attended the symposium, representing most Canadian provinces, the United States, Europe, and Japan. Governments, academics, industry, and non-government organizations were well represented (56, 26, 9, and 9% respectively). The symposium format included invited plenary papers, contributed papers, workshops, a panel discussion, and a highly successful field tour to see two old-forest areas.

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As with any science meeting, this conference produced its share of discussions, agreements, and disagreements. Nevertheless, considerable consensus was reached



Cathedral Grove, Vancouver Island. Winning old-growth photo by Barbara Carroll, Upper Kingsclear, NB.

among delegates on several issues. As well, plenary speakers provided various descriptions of old forests and their attributes that received favorable responses. Delegates generally agreed

that we must distinguish between primary (never logged) and secondary (logged but regenerated) forests, that old growth may develop within either but not necessarily maintain the same

> qualities or processes, and that there is a need to preserve natural processes within primary forests as benchmarks. In the case of primary forests, the processes would continue through time, even when the original old trees were eliminated by normal disturbances. Lee Frelich argued that the size (or landscape) of such primary forest reserves should be dictated by the scale of natural processes that operate within the given forest type. Many delegates noted that "old growth" is not a static state but is more exactly a continuum, and that for each forest type, the state may last for different periods of

Several authors noted the loss of old growth in some areas of the country, although in other areas the amount of remaining old forest is considerable. For example, most if not all of the old forest is gone from Prince Edward Island, but large areas of old forests remain in British Columbia. Many authors were able to relate the importance of

old growth in sustaining regional biodiversity, and Alex Mosseler and Al Gordon pointed out that old natural forests are a source of high local

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Managing Mountain Pine Beetle Populations in British Columbia

he mountain pine beetle (Dendroctonus ponderosae Hopk.) is a native insect widely distributed in western North America; from northern Mexico, through the western United States, north into British Columbia and Alberta, and as far eastward as Cypress Hills, Saskatchewan. Throughout its range, it breeds in virtually all species of native or introduced pine, but in Canada, its major host is lodgepole pine (Pinus contorta var. latifolia Engelm.). Mountain pine beetle populations are presently at outbreak levels over much of central BC, and the resultant mortality of trees is compromising efforts towards sustainable forest management.

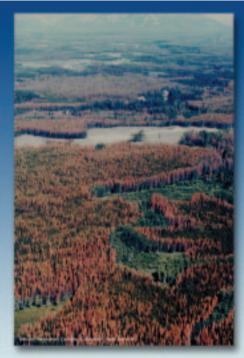
The current outbreak is not a unique occurrence. During the late 1970's and early 80's, a large outbreak spread across the Chilcotin plateau, and other areas of the province were similarly visited between 1910 and 1960. The current populations have been building since 1992, increasing dramatically since 1998, and have killed approximately 600 000 ha of lodgepole pine over 5.7 million hectares from Smithers to Quesnel.

For a mountain pine beetle outbreak to occur, two main conditions must be satisfied: First, there must be a sustained period of favorable weather over several years, and second, there must be an abundance of susceptible hosts. At present, both of these conditions are being met in central BC.

To expand rapidly to outbreak levels, mountain pine beetle populations must maintain a univoltine life cycle. If cool climatic conditions force the beetles out of synchrony with the seasons, they must overwinter in cold-susceptible life stages, leading to extensive mortality within populations. We have examined the degree-day accumulations for Smithers, Burns Lake and Quesnel and found that since 1995 the totals in all areas have consistently exceeded

833 degree-days above 5.6°C, the minimum required for a univoltine cycle.

Even if populations can maintain their seasonal synchrony, significant winter mortality will occur if, at any



Aerial photo of outbreak of mountain pine beetle in BC.

time, temperatures beneath the bark drop to -40°C. Cold causes the greatest amount of mortality early in the winter before beetles can develop cold-hardiness, or in early spring as they become active. The Chilcotin outbreak was ended by periods of extreme cold (-35°C) in the late fall and early winter of 1984 and 1985. Unfortunately, during the last five or six years central BC has not experienced a significant unseasonable cold event, thus winter mortality has not significantly affected the present outbreak. The influence of weather calls into question the potential of global climate change to affect insect population dynamics.

In the three biogeoclimatic zones where lodgepole pine is dominant in BC, fully two-thirds of the stands are more than 80 years old and therefore susceptible to mountain pine beetle attack. Interestingly, the

current age-class distribution may be outside the normal range of variability. In fact, from a distribution generated using a hypothetical fire-return interval of 100 years (generally accepted for lodgepole pine), only about onethird of stands would be in the susceptible range. Many of the existing stands are heavily stocked, even-aged, pine monocultures. They are often the aftermath of large-scale agricultural clearing, logging of highvalue Douglas-fir or larch stands, and fires in the late 1800's and early 1900's. As these stands matured, together with existing natural stands, they have been protected from fire, and generally not subjected to silvicultural treatment.

There are four distinct stages in a mountain pine beetle infestation cycle; endemic, incipient, outbreak and collapse. The most common state between outbreaks is endemic, when populations are comprised of a small number of widely dispersed beetles, usually in weakened or decadent trees. Population increase is prevented by natural factors such as host resistance, natural enemies, weather, and inter- and intraspecific competition. Populations reach the incipient stage when they escape the natural controls and generate enough beetles within stands to overcome the resistance of the average large-diameter trees. Brood survival is optimal in large trees. Incipient infestations often develop in groups of trees where tree health and/or resistance is compromised by local factors such as fluctuations in the water table, periodic flooding or pockets of root disease. In any of these situations, brood survival may increase dramatically. In the presence of abundant host trees of suitable age and size, and with sustained favorable weather, incipient infestations will progress to the outbreak stage.

Outbreaks are spread over the landscape, not confined to

Will Atmospheric Change Alter Forest Health and Growth Into the Future?

hat effect will atmospheric change have on forest health, growth, and productivity into this century? The Intergovernmental Panel on Climate Change (IPCC) recently confirmed that atmospheric CO2 concentrations have risen by nearly 30% since preindustrial times, primarily due to fossil fuel combustion. Coincidentally, emissions of oxidized nitrogen (NOx) and volatile organic compounds have increased background concentrations of the phytotoxic air pollutant, ground-level ozone (O3). Over 29% (5 300 000 square kilometers) of temperate and subpolar forest is now at risk from O₃; this will expand to 60% (11 million square kilometers) by 2100. In Canada, three-year average O3 concentrations consistently decreased between 1991 (70 µl/l) and 1994 (65 μ l/l). Since then, concentrations have actually been increasing steadily back up to 70 μ l/l in 1999. The IPCC predicts further increases in CO2 (2% per yr) and O₃ (12 to 60% in certain regions) over this century.

Experimental fumigation in chambered environments indicate that elevated CO2 and O3 impact trees in opposite ways. Elevated CO2 stimulates aboveground and belowground growth, and delays leaf senescence. Trees grown under elevated CO2 have lower foliar nitrogen concentrations and reduced levels of defense compounds. In contrast to the largely beneficial effects of CO2, O3 is detrimental to tree growth and forest productivity. Ozone has been shown to induce foliar injury, accelerate leaf senescence, decrease photosynthesis, alter carbon allocation, and decrease growth particularly in two of the most widely-distributed Canadian tree species, trembling aspen (Populus tremuloides Michx.) and paper birch (Betula papyrifera March.). Up to 1997, little research had been done on the impacts of these co-occurring greenhouse gases. Even now, we do not fully understand how interacting CO2 and O₃ will influence the composition and function of forest ecosystems.

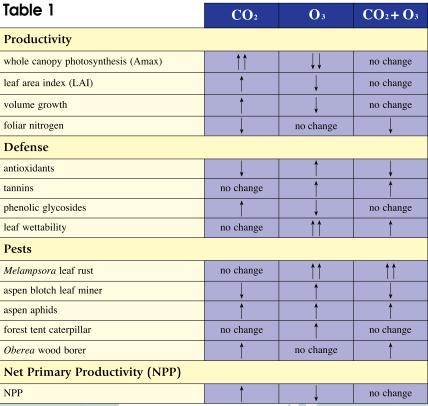
Since 1997, scientists from the Canadian Forest Service's Forest Health and Biodiversity Network (Atlantic,

Great Lakes, Pacific Forestry Centres) have been working as part of a multiagency, interdisciplinary project comprising 55 scientists from eight countries. The Free Air Carbon Dioxide Enrichment (Aspen-FACE) is the first open-air facility to examine the responses of forest trees to interacting CO2 and O3. Aspen FACE is a key experiment within the International Biosphere Geosphere Programme, and was expressly established in 1997 to study the impacts of these co-occurring greenhouse gases on aggrading northern forests in terms of carbon sequestration, physiological processes, growth and productivity, stand dynamics, interactions with pests and ecosystem processes, mineral weathering, and nutrient cycling.

Aspen FACE is situated on a 32 ha site in northern Wisconsin, USA and consists of twelve, 30 m-diameter FACE rings, assigned to treatments of atmospheric CO_2 [ambient and 560 l/l (ambient + 200 l/l)], elevated O_3 [1.5x ambient (circa 50 μ l/l 12-hour daytime average during the growing season)], and elevated CO_2+O_3 . The rings are inter-planted at 1 x 1 m spacing with communities of trembling aspen (five genotypes), trembling aspen/paper

birch and trembling aspen/sugar maple (Acer saccharum Marsh.). During 1996-2001, the Aspen FACE project has been primarily supported by the US Department of Energy (\$2.6 million US) and by companion grants (\$4.7 million US) from the US Forest Service Northern Global Change Program, Michigan Technological University, USDA Research Initiatives, US National Science Foundation, UK Natural Environmental Research Council, British Ecological Society, and the Praxair Foundation. Canadian participation has been supported through a three-year grant from the Federal Panel on Energy Research and Development (PERD), and operating funds allocated through the Canadian Forest Service-Forest Health and Biodiversity, and Climate Change Networks.

Following the first three years (1998-2000) of fumigation, the suite of responses in the young, aggrading forest to elevated CO₂ and/or O₃ have been remarkably consistent across species and genotypes with differing O₃ tolerance. Aspen canopy photosynthesis was strongly stimulated by CO₂ and strongly inhibited by O₃ leading to similar



Source: Karnosky, et al. (2002)

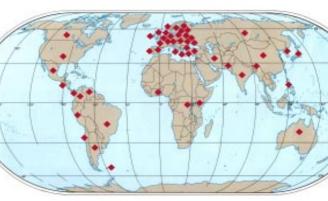
National Tree Seed Centre

he National Tree Seed Centre (NTSC), located in Fredericton, N.B. at the Canadian Forest Service - Atlantic Forestry Centre, was established about 35 years ago to obtain, store, and provide seed free of charge for research. This is the only Seed Centre in Canada with a national mandate to obtain and store tree and shrub seed for conservation and research purposes. This involves ensuring the known origin and quality of the seed, collecting baseline data, and developing effective testing methods and procedures. Upon request, staff provide seed to researchers around the world. The Seed Centre also plays an active role in gene conservation of tree and shrub species native to Canada. The long-term goal is to store representative samples from throughout the natural ranges of all Canadian species.

Seed is procured in several ways. Many of the collections are made by Seed Centre staff but others are obtained through cooperation with other Canadian Forest Service Centres, provincial forest services, forest industries, and other agencies or through exchange, purchase or donation. Seed is collected from natural stands or plantations of known seed origin. The seed is normally collected in good seed years to ensure high genetic and physiological quality and from a number of trees in order to have a representative genetic sample of the population. The Centre has seed from over 100 Canadian tree and shrub species, as well as 100 exotic species for a total of over 11 000 individual seedlots.

Stored seed originates from natural stands and populations. It is these sources and information about

the way the seedlots were collected that scientists and researchers are most interested in obtaining. Seed is collected from average quality stands and trees. No effort is made to collect from phenotypically superior trees. Conserving diversity is an important aspect. If genetically improved seed is requested, the



Seed requested and received from the NTSC from 1968-2001.



Dale Simpson and Bernard Daigle of CFS' National Tree Seed Centre, Fredericton, NB.

client is directed to either provincial government or industry sources. As tree improvement programs involving the production of genetically improved seed continue to develop, little or no seed of commercial tree species will be collected from natural stands. Therefore, the Centre's collection will become increasingly valuable for gene conservation.

The Centre stores small quantities of seed from many sources representing many species. A typical collection would consist of about 100 grams: 5 000 - 50 000 seed depending on the species. On the other hand, provincial government seed centres store large quantities (hundreds of kilograms) of seed from fewer numbers of commercial species. This is because provincial government seed centres provide seed for reforestation programs

involving millions of seedlings whereas the NTSC only

provides small quantities (500 - 1 000 seed) for research.

The NTSC is a well-known supplier of seed for research and requests for seed are received from around the world.

Researchers from provincial

and federal government agencies and universities are the principal clients. Seed has been used for a number of diverse projects, such as species introduction, provenance trials, isozyme studies, germination tests, molecular investigations, and tissue culture, to name a few. Most seed is shipped to Canadian clients, however, about 20% of the requests are received from foreign countries. Seed has been shipped to over 50 countries on all continents except Antarctica (see map).

Seed is primarily requested from Canadian species and about 80% of the seed provided is from native species. The remainder is from non-native species that the Seed Centre acquired over the years. As these non-native seedlots are exhausted they will not be replaced. If a request cannot be provided, the client is directed to other seed centres that have that material in storage.

Gene conservation is an important aspect of the Centre's work. As natural stands are harvested the sites are increasingly being reforested with genetically improved seedlings grown from seed collected in seed

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individual stands, and large increases in infested areas occur annually. Due to the sheer number of beetles, populations are very resilient and can rebound even following large-scale mortality. In the absence of a significant, unseasonably cold winter, outbreaks will kill the large-diameter trees first, then beetles move into progressively smaller diameter classes until most mature pine trees > 15cm diameter have been killed. An outbreak collapses when the supply of suitable hosts is exhausted.

Mountain pine beetle populations initially appear to grow relatively slowly. The question arises: What level of control must be achieved and how often, to slow or stop an increasing population? The general concept is straightforward. To maintain a static population you must remove a proportion of infested trees in each year equivalent to 1-1/R. In other words, if the population is tripling (R = 3), then two-thirds of all infested trees would have to be destroyed before the flight period each year. Obviously, to reduce the population, the removal rate must exceed two-thirds in this example.

With the above concept in mind, forest managers need to consider their control efforts in light of the four stages of infestation.

Management efforts will have their greatest impact on an endemic population. Relative to the potential rate of increase and the number of trees involved, removal of any of the infested stems would suppress the population, and perhaps even cause local extinction

Depending on the size, number, and accessibility of areas involved, incipient infestations may still be amenable to control. Infested trees can be salvaged or subjected to direct control methods such as harvest, fell-and-burn, peeling, or pesticide monosodium methanearsonate (MSMA) treatment. Such treatments may provide the manager with

opportunities to re-establish a mosaic of age classes and species diversity. Unless the population is eliminated or reduced to endemic levels, the detection and treatment must be repeated annually to prevent outbreak.

An incipient population may take only two to three years to develop into a full outbreak. The number of trees killed annually is often in the management of the host resource. We cannot do anything about the first requirement for an outbreak - sustained favorable weather - but we can certainly affect the availability of susceptible hosts. Because approximately two-thirds of the lodgepole pine in BC is \geq 80 years old and thereby susceptible to the mountain pine beetle, large-scale outbreaks are very likely in the

The mountain pine beetle has a one-year life cycle throughout most of its range. Adult beetles fly usually in late July or early August and select trees to attack. As they begin excavating galleries within the phloem, they produce pheromones that attract more beetles. This results in mass attack that overcomes the tree's defence.

After mating, the female extends the gallery upwards, constructing niches along the sides in which she lays eggs that hatch in about a week. The larvae mine laterally in the phloem as they grow throughout the summer and early fall, entering winter as third or fourth (i.e. last) instars. With the onset of warm weather in the spring, larvae resume feeding until they fully develop and pupate in early summer. Pupation requires about two weeks, after which the young adults feed until they reach full maturity by mid-July.

Dispersing mountain pine beetles carry spores of blue stain fungi on their bodies and in mycangia, small compartments within their mouthparts. As a mass attack develops, the host is inoculated with the fungus, which rapidly kills the phloem and spreads through the sapwood, interrupting translocation of water and nutrients, and stopping the tree's defensive resin flow. The combination of blue stain inoculation with larval mining invariably results in tree death.



millions and may encompass hundreds of thousands of hectares. The rate of increase may not be more than that of an incipient population, but its sheer size renders most management tactics ineffective. Large-scale outbreaks potentially set the stage for another similar event some years in the future, as the residual trees or regeneration reach maturity simultaneously.

The current outbreak is beyond control, but how does the future look?

Long-term impact of the mountain pine beetle can only be mitigated if we shift our focus away from the beetle and on to

future. Although we may argue the reasons why the present age-class distribution for lodgepole pine may be skewed, it is virtually axiomatic that if we can manage our forests to achieve a species mix and age distribution similar to the one we would expect from more frequent wildfires, the potential for large mountain pine beetle outbreaks would be dramatically reduced.

Allan Carroll and Doug Linton Pacific Forestry Centre

continued from page 1... Old-growth forests: a science perspective

genetic diversity. However, trying to understand what old forests looked like before European colonization is difficult, at least in eastern Canada, as was noted by several of the casestudy speakers.

At the broadest scales, efforts are being made to characterise and map Canada's forests, including unmanaged stands. These efforts take on national and international significance as Canada participates in various international forestry conventions that subscribe to the importance of primary forest on a global basis. Difficulties arise in determining how to define primary old forests and map them at large scales. In preserving forest areas, Alton Harestad noted that the

generally accepted figure of 12 percent has little biological basis, but rather is more related to what we, as a society, feel we can protect. This concept



Ian Thompson addresses a group during the oldgrowth symposium field tour.

closely corroborated the point raised by Hamish Kimmins that old-growth is as much about a feeling, as it is about science.

The organizing committee is now sifting through the many contributions and working towards publishing a book based on the conference. Their objective is to have the book ready in time for the World Forestry Congress, to be held in Quebec City, September 21-28, 2003. The organizers were pleased with the outcome of the conference, and congratulate the participants and presenters for their insights and diligent preparations.

Ian D. Thompson Great Lakes Forestry Centre

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trends in leaf area index, with O3 dominating the responses under the predicted future scenario for CO₂ + O₃. After exposure to elevated CO2, the aboveground volume of aspen stands was 40 % above those grown at ambient CO2 and there was no indication of a diminishing growth trend. In contrast, elevated O₃ resulted in a volume decrease of up to -27 % in four of five genotypes. What is particularly interesting is that in the CO2+O3 treatment, O3 completely offset the growth enhancement by CO₂, both for O₃ sensitive and O3 tolerant clones.

Work by CFS Forest Health scientists and US/UK colleagues in the Aspen FACE Insects and Disease Working Group has demonstrated that elevated CO2 and O3 caused changes to physical and defensive leaf chemistries at a scale important to insects and disease, and that these have in short order, affected pest performance as outlined in Table 1. We have shown that primary changes to aspen leaf cuticle have enhanced Melampsora medusae leaf rust infection five-fold under elevated O3. When combined with O3, CO2 did not offset the negative effects of O3 on general pest (insect and disease) status. The stimulation in antioxidant production due to O3 is indicative of the well-described "wounding response". Increased tannin amounts due to O3 and CO2+O3 also represent a defensive, phytochemical

response. Sap-feeding aphid populations were generally increased due to CO₂, O₃ and CO₂+O₃ while aspen blotch miner decreased due to fumigation. In contrast, exposure to CO₂ did not alter performance of the forest tent caterpillar (*Malacosoma*



Aspen FACE site, Wisconsin, USA.

disstria). Yet, O₃ increased forest tent performance. Wood borer activity tended to be stimulated due to CO₂, but not O₃.

The Aspen FACE results to which the CFS is a valued contributor suggest that favorable model predictions (derived from artificial, chambered studies) of enhanced growth and productivity probably overestimate field performance of trembling aspen. These new empirical data lend support to previous reports by CFS scientists on the important role of pest activity and forest health in determining carbon source/sink ratios in Canada's Boreal Forest. Given the counterintuitive effects documented at Aspen FACE to date, the complex interactions of

elevated concentrations of CO_2 and O_3 and the changing climate in concert with associated biotic and abiotic stressors as reflected in NPP response, are unlikely to enhance aspen growth, survival and productivity in the future.

Operation of the Aspen FACE Project infrastructure has just been extended for another three years (2002-2005) with the awarding by the US Department of Energy of a grant (\$2.9 million US) entitled Genetic Differences and Resulting Life Histories Interact with Rapidly Rising Atmospheric CO₂ and O₃ to Control the Rate and Fate of Photosynthate Accumulation and the Cycling of C and N in Northern Forests to D.F. Karnosky, K. S. Pregitzer (Michigan

Technological University), D.R. Zak (University of Michigan), R.L. Lindroth (University of Wisconsin), M.E. Kubiske (USDA Forest Service-North Central), K.E. Percy (NRCAN, CFS-Atlantic Forestry Centre), G.R. Hendrey (US DOE-BNL) and J.D. Isebrands (USDA Forest Service-North Central).

Kevin Percy Atlantic Forestry Centre

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orchards. Therefore, with the exception of the NTSC staff and the Canadian Forest Service, little or no seed of commerical tree species is being collected from natural stands. Samples from natural stands and threatened or unique populations are stored to preserve the genes and provide a source of germplasm for future research or restoration. It is important to know that seed will remain viable a long time, especially when it is collected from unique populations or stands that may be threatened in some way, so it can be conserved for the future.

Storage temperature and seed moisture content are the most important factors influencing storage capability. There are generally two types of seed storage behavior in the temperate tree and shrub species. The first type involves orthodox seeds (tolerant to drying, sealing, and subfreezing storage) such as most conifers and small-seeded hardwoods. These are stored in airtight glass jars in walk-in freezers maintained at -20°C. Seed is dried to a moisture content of 5 - 8% before storage. In contrast, seed of some recalcitrant hardwood species

(intolerant to drying, sealing and lower temperature storage) such as oak and silver maple cannot be stored for long because they can be neither dried nor frozen. This seed is stored at +4°C with some air exchange and collections are made frequently to maintain a viable supply.

Quality or viability of the seedlots is monitored by conducting germination tests. These tests are carried out according to prescribed rules and procedures. Due to the number of different species that are tested, a variety of pre-germination treatments must be employed in order to maximize germination. Seed is germinated in special boxes placed in cabinets where light, temperature, and humidity are strictly controlled.

Over the history of the Seed Centre, a tremendous volume of germination test data has been collected. Such a dataset is unique because of the number of tests conducted on hundreds of species and the fact that testing is repeated on seedlots over time. These data are important to demonstrate long-term

storage potential. The table illustrates, for a number of species, how well seed retains viability when properly stored. Generally, seed of coniferous species can retain high viability for a long period of time. The exceptional storage capability of the two aspen species is quite remarkable because the seed is very small and is considered short lived. Balsam fir has the lowest storage capability of conifers. One reason for this is the difficulty in removing non-viable seed during the cleaning operation. Care must be taken during collection and processing so as not to stress or damage the seed.

The NTSC continues to play an important role in storing germplasm and providing seed for research. Storage of seed from throughout the natural ranges of tree and shrub species in Canada is a long-term goal because of its national mandate. As well, collaboration with other seed centres in Canada and other countries will continue to strengthen the Centre's role in research and conservation.

Dale Simpson Atlantic Forestry Centre

Species	Years in Storage	Germination (%)
Acer rubrum (red maple)	14	92
A. saccharum (sugar maple)	12	72
Betula alleghaniensis (yellow birch)	28	85
Populus grandidentata (largetooth aspen)	32	63
P. tremuloides (trembling aspen)	29	72
Abies balsamea (balsam fir)	21	73
Larix laricina (tamarack)	18	92
Picea glauca (white spruce)	33	92
P. mariana (black spruce)	30	95
P. rubens (red spruce)	45	80
P. sitchensis (Sitka spruce)	31	92
Pinus banksiana (jack pine)	40	87
P. contorta var. latifolia (lodgepole pine)	33	90
P. resinosa (red pine)	42	83
P. strobus (white pine)	23	97

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