

Ecology and Silviculture of Trembling Aspen

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Abstract

Trembling aspen (*Populus tremuloides* Michx.) generally grows as clones in which stems, ranging from many thousands to only a few, are interconnected by a common root system. When clones are very large, in one recorded case involving about 47 000 stems joined together over a 43 ha area, aspen becomes a candidate for earth's most massive and oldest organism. Recent analyses suggest that aspen clones, although not individual stems, may be essentially immortal. Management of aspen requires an understanding of how its clonal nature influences responses to silvicultural steps. For many foresters it is a new experience to work with a species that differs from conifers in several important aspects. For example, aspen regulates its density without silvicultural intervention; if silviculturally thinned, aspen may respond by increased sucker production, which can hamper the intended concentration of increment in residual crop trees. A remarkable feature of clonally regenerated aspen suckers is that, after disturbance by fire or clear-cutting, a typical sequence is an early post-disturbance density of 200 000 or more root suckers per hectare, which self-thin to less than 25 000 stems per hectare by age 6 and to less than 10 000 by age 10. The initial high stem densities and subsequent rapid

natural thinning are relevant for the definition of stocking standards for aspen. This article outlines key autecological features of aspen in terms of environmental tolerances, growth and site factors, regeneration requirements, and stand dynamics. The focus is on post-1991 information, which updates other recent reviews on ecology and management of aspen. The need for management innovation is apparent now that technological progress has provided the opportunity to use aspen commercially.

In mixed stands over sixty years old the natural elimination of aspen becomes rapid—in the not distant future the aspen in mixed stands of this age will furnish an appreciable amount of pulpwood that will be used, thus avoiding the present total loss of this species.

E.H. Garman, 1929
Forestry Chronicle 5(3):28-44.

Introduction

This paper focuses on sources of trembling aspen (*Populus tremuloides* Michx.) information dated 1991, 1992, or 1993 to serve as a supplement to other recent reviews that summarized information up to early 1991. The opening

quotation from Garman, an early employee of the British Columbia Forest Service, shows that the search for links among silvics, management, and use of aspen goes back a long time in British Columbia and in the rest of western Canada. Information about these links has accumulated at a steady pace over many decades, with a notable acceleration of interest in the past decade as aspen became a key raw material in British Columbia for bleached chemi-thermo-mechanical pulp, as at Chetwynd, and oriented strandboard, as at Dawson Creek (Alberta Oil & Forestry Review Quarterly 1992).

The following sections summarize information on aspen in terms of: distribution; environmental tolerances, preferences and requirements; nutrient relations and relationships between growth and site factors; regeneration requirements; stand dynamics; and silvicultural implications of aspen's key ecological characteristics. Information is drawn from other recent reviews (DeByle and Winokur 1985; Adams 1990; Navratil and Chapman 1991; Peterson and Peterson 1992) but emphasis is on post-1990 information that updates these recent reviews.

The present paper is based on the idea that forest managers are increasingly asking scientific questions and seeking scientific justifications for policy decisions (Namkoong 1993). As analyses by Namkoong and others reveal, forest science and forest management are being integrated by several forces. One is that forest science has progressed beyond simply answering questions posed by forest managers. Scientific answers to scientific questions on the structure and dynamics of trees and forest ecosystems can change the assumptions on which management decisions are made, and thereby influence the kinds of questions that managers ask. On this basis, Namkoong and others suggest that questions about scientific concepts can be as important to forest managers as answers to specific operational problems. We concur with that suggestion, even though other recent analysts have challenged the assumption that ecological research is the most productive avenue for determining the limits of sustainability in natural resource management (Hilborn and Ludwig 1993). Their argument is that resource managers and user groups cannot look to more ecological research as the primary tool to tell them what to do because: the rate of learning about ecological systems is slow; decisions must often be made with current knowledge before new information is available from new ecological research; and in some resource systems the only way to learn about sustainability is to exploit the system and to record what happens. The

present report is one attempt to synthesize existing information on the silvics of aspen for possible use by resource managers who must make decisions now.

Distribution of Aspen

In North America, aspen extends across an impressive 111 degrees of longitude from the extreme eastern tip of Newfoundland (52° 39' W) to the Seward Peninsula of western Alaska (163° 48' W). Aspen's north-south range spans 47 degrees of latitude from its most northerly limit in North America, on the Mackenzie River delta (68° 40' N), to an isolated stand at about 21°N latitude in Mexico. Within this broad range, the main zone of commercial potential for aspen forest products in Canada is shown in Figure 1. In keeping with this transcontinental distribution, in British Columbia aspen occurs in all forested biogeoclimatic zones east of the Coast Mountains (Figure 2). It occurs west of the Coast Mountains only along several valleys where it has a natural occurrence to the mouths of the Skeena, Kitimat, and Fraser rivers. On Vancouver Island, aspen occurs as sporadic isolated clones along the east side of the island from Campbell River to Victoria, with two outlier occurrences, one near Port Alberni and the other near Gold River.

When expressed as five classes of relative abundance in British Columbia's 14 biogeoclimatic zones, aspen was rated by Meidinger and Pojar (1991) as: abundant in the Interior Douglas-fir, Sub-Boreal Spruce, and Boreal White and Black Spruce zones; common in the Ponderosa Pine, Interior Cedar-Hemlock, and Montane Spruce zones; present but uncommon in the Bunchgrass, Sub-Boreal Pine-Spruce, Spruce-Willow-Birch, Coastal Douglas-fir, Coastal Western Hemlock, and Engelmann Spruce-Subalpine Fir zones; and absent in the Mountain Hemlock and Alpine Tundra zones.

Classification work by the Research Branch, Ministry of Forests, to develop a correlated site series classification of British Columbia's forest ecosystems (D. Meidinger, pers. comm., Aug. 1993) reveals that aspen occurs as a seral species in an exceptionally large number of site series in the province. As examples, Table 1 lists, for each forest region, the biogeoclimatic zone in which aspen is represented in the greatest variety of site series. The last column of the table lists the number of site series in which aspen is a seral species, in the zone that has the greatest variety of aspen-related ecosystems in each forest region east of the Coast Mountains.

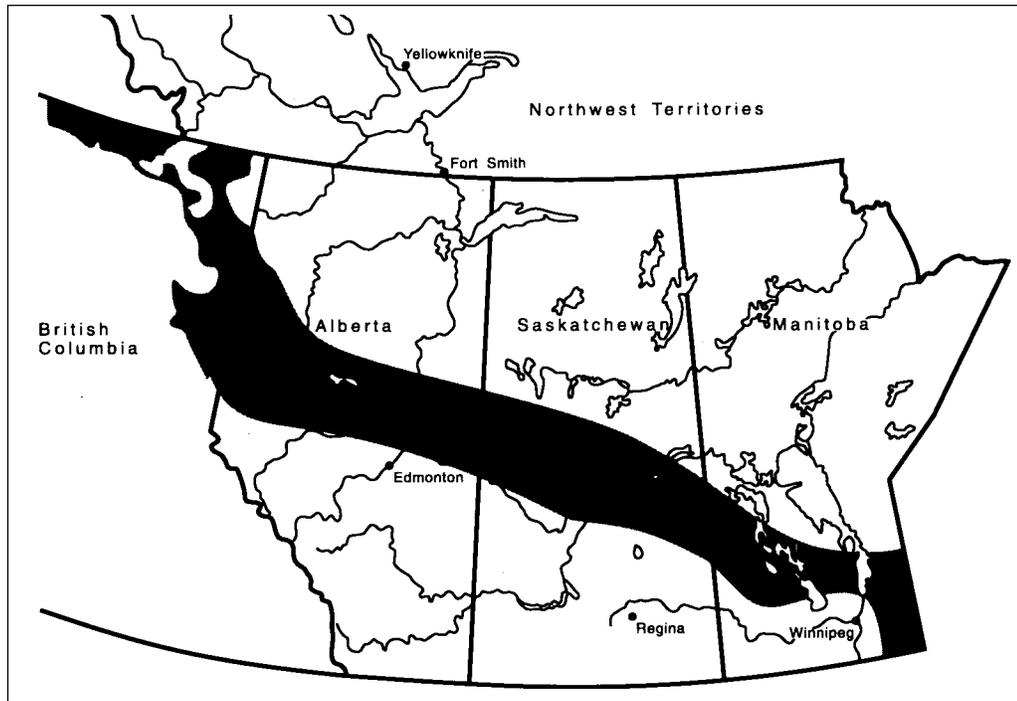


Figure 1. The main zone of commercial potential for aspen forest products in Canada extends from southeastern Manitoba to northeastern British Columbia. Figure courtesy of Canadian Forest Service, Edmonton, based on information mapped by Fitzpatrick and Stewart (1968).

Table 1. The biogeoclimatic zones in which aspen is represented in the greatest variety of site series, for each forest region in British Columbia

Forest region	Biogeoclimatic zone within forest region where aspen occurs in the greatest variety of site series	No. of site series with aspen
Cariboo	Interior Douglas-fir	21
Prince Rupert	Interior Cedar-Hemlock	22
Kamloops	Interior Cedar-Hemlock	24
Nelson	Interior Cedar-Hemlock	24
Prince George	Sub-Boreal Spruce	52

Aspen’s Environmental Tolerances, Preferences, and Requirements

The guidelines recently prepared by the Silviculture Interpretations Working Group (1993) provide a concise tabular summary of selected silvical characteristics of British Columbia’s main tree species, including aspen. From that data summary, aspen’s characteristics are listed in Table 2.

Aspen tolerates a wide range of conditions but grows best in well drained, moist, loamy soils. Aspen will not grow in permanently saturated soils (MacKinnon et al. 1992). Table 3 provides a summary of site conditions associated with good or excellent aspen growth, derived from a broad geographic range of observations. Table 4 is a summary of statements from the literature to corroborate aspen’s tolerance of a broad range of climatic, site, nutrient, and moisture conditions.



Figure 2. Natural distribution of aspen in British Columbia, as mapped by Krajina et al. 1982.

Table 2. Selected silvical characteristics for aspen in British Columbia (Klinka et al. 1990; Silviculture Interpretations Working Group 1993)

Distribution along soil moisture gradient:		Distribution along soil nutrient gradient:	
Very dry	less frequent	Very poor	absent
Dry	frequent	Poor	less frequent
Fresh	very frequent	Medium	frequent
Moist	very frequent	Rich	very frequent
Wet	less frequent	Very rich	very frequent
Shade tolerance ranking:		Potential for natural regeneration:	
Very shade tolerant	–	In the shade	low
Shade tolerant	–	In the open	high
Moderately shade tolerant	less frequent	Spatial requirements	high
Shade intolerant	frequent		
Very shade intolerant	very frequent	Vegetative reproduction from root suckers and stump sprouts	

Table 3. Sample descriptions of site conditions associated with good or excellent aspen growth

Site characteristics	Location	Reference
Nutrient-rich substrates, especially calcium-rich soils derived from limestone; hygic hygrotome and subeutrophic hygrotome	British Columbia	Krajina et al. 1982
Water table between 1.0 and 2.5 m	British Columbia	Haeussler et al. 1990
Fresh to moist (good to moderate) soil moisture and sandy loam or clay loam (not sand and clay) soil texture	Alberta, Saskatchewan, Manitoba	Steneker 1976
Soils with free lime or with high calcium content	Ontario	Heeney et al. 1980
Silt or clay loams with a silt and clay content of 50–70% and a fresh to very fresh moisture regime	Lake States	Heeney et al. 1980
Water table 0.7–2.0 m below the surface	Lake States	Fralish 1972; Stoeckler 1959; Wilde and Pronin 1949
Silt plus clay content in excess of 31% (percent of total cubic volume in upper 1 m of soil) and depth to water table greater than 60 cm	Lake States	Brinkman and Roe 1975
Porous, loamy, humic soil with an abundance of lime	Lake States	Zehngraff 1947
Loam and silt loam soils on boulder clay or clayey moraine	Lake States	Kittredge and Gevorkiantz 1929; Kittredge 1938
Loams with heavy (clayey) subsoil and moderately high water table	Lake States	Roe 1934, 1935
Rich herbaceous vegetation	Lake States	Kittredge 1938; Roe 1934

Table 4. Sample statements from the literature on aspen's tolerance regarding climatic, site, nutrient, and moisture conditions

Condition	Source
Aspen grows on soils with a wide range of soil fertility; good aspen sites are characterized by a markedly high content of Ca, Mg, K, and N.	Fowells 1965; DeByle and Winokur 1985
Soils that have free lime, or have an otherwise high content of Ca, seem to produce the best aspen.	Heeney et al. 1980
Aspen is best adapted to soils of intermediate to high pH; however, it has also been recorded as a successional species on sandy areas where soils are very acidic.	Bell 1991
Aspen is tolerant of sites ranging from xeric to hygric.	Haeussler et al. 1990
Soil moisture is the most important factor in aspen productivity because this species has relatively poor stomatal control of water loss.	Davison et al. 1988
Aspen succeeds on dry sites despite relatively high transpiration rates, probably because of its deep and extensive root system and low leaf area.	Sucoff 1982
Because of its rapid growth and high nutrient demand, aspen has an important role in nutrient cycling.	DeByle and Winokur 1985; Perala 1990
Aspen's frost resistance is high, shade tolerance is low, and flood resistance is very high; nutritional requirements are about as high as those for white spruce.	Krajina et al. 1982

It is in relation to light that aspen has its most demanding requirements. Bell (1991), citing various other sources, described aspen's light requirements as follows: it is a shade intolerant species requiring full sunlight for survival and growth (Klinka et al. 1990); aspen cannot reproduce successfully under its own shade (Ohmann 1982); high light levels are required to stimulate production of root suckers and to ensure their continued, vigorous growth (Haeussler et al. 1990).

In relation to shade tolerance and relative preference along a soil moisture gradient, aspen's ranking relative to British Columbia's other main tree species is summarized in Table 5 from information compiled by Klinka et al. (1990).

If ranked in relation to British Columbia's 25 other main tree species, in terms of the soil nutrient gradient aspen is most frequent at the rich and very rich ends of the gradient, with the same ranking as grand fir, white spruce, western white pine, ponderosa pine, balsam poplar, black cottonwood, and red alder. Only bigleaf maple and Sitka spruce have a ranking higher than aspen at the very rich end of the soil nutrient gradient (Klinka et al. 1990). All of the province's other 17 tree species are ranked by Klinka and co-workers towards the poor end of the soil nutrient gradient relative to aspen's greatest frequency on rich and

very rich sites. Of these 17 species, western redcedar comes closest to aspen's preferences for rich and very rich sites, with jack pine and black spruce predominant at the very poor end of the soil gradient.

When tolerance to growing season frost is compared for British Columbia's 26 main tree species, aspen ranks in the high frost tolerance group of species, which also includes black cottonwood, balsam poplar, paper birch, mountain hemlock, tamarack, lodgepole pine, jack pine, whitebark pine, and black spruce (Silviculture Interpretations Working Group 1993).

Nutrient Relations and Relationships Between Growth and Site Factors

The main nutrient relations for aspen are summarized in Table 6. Although there is abundant information on aspen's growth on naturally occurring sites of varying quality, it is instructive to note recent information on responses to human-induced site changes. Reed and Hyde (1991), and other earlier investigators, have noted the rise of water tables after aspen is harvested or burned. Elevated water tables reduce aspen suckering and sucker growth rates, in

Table 5. Relative ranking of aspen compared to British Columbia's 25 other main tree species in terms of shade tolerance and preferences along a soil moisture gradient. In the columns below species are listed in descending order from very shade tolerant to very shade intolerant, and from those with their greatest frequency on very dry sites to those with greatest frequency on wet sites (Klinka et al. 1990)

Species more shade tolerant than aspen	Species preferring drier sites than aspen	Species preferring wetter sites than aspen	Species less shade tolerant than aspen
Pacific silver fir	ponderosa pine	lodgepole pine	bigleaf maple
western hemlock	limber pine	red alder	white spruce
subalpine fir	jack pine	limber pine	Pacific silver fir
mountain hemlock	subalpine larch	whitebark pine	grand fir
western redcedar	western larch	western larch	Engelmann spruce
black spruce	whitebark pine	subalpine larch	western redcedar
Alaska yellow-cedar	lodgepole pine	jack pine	subalpine fir
grand fir	Douglas-fir	balsam poplar	Sitka spruce
western white pine	paper birch	cottonwood	red alder
Douglas-fir	western hemlock	paper birch	Alaska yellow cedar
white spruce	mountain hemlock	tamarack	black spruce
Engelmann spruce	western white pine		balsam poplar
bigleaf maple			black cottonwood
Sitka spruce			tamarack
ponderosa pine			

Table 6. Nutrient relations of aspen

- Aspen rapidly takes up large quantities of nutrients, which are stored in woody tissue, particularly bole bark and bole wood (Pastor 1990; Ruark 1990).
- Aspen is adapted for rapid growth and high nutrient uptake early in stand development (Peterson and Peterson 1992).
- Aspen retains nutrients effectively within the ecosystem; leaching losses are minimal and decrease quickly after fire or clearcutting (Hendrickson et al. 1987; Pastor 1990; Ruark 1990).
- Carbohydrates are stored below ground in long-lived clonal root system, and the roots have high nutrient uptake rates (Tew 1970; Ruark and Bockheim 1987).
- Aspen functions as a nutrient pump (Corns 1989); aspen leaves have higher nutrient content than conifer needles on the same site (Young and Carpenter 1967; Troth et al. 1976).
- Aspen leaf decay rates are strongly influenced by temperature and less influenced by moisture (Taylor and Parkinson 1988). Decay of aspen's waxy leaves is faster when mixed with nitrogen-rich alder leaves (Lousier and Parkinson 1978; Taylor et al. 1989).
- A large proportion of litter decomposition (75% in one study) takes place between December and March at temperatures between 0° and -5° C (Coxson and Parkinson 1987).
- With its high nitrogen requirements aspen is very sensitive to nitrogen supply (Bonan 1993); because conifers are more efficient than deciduous species in their use of N, conifers rather than hardwoods (including aspen) tend to dominate on N-poor sites.
- Rates of forest floor decomposition and nutrient turnover are more rapid under aspen than under spruce (Perala and Alban 1982).
- There is greater biomass and litter fall of understory vegetation under aspen than under conifers, and greater stemflow in aspen than in spruce (Gordon 1981).
- More rapid breakdown of aspen and birch litter relative to conifers accounts for the shorter residence time of nutrients in mixedwood stands with a high proportion of hardwoods (Gordon 1981, 1983).
- Fertilization trials in aspen and birch in Alaska consistently showed growth response to N but not to P and K (Van Cleve and Oliver 1982; Van Cleve et al. 1983).

extreme cases creating sites no longer productive for future tree crops. In general, aspen should not be harvested in depressional areas, with the uncut stands left to support wildlife habitat and forest biodiversity management objectives.

Regeneration Requirements

For seed production, aspen has been reported to have a minimum seed-bearing age of 10–20 years compared to the following minimum seed-bearing ages for aspen's common boreal associates (Schopmeyer 1974): lodgepole pine, 5–10 years; balsam poplar, 8–10 years; black spruce, 10 years; paper birch, 15 years; and white spruce, 30 years.

The earliest known age of vegetative reproduction is the report by Farmer (1962) of a 1-year-old aspen seedling producing root suckers. Aspen's requirements for vegetative reproduction are well understood. Suckering is inhibited by auxin translocated to the roots from growing shoots and leaves, a phenomenon called apical dominance. Disturbances that damage, cut, or kill stems will reduce the flow of auxin into the clonal root system and will result in root sucker production (Schier 1981). For the present review, the most important point for an aspen silviculturist is that there are constraints to the regenerative capacity of aspen root systems, as summarized in Table 7.

Clone Size and Stand Dynamics

One aspen clone at the south end of the Wasatch Mountains in Utah has been nominated as the most massive living organism in the world. Made up of about 47 000 stems, this clone covers about 43 ha (106 ac). The clone is estimated to weigh 5.9 million kg, nearly 3 times heavier than the largest giant sequoia (Grant 1993). Along with large clone size goes potentially great clone age. There has been speculation that south of the limits of continental glaciation in the western United States some aspen clones may reach an age of many thousands of years. Grant suggested that with vegetative reproduction there is no botanical reason why aspen clones could not be essentially immortal.

For unknown reasons, clones tend to be much smaller in the boreal parts of aspen's range than they are in the southern Rocky Mountains. Some clones mapped by A.K. Hellum near Smith, Alberta, are shown in Figure 3,

ranging from only 35 stems in a small (266 m²) clone to 1002 stems in a 4900 m² clone. In Manitoba, studies have also shown most clones to be a fraction of 1 ha in area; in what may be an extreme example of small clones, Steneker (1973) observed an estimated 1000 clones/ha at one Manitoba study site.

One of aspen's most important silvical features is the rapid reduction in number of stems/ha as a result of natural mortality in the first few years of development in sucker-origin stands. The decline in numbers of suckers with age is shown for various published sources in Table 8. Typically, the least vigorous suckers die during the first 1 or 2 years. Competition reduces most clumps of suckers to a single stem by the fifth to tenth year after cutting (Turlo 1963). There is a wide range of acceptable early stand densities for sucker-origin aspen. One reason may be the tendency for stands to end up with a relatively similar density, in the range of 20 000–25 000 stems/ha by approximately age 6, whether sucker density the first year after harvesting is as low as 44 000 or as high as 225 000 stems/ha (Table 8).

A Synopsis of Some Key Findings from the 1991–1993 Aspen Silvics Literature

To avoid a long review article, this section focuses on a tabular summary of highlights from the 1991–1993 literature relating to aspen silvics and silviculture (Table 9). The paragraph below selects one example from this list of recent findings, dealing with relations between intensity of forest tent caterpillar outbreaks and the amount of forest edge created by harvesting. This example, out of many that could have been selected from Table 9, stresses that specific advances in our knowledge of ecosystem processes involving aspen can change the way we plan the management and silvicultural manipulation of the aspen resource.

The example selected is recent evidence from Roland (1993) that increased clearing and fragmentation of boreal forests, by forest harvesting or clearing for agriculture, may be contributing to increasing severity of outbreaks of aspen's main defoliator, forest tent caterpillar (*Malacosoma disstria* Hübner). The observation that outbreaks are of longer duration in areas that have high structural heterogeneity, expressed as km of forest edge per km², is thought

Table 7. Limitations on the regenerative capacity of aspen

Condition	Reference
• Regenerative capacity of aspen roots is not unlimited; carbohydrate reserves can be exhausted by grazing, repeated cropping or killing of sucker stands, or insect defoliation.	Perala 1990
• Repeated spring burns eventually cause significant reduction in sucker density.	Buckman and Blankenship 1965
• Suckering is inhibited when soil temperature is less than 15° C in the soil depth (7–12 cm) where most sucker-producing roots occur.	Maini 1967; Navratil 1996
• Multiple effects of partial cutting and competition from hazel and alder can limit sucker production.	Doucet 1989
• Inhibiting effect of low soil temperature can reduce suckering capacity of aspen.	Peterson et al. 1989b; Navratil 1991
• Thick duff layer, dense shrubs and grass, especially <i>Calamagrostis</i> , can delay soil warm-up and aspen regeneration.	Hogg and Liefvers 1990
• Summer harvest may reduce the number and vigor of suckers when root carbohydrate reserves are lower.	Schier et al. 1985; Bates et al. 1990; Navratil 1991
• Disturbance and compaction from skid trails and landings, and interrupted drainage in harvested areas can limit sucker production.	Expert Panel on Forest Management in Alberta 1990
• Harvesting impacts resulting in soil compaction and increased bulk density, especially in wet soils, and damage to aspen roots can restrict aspen regeneration.	Zasada and Tappeiner 1969; Shepperd 1993
• Often on the most productive boreal mixedwood sites aspen regeneration can be inhibited by invasion of alder and willow, a thick duff layer, a rise in water table after harvest, low soil temperature, increase in balsam poplar competition, or soil compaction.	Navratil et al. 1991
• Aspen roots have low tolerance for high soil moisture content; waterlogging after harvest can reduce suckering.	Yang and Fry 1981; Bates et al. 1990
• Soil compaction, root disturbance, excessive soil moisture, and reduced carbohydrate levels resulting from harvesting impacts are all important constraints for aspen regeneration.	Kabzems 1996

Table 8. Number of aspen suckers per hectare in relation to age

Reference (location)	Age (years)										
	1	2	3	4	5	6	7	8	9	10	17
Crouch 1983 (Colorado)	76 758	74 198	55 285	36 176	24 513	20 707	17 816	–	–	–	–
Crouch 1981 (Colorado)	–	–	–	–	–	18 021	13 135	10 959	7 455	6 417	–
Perala 1984 (Minnesota)	128 045	91 095	63 765	43 510	29 790	22 005	16 190	–	–	–	–
Weingartner 1980 (Ontario)	46 800	41 400	31 400	–	–	–	–	–	–	–	–
Pollard 1971 (Ontario)	–	–	–	31 000	29 000	26 000	22 000	–	–	–	–
Bella 1986 (Saskatchewan)	74 000	59 000	48 000	47 000	38 000	27 000	–	–	–	–	9000
Steneker 1976 (prairie prov.)	225 000	162 000	130 000	85 000	50 000	–	–	–	–	–	–
Steneker 1976 (prairie prov.)	44 000	40 000	35 000	33 000	29 000	21 000	–	–	–	–	–
Bella and DeFranceschi 1980 (highest density class, Alta./Sask.)	–	280 000	190 000	125 000	80 000	–	–	–	–	–	–
Bella and DeFranceschi 1980 (lowest density class, Alta./Sask.)	–	160 000	110 000	75 000	50 000	–	–	–	–	–	–

Table 9. Highlights from the 1991–1993 literature relating to aspen silvics and silviculture

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- Aspen clones can achieve a biomass greater than any other species on earth (Grant 1993); one 47 000 stem clone in Utah occupies 43 ha and has an estimated biomass of 5.9 million kg, three times larger than the largest giant sequoia and equivalent in weight to over 100 000 sheep.
 - Aspen clones may have a longevity greater than the thousands of years previously suspected (Grant 1993)—possibly, as with *Sphagnum*, being essentially immortal.
 - Natural establishment of aspen seedlings has recently been documented at 925 to 2708 seedlings per hectare in topographic depressions; in riparian zones burned down to mineral soil seedling densities as high as 11.5 million seedlings per hectare have been recorded (Kay 1993).
 - Aspen sucker regeneration after clearcutting is not automatically guaranteed, especially on landings and feller-buncher skidroads where soil compaction occurs (Reed and Hyde 1991; Shepperd 1993). Bulk density increases are known to persist for at least 12 years (Shepperd 1993).
 - Root damage by compaction from logging activities can occur without apparent disruption of the soil profile (Shepperd 1993), especially to fine roots and roots in saturated soils.
 - Post-treatment assessment to determine the effectiveness of pre-harvest aspen control using hack and squirt and girdling to reduce post-harvest suckering found that no one treatment gave a significant reduction in sucker density in the year four assessment (Bancroft 1993).
 - Species richness, total abundance, and species diversity of breeding birds increase with increasing age of successional stage of aspen (Pojar 1993).
 - Avian communities of old aspen stands are distinct from and more diverse than those of younger aspen stands (Nietfield and Stelfox 1993).
 - Large deciduous trees increase vegetation diversity and are important to a wide range of birds during summer breeding, and large dead hardwoods are an important source of snags (Klenner 1991).
 - Some terrestrial vertebrates that require or use live hardwoods or hardwood habitats include: Red-naped Sapsucker; Western Kingbird; American Redstart; Ruby-crowned Kinglet; Lewis' Woodpecker; Barred Owl; Eastern Kingbird; Nashville Warbler; Cedar Waxwing; Downy Woodpecker; snowshoe hare; beaver; moose; and white-tailed deer (Klenner and Kremsater 1993).
 - Unanswered decay questions centre on whether aspen originating from cutovers are more defective than their parent stands (Basham 1992).
 - There have been large over-estimates of the extent of stem decay in aspen because researchers have not differentiated between stain and decay and have referred to both as decay or rot (Basham 1991).
 - One of the major difficulties encountered with decay studies is the definition of what is decay, incipient decay, and stain. For example, large woody galls are found on aspen stems but little decay or stain is found in stems that have black galls (Mallett 1992).
 - Research to assess whether aspen aids in establishment of white spruce indicated that in northeastern British Columbia temperature and moisture ameliorations during white spruce germination are the most likely benefits of aspen canopies (Kabzems and Lousier 1992).
 - Annual photosynthesis and total maintenance respiration are greater for aspen than for white spruce (Hunt and Running 1992).
 - After 3–4 years of severe defoliation by forest tent caterpillar, radial growth of aspen drops significantly, and growth may not recover to expected levels for 2–3 years after defoliation ceases (summarized by Moody and Amirault 1992).
 - Increased fragmentation of boreal forests, either by harvesting or clearing for agriculture, may be contributing to increasing severity of outbreaks of aspen's main defoliator, forest tent caterpillar (Roland 1993).
 - Plant communities under aspen overstory are remarkably similar, from Alaska through Alberta to eastern Canada (La Roi 1992).

(continued)

Table 9. Highlights from the 1991–1993 literature relating to aspen silvics and silviculture (continued)

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- After harvesting, more than 98% of the aspen stems recorded in the first 6 years were established in the first growing season after cutting (Krasny and Johnson 1992).
 - There is evidence that clonal connections between young aspen stems may play a role in speeding up the self-thinning process (Krasny and Johnson 1992).
 - After a fire, vigorous aspen regeneration by root suckering is normal, due to the combined effect of two conditions: the reduction of apical dominance to a minimum; and increased soil temperatures. However, there are exceptions; suckering may be limited where: the rooting zone remains cool after the fire as a result of a moist duff layer; sap flow had been initiated before and during the burning period; and root carbohydrate reserves may have been inadequate to promote suckering late in the growing season (Quintilio et al. 1991).
 - Thinning of aspen is not taken seriously, but in the Lake States thinning could shorten rotations for the purpose of production of aspen pulpwood and mitigate the imbalance of age classes in that region (Perala 1991).
 - When researchers suggest thinning in aspen it is often in relation to mixedwood stand development; for example, Weingartner (1991) suggested that precommercial thinning of aspen may be required to maintain or enhance stand vigour early in the rotation. In boreal mixedwoods, this early release can increase the coniferous component or accelerate the growth of planted conifers, and can also maintain the value of the stand for wildlife habitat.
 - Management techniques that work *with* rather than *against* nature will permit advantageous use of aspen's ease of regeneration, rapid growth, and early maturation; this is especially important because in Canada aspen comprises 80% of the total merchantable *Populus* standing timber (Morley and Balatinecz 1993).
 - There are many agents or processes that cause decay and stain in aspen, all of which have complex interactions within the ecosystem. Decay fungi, particularly *Phellinus tremulae*, are as much a part of aspen ecosystems as are the aspen hosts. Therefore, the search for one or a few factors that are strongly correlated with stain and decay is impaired by these interactions (Lewis 1996).
 - Although foliar pathogens such as *Venturia macularis* and *Melampsora medusae* are commonly encountered in aspen, they usually affect only young stands or suppressed trees. *Phellinus tremulae* remains as aspen's most damaging heart rot. *Hypoxylon mammatum*, which causes high levels of stand damage elsewhere in North America, is infrequent in British Columbia aspen stands. Two canker pathogens, *Encoelia pruinosa* and *Valsa sordida*, and two root and butt pathogens, *Armillaria sinapina* and *Bjerkandera adusta*, require more documentation of their significance for aspen management in British Columbia (Callan 1996).
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to be related to the effect of habitat structure on the virus and parasitic fly that are the main causes of decline in tent caterpillar populations. Fragmented aspen stands may limit dispersal of parasites and/or transmission of pathogens of tent caterpillar. Roland (1993) suggested that the resulting pockets of high host density, relatively free of tent caterpillar's natural enemies, serve as local sources of dispersing moths. This process could allow rapid increase during the early phase of a tent caterpillar outbreak, and it could also keep mean densities of tent caterpillar high when populations are declining in unfragmented forest areas. Small aspen stands, located within continuous forest dominated by non-host tree species, could also isolate caterpillar populations, limit movement of natural enemies, and prolong caterpillar outbreaks. However, differences

in duration of outbreaks were more strongly positively correlated with the amount of stand edge than with the overall amount of aspen present per unit area of boreal mixedwood forest. In addition to the role that natural enemies may have in tent caterpillar's greater outbreak duration in areas of greater forest edge per unit land area, another biological phenomenon is suspected, which is that many lepidopteran insects lay more eggs along edges of host plant patches than in the interior of patches. Bands of high host abundance along boreal mixedwood stand edges could act as local sources to maintain high regional tent caterpillar densities for several years beyond the collapse of outbreaks in more continuous forests.

Silvicultural Implications of Aspen's Key Ecological Characteristics

A key feature of aspen's silviculture is that regeneration techniques require a focus on management and protection of clonal root systems. An example of clone distribution is shown in Figure 3. There are some important features of aspen's biomass accumulation rates and production structure during early development of sucker stands that also distinguish aspen from its companion conifer species. The first is aspen's very rapid early height growth compared to white spruce. Figure 4 provides comparative data from Alberta, with aspen over 6 m at age 10 and natural seedlings of white spruce averaging less than 1 m tall at age 10. Aspen is but one of three barriers that white spruce natural regeneration must overcome to be free-growing. The three barriers are shown in Figure 4 as A (aspen competition barrier for white spruce seedlings at about 2.5 m before spruce is free growing above the aspen), snowshoe hare browsing of white spruce up to about 1.8 m of spruce seedling height (barrier B), and barrier C, *Calamagrostis* competition for spruce up to the average height of *Calamagrostis* (about 1.2 m).

Another important feature of aspen's early growth is the exceptionally high absolute amount of foliage biomass in young stands. Figure 5 is a composite of various data sources and shows some Alberta aspen stands under 20 years of age that support over 12 t/ha of foliage dry weight compared to 5 t/ha or less in aspen stands over 50 years of age. Expressed another way, foliage biomass as a percent of stem wood biomass is very high in stands under 35 years of age compared to stands 40 years or older (Figure 6). These production structure data indicate the magnitude of aspen's well documented early growth rates, involving a large photosynthetic factory (leaf biomass) relative to total above-ground standing crop. The large amount of foliage per unit land area in young aspen stands is an important aspect of browse production for wildlife that feed on aspen foliage and succulent young twigs.

For the concluding section of the paper, it is helpful to summarize some of the main silvicultural differences between aspen and conifers (Table 10), with items listed in no intended order of importance. Original sources of information for Table 10 can be found in references contained in earlier tables of this paper, or in more comprehensive reviews such as Peterson and Peterson (1992).

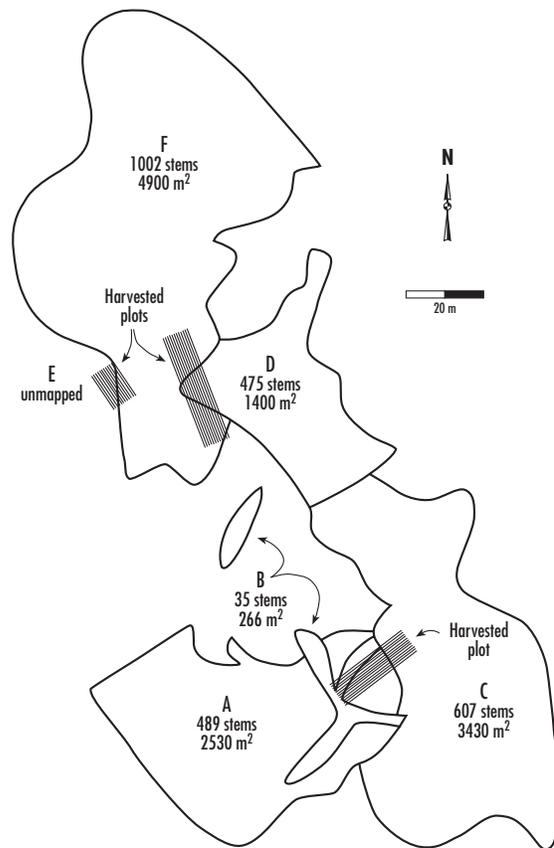


Figure 3. Example of clone distribution, ranging from 35 to 1002 stems per clone, in a study near Smith, Alberta. Figure courtesy of Canadian Forest Service, Edmonton.

Table 10 summarizes the main silvicultural implications of aspen's key characteristics. In addition to the items listed in Table 10, several examples of little discussed aspects of aspen silviculture deserve mention. The first example is the increasing realization that there are cases of less than satisfactory aspen regeneration following disturbance. In areas of commercial aspen harvesting near Hudson Bay, Saskatchewan, aerial photographs that spanned 30 years were examined by Reed and Hyde (1991) to determine: the effect of aspen parent stand conditions on post-disturbance regeneration levels; effect of site on aspen regeneration levels; density and distribution of aspen suckers on burned and cutover sites; impact on density and distribution of aspen suckers from the effect of increased level of the ground water table, soil compaction on skid trails, or damage to the root zone of the parent stand; and effect of season of harvest on subsequent density and distribution of regenerating suckers. Key findings of this study were that: well-stocked regeneration of aspen

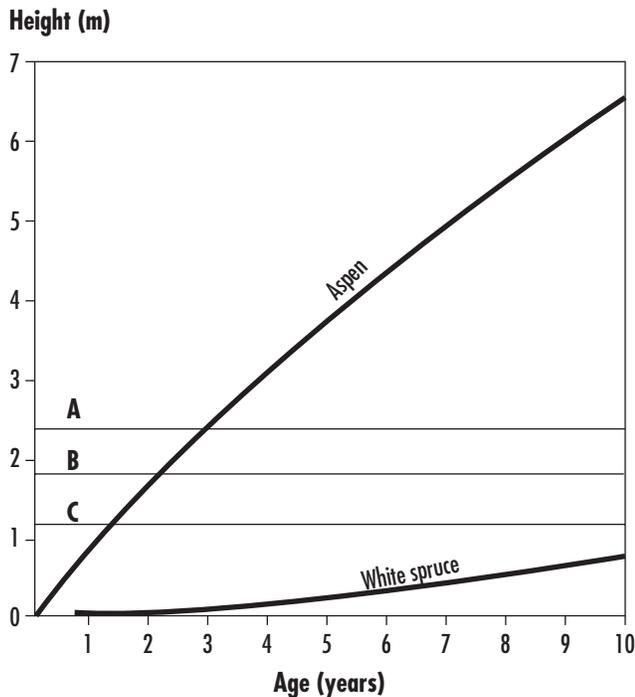


Figure 4. Height of Alberta and Saskatchewan aspen suckers and wild seedlings of white spruce in Alberta during the first 10 years of mixed-wood stand development. White spruce does not respond to a single treatment for release from aspen until the spruce is at least 2.4 m tall (barrier A); browsing by snowshoe hare is significant until white spruce seedlings are approximately 2 m tall (barrier B); competition from *Calamagrostis canadensis* is significant until spruce exceeds the maximum height (1.2 m) of *Calamagrostis* (barrier C). Data sources for this graph are identified in Peterson (1988). Figure courtesy of Canadian Forest Service, Edmonton.

occurs after clearcutting hardwood, but reduced stocking levels result when residuals were left; depression areas that are harvested lead to an increase in the non-productive land base; and hardwood regeneration stocking levels on burned areas do not appear to maintain stocking levels comparable to clear cutovers on similar sites, possibly because of raised water tables and greater root damage on burned areas compared to clearcuts. Where hardwoods were clearcut, natural regeneration of aspen was good to excellent; where a residual crown closure of 10–30% was left, natural aspen regeneration was very uneven and

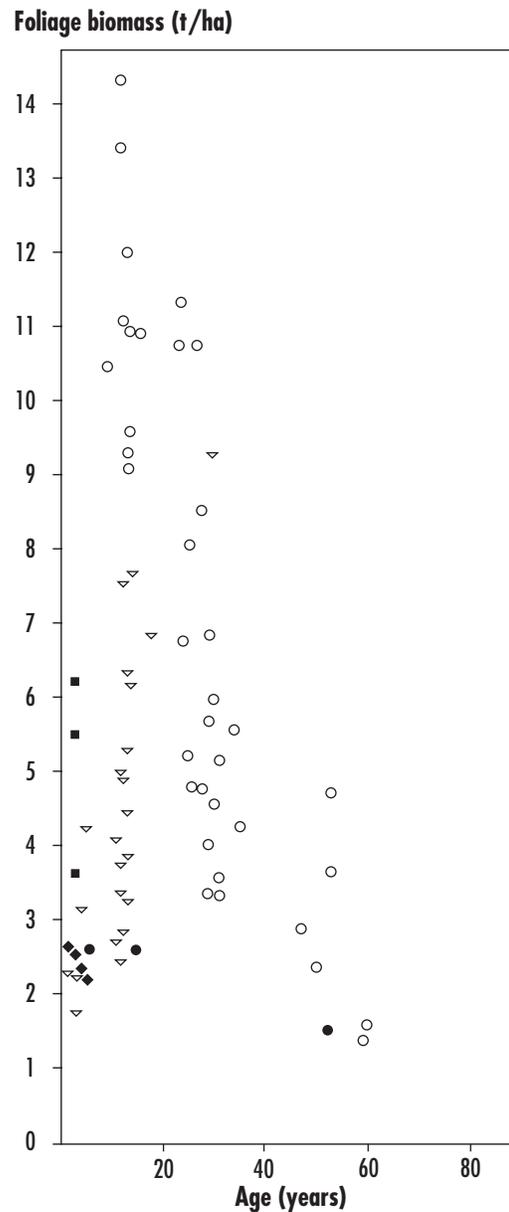


Figure 5. High foliage biomass (t/ha dry weight) in young aspen stands, based mainly on Canadian Forest Service data from ENFOR Project P-205 in north-central Alberta (Peterson et al.). For comparison, other evidence of very high foliage standing crop is shown by data from: Pollard (1971) for Petawawa, Ontario; Zavitkovski (1976) for a *Populus tristis* plantation near Rhinelander, Wisconsin; Bella and DeFranceschi (1980) for 2–5 year aspen stands in Alberta and Saskatchewan; and Peterson et al. (1982) for dense aspen stands in Alberta and Saskatchewan.

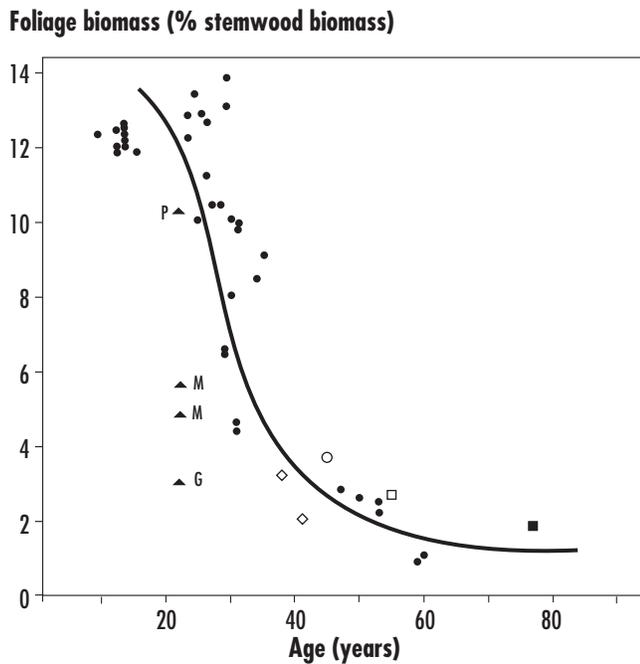


Figure 6. High proportion of foliage biomass (dry weight) as percentage of stem wood biomass in young aspen stands, dropping to low percentage at stand ages over 40 years. Data sources are from: Bray and Dudkiewicz (1963) for Dorset, Ontario and Park Rapids, Minnesota; Peterson et al. (1970) for Kananaskis, Alberta; Jones and Trujillo (1975) for Arizona stands in good (G), medium (M) and poor (P) sites; Crow (1978) for Wisconsin aspen; Van Cleve et al. (1983) for Fairbanks, Alaska; and unpublished data from Canadian Forest Service ENFOR Project P-205 in north-central Alberta (Peterson 1989a).

reduced compared to clearcuts; and with 30–50% of residual crown closure, natural regeneration was non-existent, resulting in a site where management to promote the next crop of hardwoods was virtually impossible.

It is notable that the aspen reproduction differences recorded near Hudson Bay, Saskatchewan were a result of changes in harvesting technology. For example, Reed and Hyde (1991) observed that a switch to feller bunchers around 1980 led to creation of more skid trails than prior to 1980. Because aspen does not regenerate well on landings and major skid trails, clearcuts created in the era before feller bunchers had better stocking levels than areas

where feller bunchers caused greater soil compaction and resulted in greater root damage to aspen's root systems. The resulting reduction in aspen stocking levels and growth rates also contributed to raised water tables. Even some winter harvested areas had reduced aspen regeneration after the introduction of feller bunchers, although less so than with summer harvests.

There is inconclusive information on the effects of season of harvest upon sucker regeneration (Bates et al 1990; Navratil 1991). In the Fort Nelson District, Canadian Chopsticks Ltd. observed better aspen regeneration from summer logging than from winter harvests, whereas the opposite seems true in the South Peace Timber Supply Area (Robinson 1993). In Manitoba-Saskatchewan, Steneker (1976) indicated better sucker production from summer harvesting that destroyed shade-producing understory shrubs. However, Bella (1986) reported that after 5 years there was no difference in sucker density between summer- and winter-logged areas.

A recent review of manual brushing in British Columbia (Hart and Comeau 1992) indicated that aspen suckers are produced much more profusely after overstory aspen are cut than if they are girdled. There is also evidence that site factors may influence aspen's suckering ability; for example, on very dry to dry sites in the Cariboo Forest Region, aspen usually does not sucker. Timing may also influence the effectiveness of cutting aspen as a silvicultural brushing method. The Hart and Comeau review indicated that in the Williams Lake Forest District aspen is cut in July and August to minimize sprouting. There are also reports of reduced aspen sprouting when aspen is cut during the dormant season. These and other limitations to the regeneration capacity of aspen are summarized in Table 7.

In relation to wildlife, the habitat roles of aspen stands need to be analyzed as would be done for any other major tree species. An accepted procedure is to recognize that forest ecosystems can provide five basic requirements for wildlife: food; water; cover for hiding; cover from weather; and living space (Klenner and Kremsater 1993). Several interviews and workshops held in conjunction with a recent problem analysis of hardwood management in relation to British Columbia wildlife (Enns et al. 1993) urged acceptance of hardwood species as a silvicultural endpoint if silviculture is to be successful in hardwood management. This concern was directed partly at the common practice of converting backlog not-sufficiently-restocked (NSR) stands to conifers, a step that is today viewed by some

Table 10. Some silvical differences between aspen and conifers

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1. Unlike conifers, aspen grows in clones made up of many genetically identical stems per clone.
 2. Aspen's suckering provides more rapid natural regeneration of disturbed sites than is possible with conifers.
 3. During stand development, aspen is better than conifers at regulating its density through self-thinning.
 4. Aspen's shorter life span and lower age of maturity, relative to conifers, makes aspen a more likely candidate for short-rotation management; the shorter natural life span also allows aspen stands to progress more quickly than conifers through structural changes that are important for wildlife; natural production of snags, cavity-nesting opportunities, and creation of decay-laden foraging sites in branches and stemwood all occur earlier in aspen than in conifer stands.
 5. Aspen, like several other deciduous species, has a higher rate of photosynthesis per unit foliage of biomass than do conifers.
 6. Unlike conifers, aspen is a very effective capturer of carbon during rapid growth in its first 20 years of stand development, before there is a conifer overstory; this high rate of carbon fixation in early aspen stand development is balanced by high rates of carbon release between 100 and 150 years during aspen stand breakup, a carbon release period that occurs earlier than in conifer stands.
 7. Aspen's bark is more susceptible to physical damage than that of conifers, a factor contributing to greater susceptibility to stem decay than in conifers.
 8. Despite aspen's greater susceptibility to stem decay, it is less susceptible to root diseases than are conifers, especially *Armillaria*.
 9. Aspen can serve as a nurse crop for conifers, but the reverse is not true of conifers.
 10. Aspen has higher nitrogen concentrations in twigs and branches than do conifers, a feature of importance to some species of wildlife; aspen also accumulates larger amounts of Ca than do conifers.
 11. Aspen foliage has higher N, lower lignin, and lower lignin:N and C:N ratios than conifer foliage.
 12. Overall, aspen ecosystems have more rapid turnover of nutrients than do conifer ecosystems.
 13. Aspen forests allow more groundwater recharge than conifer forests by intercepting less water, but aspen also depletes soil water faster and to greater depth than do conifers.
 14. Aspen stands typically have a greater diversity of understory shrub and herb species, and therefore sometimes greater biodiversity and wildlife habitat values, than do conifer stands.
 15. Aspen, with other hardwoods, influences wildlife habitat more rapidly than do conifers because the rapid early hardwood growth results in early creation of vertical structure, and an early abundance of biomass of browse and forage value.
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resource managers as counter-productive, since many aspen-dominated brushy or NSR stands are now used by wildlife and will be used for aspen pulp or panelboard raw material in the future.

Aspen's geographic range in British Columbia places this resource in contact with many locations where the cattle industry is interested in the use of the same land base. There are two examples of cattle-aspen interactions that deserve to be singled out because they provide new perspectives on how we view the aspen resource. The first example is that, in relation to range conditions, aspen can serve as an indicator species. In various parts of western North America, range managers have assessed range to be in satisfactory condition when aspen suckers are present,

and unsatisfactory if they are absent (Greenway 1990). Aspen cover is important to the range manager not only for its own sake but also for the often diverse herb-grass understory forage beneath aspen. The vitality of aspen stands cannot be taken for granted, so management to maintain forage production may be needed in some cases to prevent livestock-induced transitions from aspen to brush or to brush-conifer ecosystems. On disturbances created by fire or clearcutting, or around old beaver ponds, aspen shoots should be abundant. If they are not, over-browsing should be suspected (Greenway 1990).

The second example relates to information that continues to be gathered on the potential role of cattle for thinning aspen. Work of the Hardwood/Mixedwood Steering

Committee (Robinson 1993) confirmed that aspen stocking numbers can be very high in hardwood cutblocks in northeastern British Columbia, and such dense sucker stands do not provide good forage for cattle. One way to entice cattle into such cutblocks is to sow some tame forage, with the potential of some thinning by livestock trampling of suckers. Further documentation is required for these aspen-cattle relationships.

As a last example, a recent detailed analysis of fire and vegetation dynamics of the boreal forest (Johnson 1992) suggested that we are still poorly informed about the effects of the high intensity fires that occur, on average, about once a century in the boreal forest. Johnson's premise is that the boreal landscape is a result of these infrequent, large, high intensity fires. For aspen, the important point is that local variations in humus conditions after fire, and survival of groups of trees after large high intensity fires, have been largely ignored as topics for detailed research.

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Sustained Aspen Productivity on Hardwood and Mixedwood Sites

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Abstract

Sustained aspen productivity after harvesting of hardwood and mixedwood sites is dependent on the amount and quality of aspen regeneration. Aspen suckering is inhibited by low soil temperatures, and soil temperature management may be required on many sites. To enhance soil warming and to encourage adequate suckering, shading by residual trees, shrubs, herbaceous cover, *Calamagrostis* grass, and log decks should be minimized. Disturbance or removal of insulating soil organic horizons by scarifying or burning will also improve soil temperatures but should not be done after suckering has begun. Sucker densities and growth rates are reduced on skid trails and landings, proportionate to disturbance intensity. Affected areas can be kept to a minimum by optimizing layout of extraction roads and designated skid trails.

Small clumps of up to 35 residual mature trees of balsam poplar (*Populus balsamifera*) left in clearcut blocks do not significantly affect the density and growth of aspen regeneration.

Harvesting white spruce-dominated mixed stands results in successional desynchronization, early-seral microclimate but late-seral forest floor conditions, thus increasing soil temperature problems. In harvesting

these mixed stands, the number and spatial distribution of aspen parent trees is critical, a minimum of 50–60 stems per hectare are required in order to obtain acceptable regeneration of aspen.

Silvicultural systems other than clearcutting in large blocks reduce aspen regeneration and future yield of aspen.

Introduction

Increased utilization of trembling aspen and balsam poplar over the last two decades in Canada and the USA has prompted the production of several review publications describing ecological and silvical characteristics of aspen and balsam poplar (DeByle and Winokur 1985; Bates et al. 1988; Peterson and Peterson 1992).

Challenges and implications to both forest management and management of other resources from the increased aspen harvest have also been examined and addressed:

- Hardwood management problems in Northeastern British Columbia: An information review (Peterson et al. 1989)
- Aspen symposium in 1989 in Minnesota (Adams 1990)
- Aspen symposium in 1990 in Alberta (Navratil and Chapman 1991)

The quality of aspen regeneration on hardwood and mixedwood cutblocks does present some real concerns (Bates et al. 1990; Expert panel on forest management in Alberta 1990; Waldron 1993) that need to be examined and resolved if we are serious about the goal of sustainable development as it applies to hardwood production.

In this paper we discuss the perceived and observed problems in achieving sufficient aspen regeneration to sustain aspen productivity after harvest of hardwood and mixedwood stands. Retrospective observations from older hardwood cutblocks in the Prairie region and results drawn from the Mixedwood Silviculture Research Program at Northern Forestry Centre, Canadian Forest Service, Edmonton will be used. Through research, a perceived problem may be found not to be a problem at all. We present the results of such a case study.

Soil Temperature Management

There are two clear relationships known to be involved in aspen suckering. The first, apical dominance, involves the ratio of growth regulators—auxins and cytokinins—in the roots. The second relationship, between soil temperature and suckering, can be the principal and controlling factor with or without apical dominance. It is generally accepted that increases in soil temperature, resulting from increased solar radiation following logging, are the most critical requirement for sucker stimulation (Peterson et al. 1989).

Low soil temperatures have been suggested in several reports as the reason for poor suckering in northern regions and on soils insulated with thick duff layers (Peterson et al. 1989; Navratil et al. 1990). In Alaska, aspen is found chiefly on southern exposures. This was attributed to low soil temperature on other exposures.

Temperature Thresholds for Suckering

Maini and Horton (1966) concluded from greenhouse assays that temperatures less than 15°C (60°F) inhibit suckering. This temperature threshold of 15°C has been repeatedly reported in the literature. Published results do not make it clear how temperature influences suckering—whether it is influenced by average temperature, temperature duration, cumulative degree days, or by maximum

and minimum temperatures and variable daily temperature regime (Hungerford 1988). Zasada and Schier (1973) indicated that the diurnal change may influence suckering and that low minima may suppress suckering regardless of maxima.

There are known clonal and regional differences in suckering responses to temperature. Significant differences were observed among four Ontario clones when propagated at temperatures ranging from 15.6°C to 35°C (Maini and Horton 1966; Maini 1967). The same authors found that sucker production increased with increasing temperature up to 30.6°C while Zasada and Schier (1973) working with Alaskan aspen clones found that temperatures above 22.8°C appeared to inhibit sucker formation on root cuttings.

It is evident, therefore, that the soil temperature threshold and conditions that limit suckering need to be assessed for each region and site before soil temperature management is considered. Many cutblocks should regenerate well without any treatments, especially the locally warm sites. Some measure of temperature enhancement may be needed for the particularly cool sites where soil temperatures may never reach a temperature conducive to suckering.

The importance of local soil temperature assessment for securing high quality aspen regeneration is illustrated by the following example of soil temperature measurements in an aspen cutblock in the Peace River region of Alberta.

A profile of daily average soil temperatures in the first growing season after harvest is shown in Figure 1. The cutblock was winter harvested. Roadside debris (tops and limbs) from the decking areas was brush-raked into piles with minimum ground disturbance. Skid trails from winter logging were barely discernible. Mean thickness of L, F, H layers was 9.1 cm. Aspen sucker producing roots closest to the surface were at a depth of 8–15 cm. Mean daily temperatures at the depths of 7 and 12 cm, where the majority of aspen roots occurred, did not reach 12°C until the end of July. Temperatures of 12–14°C occurred for only 2 weeks in August. Suckers that developed in the area were numerous, but small, and were damaged by fall frost—indicating that they were initiated in the late part of the growing season.

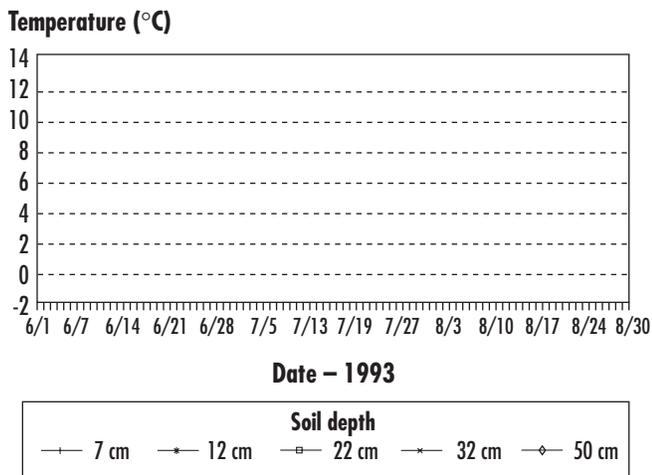


Figure 1. Mean daily temperatures, June to August, 1993, at soil depths 7–50 cm in a hardwood cutover near Manning, Alberta. (Source: Canadian Forest Service and Daishowa–Marubeni International Ltd., unpubl. data.)

Vegetative Cover

Shading by shrub and herbaceous cover can reduce solar insolation and in turn affect soil surface temperature and reduce suckering and the growth of developing suckers.

Shrubs may be a lesser problem than other vegetative cover. In Saskatchewan, a dense hazel understory was not found to be a major deterrent to aspen suckering (Peterson and Peterson 1992). Effects on soil temperature and suckering response after harvesting are not known for other shrubs that form the understory in aspen ecosystem associations (alder, willow, buffalo berry)(Corns and Annas 1986; Delong 1988; Beckingham 1993).

Field observations indicate that the dense grass cover by *Calamagrostis canadensis* can be a major deterrent to aspen suckering. *Calamagrostis*, when dominating the site, can have a two-fold effect on aspen regeneration: preventing or delaying soil warm up and exerting a competitive stress on developing aspen seedlings and suckers. John and Lieffers (1991) observed both greater mortality and lower growth rates of aspen and white spruce found in association with grass as opposed to shrubs or other trees.

The impact of *Calamagrostis* on aspen regeneration may be greatest when harvesting open stands, where *Calamagrostis* cover is well established prior to harvest and expands after harvest (Lieffers et al. 1993). A similar result is observed in open areas where soils are disturbed.

Landings, for example, are rapidly colonized and dominated by *Calamagrostis* within 3 years after disturbance (Hogg and Lieffers 1991). A delayed colonization of landings by aspen of seed origin and very slow growth of aspen seedlings under *Calamagrostis* cover has been observed (Navratil 1991). In harvested areas where dense aspen regeneration captures most of the leaf area capacity of the site immediately after harvesting, *Calamagrostis* cover is reduced proportionally to aspen density.¹

Calamagrostis Cover and Soil Temperature

Effects of *Calamagrostis* on soil temperature are substantial. *Calamagrostis* builds up a thick layer of litter that insulates the soil surface. Under a bed of *Calamagrostis* the summer soil temperatures at 10 cm were 4°C cooler than on sites with no aboveground cover. The maximum temperature in soil under grass was 12°C (Hogg and Lieffers 1991), 3° below the 15°C threshold for aspen suckering discussed previously.

It is very likely that heavy grass cover on old skid trails is the main factor limiting ingress of aspen roots and suckers from the stocked areas adjacent to skid trails. Soil compaction may also be a factor.

A pre-harvest assessment should be done to determine the density and spatial distribution of *Calamagrostis*. If there is significant grass coverage in the understory prior to logging, there will be a rapid spread when the stand is clearcut (Lieffers et al. 1993). Unless the grass rhizomes are killed by a burn or other means, the likelihood of aspen regeneration developing at an acceptable density and growth rate is very low.

Insulation by Soil Organic Layers

The thickness of organic layers greatly affect soil temperatures in the boreal forest prior to and after harvesting. Any ground disturbance or removal of organic layers by logging, scarification, or fire results in warmer soil temperature in the upper layers of soil profile. This should result in increased density of aspen.

In the interior of Alaska, the removal of the organic layer had a remarkable effect on soil temperature. In the winter harvested area, the removal of the organic layer increased soil temperature in late June from about 12°C to about

¹ S. Navratil, unpublished 3rd and 5th year data from vegetation management trials in Alberta.

20°C at a depth of 10 cm. In the summer harvested area, the soil warming effect was less (Dyrness et al. 1988).

In the Prince George Region there was a 6°C mean difference in afternoon soil temperatures at the depth of 5 cm between the untreated plots and plots with removed organic layers. Temperatures were intermediate on clipped plots where the vegetation cover was removed without disturbing the organic layers (Dobbs and McMinn 1977).

Use of Summer Logging for Soil Temperature Increase

Summer logging provides more disturbance to both organic layers and ground vegetation than does winter logging. It has also been reported to promote root suckering of aspen (Bella 1986; Perala 1972).

Harvesting in the frost free season, or site preparation treatments with anchor chains, have been recommended in stands with heavy shrub vegetation (Steneker 1976). Late summer harvesting in particular destroys shrub cover and exhausts its energy reserves, thus clearing the way for soil temperature increases and aspen suckering.

Consideration of summer logging to promote aspen suckering on heavy textured or wet soils should include an assessment of the risk of soil degradation and root disturbance by heavy equipment. Sensitive sites typically have poorer aspen stocking after summer harvesting as compared to winter harvesting (Bates et al. 1990; Alberta Forest Service data *In* Navratil 1991).

A detailed pre-harvest silvicultural plan, containing soil sensitivity information to guide choice of season for harvesting and its potential to optimize regeneration and minimize detrimental soil disturbance, has been accepted in practice in British Columbia (e.g., British Columbia Forest Practices Code 1993).

Use of Scarification for Enhancement of Suckering

Disturbing the surface organic layers by scarification can promote aspen suckering. The timing and intensity of treatments are crucial for achieving the high quality aspen regeneration desired. Improper timing and intensity can be detrimental to aspen regeneration and aspen quality. Scarification should be light and done immediately after harvesting, before any suckering has occurred.

Light scarification, applied in the spring to cutovers harvested in the dormant season, increased suckering both in percent stocking and in density of aspen suckers over unscarified cutovers (Weingartner 1980). Light scarification with drag chains equipped with no or one attached shark finned barrel resulted in gains of 60–78% and 16–56% density over the untreated areas in the first and second years, respectively. Slightly heavier scarification with drag chains and several barrels increased aspen density even more than light scarification, but was associated with a decline in height growth.

Heavy scarification, such as disking or disk trenching, can also promote initial aspen suckering (Sandberg 1951; Brinkman and Roe 1975),² but the initial gains in aspen density are short-lived and can be misleading. Since young suckers depend on the original parent root system, mortality of suckers on disturbed parent roots is higher. Furthermore, after disking, both the growth rate of the aspen stand and the internal quality of individual stems are reduced.

A decrease in height growth was noted up to 10 years after disking (Sandberg 1951). We have found a direct relationship between the degree of root segmentation by disking and height growth of suckers after treatment.³

A combination of heavy scarification and treating after suckering has begun is particularly detrimental (Basham 1988). Measurements 10 years after disking a 3-year-old aspen sucker stand revealed substantial reductions in aspen growth. Damage to the parent root system significantly reduced stem growth, and the effects were still increasing 10 years after scarification. The extent of advanced stem decay averaged 7% in severely wounded, scarified stems as compared to 0.2% in non-scarified aspen suckers. Basham (1988) concluded that the scarified trees will likely be of lower quality at harvestable age and more susceptible to windthrow or breakage.

Prescribed Burn

In regions with cool soils or on sites with heavy grass cover, prescribed burning may be necessary for managing for aspen. Where fire can be safely used it has been an efficient regeneration tool, not only for promoting aspen suckers, but also for generating suitable exposed mineral soil seedbeds for aspen seedlings to exploit (Perala 1991).

² Navratil and Hayward, Can. For. Serv. (in press).

³ Ibid.

In a prescribed burn on an aspen site in Idaho (Hungerford 1988), soil temperatures to the depth of 30 cm were as much as 13°C warmer than those on an unburned site. From June to August in the first year after burning, soil temperatures were significantly higher in burned areas. However, by the second year, there were no temperature differences for most months, due to rapid regrowth of vegetation and emergence of aspen suckers. Temperatures on burned plots were favourable for higher levels of sucker initiation than temperatures on unburned plots (Hungerford 1988).

Prescribed burning may be particularly useful when harvesting late successional stages of mixedwood stands, with aspen as the reforestation goal. Such stands are characterized by thick duff layers and sporadic distribution of aspen under a white spruce canopy. Amelioration of soil temperature by prescribed burn or other measures may be needed to obtain adequate aspen suckering from sparse parent root systems. Clearcutting of a predominantly white spruce stand, followed by broadcast slash burning, resulted in temperatures twice as high as those in areas clearcut only (Dyrness et al. 1988).

Burning at low and moderate fire intensities or when the surface soil is damp may be needed to protect shallow aspen roots. High intensity fires on sites with heavy coniferous slash can be detrimental to suckering. Strategies for prescribed burning on aspen sites are described by Perala (1974), Alexander (1982), and Brown and Simmerman (1986).

Harvesting Patterns and Silvicultural Systems

The intolerance of aspen to shade and the temperature requirements for suckering dictate that as many residual trees should be removed during harvest as economically practical. There is a close relationship between the residual canopy and aspen stocking, particularly if the residual canopy contains spruce (Waldron 1963).

Shading by residual trees and adjacent stands reduces soil temperature and hence the growth of suckers. Openings of about 0.4 hectares provide minimally acceptable conditions for regenerating aspen (Perala and Russell 1983).

Clearcutting in strips and longitudinal cutblocks should maximize the amount of light and insolation. Clearcut strips aligned north-south with a width equal to or less

than stand height received proportionally less daily light as compared to a nearby open field (Berry 1964). In Northern Ontario, 20 m wide strips with the long axis in a north-south direction had lower aspen density than the adjacent clearcut.⁴

Solar exposure can be maximized in strip clearcuts by varying the orientation, shape, and sizes of cutblocks. This may be a worthy objective for simultaneous regeneration of aspen and white spruce where higher soil temperatures are desirable. Guides and programs are available to aid in designing cutovers to meet particular forest management objectives (e.g., Halverson and Smith 1979; Harrington 1984).

Sustained aspen productivity can only be achieved with the clearcutting, even-aged silvicultural system. Partial cutting leads to a decline in stocking and growth of aspen (e.g., Doucet 1989).

The concept of a two-staged harvesting system, as applied to mature aspen stands with immature white spruce understories, relies on the concurrent yield of white spruce and aspen in the second harvest (Brace and Bella 1988). Aspen is expected to regenerate after the first harvest of aspen overstory and release of white spruce. However, the released white spruce understory may provide enough shade to reduce aspen stocking and growth to less than adequate levels. Furthermore, the canopy space available for aspen at rotation age may be limited and vary greatly depending on the density and spatial distribution of the released white spruce.⁵

Log Decks on Landings

Log decks kept on site for an extended time during the growing season tend to delay soil warm-up and may have an additional negative impact on suckering. The ongoing respiration in aspen roots can exhaust carbohydrate supplies if there is no replenishment from the aboveground shoots or new suckers. This may eventually lead to the loss of root vitality, and the inability to initiate suckers.

⁴ D. Weingartner, OMNR, personal communication, 1993.

⁵ Unpublished TASS simulations by B.C. Ministry of Forests Research Branch and Canadian Forest Service.

Soil Moisture Management

The sensitivity of suckering to soil aeration has been known for a long time. Besides the first report in 1911 (Weigle and Frothingham 1911), the published experimental data are limited to one report by Maini and Horton (1964). In a greenhouse assay they found that the maximum number of aspen suckers developed at the 7% moisture content level of the soil (rooting medium). Suckering was reduced at 10–20% soil moisture and no suckers were produced under saturated (25%) and flooded (27%) moisture conditions.

Field observations attributing poor aspen suckering to poor soil aeration are common. Examples are noted on level sites (Bates et al. 1990), those with a high or elevated water table, and on sites with interrupted drainage patterns (Crouch 1986; Expert panel on forest management in Alberta 1990 Sims et al. 1990). Suckering failure and subsequent sucker mortality has been observed in Colorado where the water table, raised by clearcutting, combined with higher precipitation, caused harmful soil moisture conditions (Crouch 1986).

The areas of cutblocks affected by excessive soil moisture can be large or small. Poor regeneration can be limited to small areas of depressions, that in the parent stand prior to harvesting were likely occupied by balsam poplar. Enclaves of depressions can be delineated by pre-harvest silviculture prescriptions and should preferably be left standing. These wet areas commonly do not successfully regenerate to aspen and as islands of mature trees (usually balsam poplar) they function in water removal through transpiration as well as providing benefits to other forest resources (see the section “Balsam Poplar Residuals”).

Large areas of poor drainage may be inherent to the site or may result from interrupted drainage by roads or ruts and from reduced transpiration after harvesting. Prevention of excessive soil moisture is difficult. Improved harvest planning, including a detailed site inspection prior to harvest, can help avoid inappropriate road construction or harvesting in the wrong season, which create ruts that impede lateral water flow.

Harvesting Disturbance

In all regions where aspen is commercially harvested, observations indicate that areas with severe harvesting disturbance to soil and roots have not regenerated and that the lack of regeneration has been long lasting (Zasada and Tappeiner 1969; Jones 1975; Jones 1976; Schier et al. 1985; Bates et al. 1990; Shepperd 1993).

In older hardwood cutovers harvested by conventional systems in Saskatchewan and on more recent cutovers in Alberta a 20–30% site disturbance due to soil compaction on skid trails and landings, and interrupted drainage was observed (Expert panel on forest management in Alberta 1990; Waldron 1993).⁶ This has raised the concern about potential understocking and relatively poor growth of aspen. In one area a falldown of 15% in AAC was postulated (Waldron 1993).

Localized disturbances are differentiated into three types: extraction roads, landings, and skid trails.

Extraction Roads

Constructed for hauling wood from the cutblock, roads can be temporary or permanent. In forest estate planning, in general, a network of roads is judged to be an asset and an investment. It seems very unlikely that any amount of reclamation could bring the hauling road landbase into full productivity for hardwoods. The opportunities exist to optimize road design and road spacing in harvest plans by utilizing long reach and long distance forwarding, techniques which minimize all three types of disturbances.

Landings

With winter harvesting, when log decks are hauled prior to the spring thaw, landings should have limited impact on aspen regeneration. The removal of surface soil horizons during the construction of landings, and spreading them back afterwards, is not acceptable on hardwood sites. Such a practice destroys roots and damages the regenerative capacity of aspen.

⁶ Unpublished TASS simulations by B.C. Ministry of Forests Research Branch and Canadian Forest Service.

Landings with heavily disturbed soils are dominated by *Calamagrostis* within about 3 years (Liefers et al. 1993). At the same time, they are gradually colonized by aspen and balsam poplar seedlings. Stocking of aspen on landings in one study area ranged from 40 to 60% (Navratil 1991). Aspen on landings (predominantly of seed origin) was of a substandard size and growth and unacceptable for maintaining original stand productivity. Seeding of landings with conifers may be a viable alternative, providing enclaves of wildlife cover and adding to the forest's biodiversity.

Skid Trails

Severe soil structural damage occurs where skidding results in deep ruts. Heavily disturbed skid trails resist aspen ingress from the adjacent areas and can be visible for 15–30 years after harvest. Regeneration by suckering can be poor or absent. Growth decline can occur on trees growing on skid trails, even where no surface soil disturbance is visible. Less visible damage is associated with compaction and other physical changes in soil and can also be long lasting. Soil compaction in the boreal forest of Alberta may persist for several decades due to characteristics of local soils (Corns 1988). Increases in soil bulk density in aspen cutblocks have persisted for up to 12 years after harvest in Colorado (Shepperd 1993).

From a detailed study of skid trails in Colorado, Shepperd (1993) concluded that:

- significant compaction can occur regardless of soil moisture conditions;
- high organic matter content in the upper soil profile can decrease the compaction effect;
- compaction increased with each succeeding pass of a tractor where later passes contributed less to the total compaction effect; and
- root damage, especially to fine roots, can occur without apparent disruption of the soil profile and is more extensive in wet soils.

In the retrospective study of skid trail impact on aspen regeneration in central Alberta, we assigned a light, moderate, or heavy impact to various parts of skid trails according to an estimated amount of traffic (Table 1).

Table 1 summarizes aspen density and growth on the wheel tracks of skid trails, in between the tracks and off the trails in the adjacent stand. The greatest reduction in aspen density and growth was in the areas of wheel tracks and slightly less in the centre parts of skid trails when compared to the adjacent undisturbed stand.

Table 1. Density and growth of aspen on skid trails of different impact classes (means from five cutblocks)

Impact class	Location	Density (trees/ha)	Density reduction relative to stand (%)	Total height (cm)	Height reduction relative to stand (%)	Annual mean height in last 3 years (cm)	Annual mean height reduction relative to stand (%)
Low	Stand	39 934		192		19.7	
	Trail centre	18 553	54	133	31	17.8	10
	Trail track	10 395	74	132	31	16.5	16
Moderate	Stand	51 765		223		25.6	
	Trail centre	20 196	61	150	33	21.4	16
	Trail track	10 000	81	141	37	19.2	25
High	Stand	64 285		203		27.4	
	Trail centre	18 333	71	108	47	15.8	42
	Trail track	7 619	88	98	52	13.6	50

All three aspen variables—density, total height, and 3-year mean periodic height increment—showed a reduction when going from low to moderate to heavy impact. In the heavy impact parts of skid trails the reductions in density and total height of aspen were 71–88% and 47–52%, respectively. Reductions in the mean periodic height increment in the last 3 years indicate that soil disturbance continues to reduce growth several years after harvest.

Skid trail impacts on aspen regeneration are evident. What does it mean in terms of aspen productivity and how much should we invest to rectify it? Our ability to predict the degree to which compaction will affect site productivity for hardwoods is limited (Alban 1991). Thus, at present, cost-benefit analysis (weighing costs of reducing skid trail impact versus the gains in yield) may not be possible.

The most biologically appropriate way to minimize soil disturbance on skid trails is to harvest only when soils are frozen or covered with snow. Another feasible approach would be to minimize the affected area by restricting skidding to pre-planned, designated skid trails. In fact, data from European coniferous forests, where networks of designated skid trails are common, show that very little productivity is lost because the trees adjacent to skid trails utilize available light and compensate by increasing radial growth (Eriksson Chroust 1989; 1987).

Work on site sensitivity rating systems has begun in Alberta and British Columbia,⁷ and will be helpful in deciding where to employ low impact equipment such as wide tired skidders, or deciding which blocks must be sequenced for winter harvest.

Balsam Poplar Residuals

Balsam poplar grows in association with aspen to varying degrees. In the Prairie region, balsam poplar commonly comprises a significant proportion (30% or more) of aspen stands (Winship 1991). In Alberta, balsam poplar represents about 15% of the provincial deciduous inventory.

Until recently most hardwood operations did not utilize balsam poplar. Individual trees or groups of balsam poplar were bypassed and retained as standing residuals. The residual trees in groups provide the benefits of cover for ungulates and of nesting sites for cavity nesters. Other benefits include aesthetics, increased biodiversity, and a

possible reduction of the effects of a rising water table after harvesting.

In contrast to these benefits, concerns have surfaced regarding the potential negative impact of balsam poplar shading—lowering soil temperature and affecting aspen regeneration. Foresters have also observed a post-harvest increase in the proportion of balsam poplar versus aspen, and have expressed concern about the influence on such changes in stand composition on stand development, growth, and yield of regenerated aspen (Navratil et al. 1990).

A study designed to answer some of these questions compared aspen density and growth within and outside of 11 clumps of balsam poplar residuals 4–6 years after harvesting hardwood cutblocks in west central Alberta. The effects varied with the sizes of the clumps. Aspen density was significantly less (by 56%) inside the largest clump (consisting of 117 balsam poplar trees) as compared to density outside the clump. In two other clumps, consisting of 63 and 12 balsam poplar trees, the aspen density was 22% less (significant at $P=0.06$ and $P=0.08$). No significant difference in aspen density was found in the remaining nine clumps that ranged from 7 to 35 balsam poplar trees when compared to density outside the clump.

From these investigations we concluded that balsam poplar residuals in clumps with more than 35 stems reduce aspen density within the residuals, but effects did not extend outside of the clumps (Figure 2).

The effects on growth rates of aspen regeneration were minimal, and occurred only within the largest clumps but not outside them. The areas within the clumps and up to a distance of 10–15 m had balsam poplar densities ranging from 1000 to 5800 stems per hectare. This represents a 10% proportion of balsam poplar in a regenerated aspen balsam poplar stand.

It appears that the benefits to other forest resources from retaining balsam poplar groups in hardwood cutblocks outweigh any likely reductions in density and growth of aspen regeneration.

⁷ R. Kabzems, B.C. Ministry of Forests, personal communication.

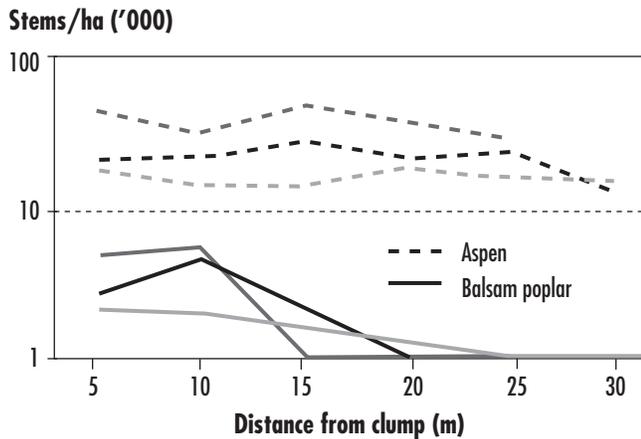


Figure 2. Aspen and balsam poplar densities in relation to the distance from the edge of three balsam poplar clumps.

Aspen Regeneration after Harvesting Mixedwoods

In the mixedwood sections of the Prairie provinces (Rowe 1972) the successional pathway of mixed aspen white spruce stands leads to an increasing proportion of white spruce in the canopy. The late successional stages are white spruce dominant stands characterized by greater litter accumulation, thicker surface organic layers, increased moss cover, and scattered distribution of aspen in the canopy, plus a few smaller, whip-type aspen under the canopy.

In the context of ecological implication, clearcutting of the late stage mixed stands results in successional desynchronization (Kimmins 1989). Clearcutting with minimal soil disturbance results in early seral microclimates but late seral forest floor conditions. These forest floor conditions, without scarification or burning, are less conducive to soil warming and thus to aspen regeneration. Desynchronization of microclimatic and soil conditions may be rectified by burning, scarification, or other treatments.

The number, spatial distribution, and vitality of aspen parent trees in the stand required for adequate suckering must also be considered.

Low numbers or poor distribution of aspen trees may indicate insufficient root densities needed for full aspen regeneration. About 4–5 m² basal area of aspen/ha are recommended for adequate regeneration (Perala 1983;

Doucet 1989; Perala 1991). As a simple guideline, assuming a mean dbh of aspen to be 30 cm, approximately 50–60 aspen trees per hectare are needed for full aspen regeneration.

Data have been collected on the areas occupied by suckers that have developed on the root systems of single aspen trees.⁸ In aspen-lodgepole-pine associations in the Alberta foothills the mean radius of single tree root systems ranged from 8 to 14 m, with the overall mean being 10.8 m. Using a 10.8 m radius, a minimum of about 30 aspen trees/ha would be needed for full aspen regeneration if they are uniformly distributed. It is prudent to use a number higher than 30 trees/ha since this calculation does not allow for clustering of aspen parent trees and overlap of root systems.

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⁸ S. Navratil, unpublished data.

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Aspen Decay and Wood Utilization

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Abstract

The process of wood decay is an integral component of ecosystem function. Dead trees are decomposed by fungi during the process of nutrient cycling. Fungi provide wildlife habitat by decaying living and dead trees, and they enhance biodiversity through the creation of gaps in the canopy. Decay fungi are also important in the short lifespan of aspen by acting as agents of mortality and decomposition. This natural decay process is perceived as causing problems only when expectations of wood yield are placed on the ecosystem, or when human activities alter normal ecosystem dynamics.

Wood decay fungi have three main strategies for obtaining nutrients from living trees. They colonize the dead sapwood created by wounding, canker infections, etc. (wound pathogens); they enter trees through branch stubs or deep wounds and colonize the heartwood (heart rots); and they infect roots of trees then grow up into the stem (root rots).

In northeastern B.C., the heart rot fungus *Phellinus tremulae* is the most common and widespread decay species on aspen (*Populus tremuloides*). It is also very important in the process of natural stand rotation. This fungus, and many of the other decay fungi, produce little external indication of their presence except for fruiting bodies, which are not always produced or conspicuous.

Because of the lack of external indicators, many attempts have been made to correlate tree variables (age, dbh,

and height) with incidence and amount of decay, but the results have been conflicting. The few attempts at correlation of site factors with decay have also shown inconsistent and contradictory results. Inconsistency in method of data collection, a wide variety of sampling locations, and other interacting biological or site factors may partly explain this.

To address these inconsistencies and to attempt to find variables, or combinations of variables that predict decay, a 2-year study was initiated that measured decay in 543 aspen trees across a wide range of dbh and age groups within the BWBSmw2 subzone. Site data (e.g., soil characteristics, topography, drainage, plant associations) were collected at each sampled tree. Regression analyses and analyses of variance were used to correlate stand, tree, and site variables with the amount of decay. None of the variables or variable combinations were able to account for sufficient variation of the dependent variable (amount of decay) to be useful as predictors, although a trend was observed between age and decay.

Although this study had several weaknesses that were a result of the sample design, the results do suggest that the process of decay in aspen is probably dependent on many features and site characteristics that have complex interactions. It is suggested that a better understanding of the biology of these decay fungi, their successional pathways, and their natural role in ecosystem function will provide more useful information for the management of aspen as a timber resource.

Introduction

The process of wood decay is an integral component of ecosystem function. Decay fungi are only perceived as problems when humans place expectations upon the ecosystem that are outside of its normal functioning, or when human activities alter normal ecosystem dynamics. Fungi are the primary agents of decay; fungal mycelia break down wood cell walls and absorb the cell wall constituents. The wide variety of woody substrate found naturally in forested ecosystems has provided an abundance of habitat niches for decay fungi.

In general, wood decay fungi employ one of four strategies in niche exploitation, although considerable overlap occurs. One strategy is to decay wood in dead trees. These fungi have high competitive abilities; they are able to quickly colonize available substrates and may be part of a natural succession of organisms. They are not able to tolerate the defense responses evoked by living trees. The second strategy is to colonize the sapwood of living trees where the sapwood has been locally killed or damaged. These fungi are adapted for rapid colonization and are known as wound pathogens. Some have the ability to spread into undamaged sapwood or heartwood. The third strategy is employed by fungi that cause heart rot. These fungi are able to infect trees through branch stubs or deep wounds, then colonize the dead heartwood (or inner portion of the stem of species such as aspen, which do not form true heartwood) within the living tree. They are generally confined to the heartwood by the defense actions of the living sapwood. The fourth strategy involves entry through the roots by root rot fungi, which have developed several mechanisms that bypass or tolerate the host's defense mechanisms. These fungi are generally not good at competing for substrate with other organisms; their niche is to reside within the roots, well protected from other wood-utilizing organisms.

Aspen is a relatively short-lived species (Fowells 1965). Decay fungi play an important role in both the death and subsequent decomposition processes that lead to natural rotation of aspen stands. Aspen is recognized as an important timber resource, partly because of its abundance (Table 1). However, the utilization of aspen is limited by the naturally high levels of decay.

Table 1. Volume estimates of aspen in British Columbia

Author	Area	Volume (millions m ³)	Assumptions
Farnden 1990	B.C.	215	age > 81 years dbh > 17.5 cm
Ondro 1989	B.C.	281	dbh > 17.5 cm top diam. = 10 cm
Peterson et al. 1992	Ft. Nelson TSA ^a Peace TSA	8.17 6.63	dbh > 17.5 cm top diam. = 10 cm

^a TSA = Timber Supply Area

Main Strategies of Wood Decay Fungi

Of the four main strategies employed by decay fungi discussed above, the last three are the most important from a wood utilization perspective. The means of entry, means of spread, and mode of action are different for each of these main strategies; they produce different results with respect to the impact of decay on the timber resource, and the effect of management activities on the amount of decay. Each of the three main strategies are discussed briefly below.

Wound Pathogens, Saprots

Fungi that cause sap rots generally begin the decay cycle by colonizing a wound surface. Spores of the fungus land on the wound, germinate, and grow into killed or injured cells. Deep wounds provide direct entry to the heartwood, and the host has little opportunity to compartmentalize the fungus. Successful colonization of shallow wounds depends on the size of the wound, host vigour, the virulence of the fungus, and previous colonization by other organisms that may have modified the substrate. The decay fungus may be limited to the dead sapwood at the wound site, or it may continue to expand into living sapwood or the heartwood. Once sufficient food base is colonized, the fungus produces a fruiting body and the cycle begins again.

Heart Rots

Heart rots infect living trees either through small twig or branch stubs, or possibly through wounds depending upon the fungus and host species. The time from infection to colonization can range from one or two years to tens of years. Once in the heartwood, the fungal mycelium expands longitudinally because the heartwood does not respond to the infection. The fungus may also grow slowly outwards, colonizing the inner portion of the sapwood. Fruiting generally occurs at a branch stub, which provides a route for the fungus to the outer surface. Most of the heart rot fungi produce a perennial sporocarp (conk), which produces basidiospores each year from a newly formed fertile layer. However, heart rots may grow for many years in the host prior to sporocarp production.

Root Rots

Root rot fungi have developed various means of avoiding or tolerating host responses to infection. Entrance to the host usually occurs through the root system from contact with infected roots. Initial colonization of the root system occurs in the cambium or within the heartwood, depending on the fungal species. Most of the root rot fungi also colonize the lower portion of the stems and can extend several metres up the tree. These fungi are generally poor competitors; by exploiting the rhizoplane and root systems, they avoid competing with saprophytic organisms that are abundant in the soil.

Type of Decay

In addition to the location of decay within the tree and the length of time since infection, the type of decay caused by the fungus has a large effect on wood recovery. Two main types of decay exist: brown rots and white rots. Brown rot fungi produce endo- and exo-cellulases and are able to rapidly break down the long chain cellulose molecule into two-sugar units, which are absorbed by the fungal hyphae for its nutrition. White rot fungi are not able to cleave the cellulose molecule randomly. Cellulose is digested slowly from the ends of the molecular chain. However, white rot fungi are also able to break down and utilize lignin by means of a variety of oxidative enzymes. Most of the decay fungi common to aspen cause white rots.

In the production of pulp, wood with white rot will yield some pulp fibres because some cellulose remains in the decayed wood. The wood also retains some of its strength and integrity. There is little to no cellulose remaining in wood decayed by brown rot fungi, and therefore the wood has no structure or strength, and no pulp is recovered.

Decay-causing Species Common to the Boreal Forest

By far the most common decay-causing species of aspen in central and northern British Columbia is *Pheleinus tremulae*, which causes a heart rot of aspen stems. The fungus is thought to enter the tree by spores landing on branch stubs. The mycelium then grows into the centre of the tree and can create extensive white rot decay columns. Except for the production of sporophores, there are no external indicators of decay.

Radulodon americanum (= *Radulum caesarium*) and *Peniophora polygonia* are two fungi that commonly cause stain in aspen with small pockets of decayed wood. Both of these fungi are thought to be part of the ecological succession of microorganisms in aspen. They may be preliminary fungi that alter the host substrate for the main decay fungi such as *P. tremulae* and *Ganoderma applanatum* (Hiratsuka et al. 1990). There are no external indicators of infection by these preliminary fungi except for the occasional production of inconspicuous sporocarps.

The above three are the fungi most commonly observed and isolated from decayed aspen. Several other fungi are occasionally found. *Trametes ochracea* (= *Coriolus zonatus*) causes a white rot of dead sapwood (Gilbertson and Ryvar den 1987). *Bjerkandera adusta* is another occasional species on aspen and also causes a white cubical sap rot. There are a few species within the genus *Pholiota* that cause white rot either in the trunk or in the roots and butt. The most common root and butt rot is caused by *Armillaria* spp., usually *A. sinapina*. This fungus infects aspen trees through the root system, particularly in trees formed by root suckers from an infected parent tree. A stringy rot, brown in colour, is produced in the centre of the butt. Infected trees may show some external symptoms such as a thin crown; otherwise, external indicators are limited to the seasonal production of sporocarps.

Impacts of Decay on Useable Volume

The magnitude of decay and losses to volume reported in studies and surveys varies widely between and within study areas. Most of the studies cannot be compared; Peterson and Peterson (1992) recognize three reasons for the inconsistencies. Firstly, existing age-decay tables were developed from sampling across a wide range of ages (and therefore a wide range of study sites) to ensure all age classes were represented. This sampling scheme allowed differences in site quality and stand history to potentially affect the relationship with decay. Secondly, incipient decay, advanced decay, and stain have not been consistently identified by different researchers. Thirdly, different sampling methods, and different criteria for assessing the percent of decay required for an entire log to be rejected, were used. Three examples of decay studies follow. A study in Ontario found that 69% of 1754 aspen trees had decay within the merchantable portion of the bole. Decay volume averaged 8.7% (6.4% caused by *P. tremulae*) for trees 41–180 years old (Basham 1958). In Alberta, 1015 aspen trees (average age of 70 years) were sampled for decay. Only merchantable trees with less than 50% decay were measured; the average percent decay of these was 8.7%. In a sample of 100 trees 80 years old or more in central B.C., Kumagai and Girvan (1990) found that decay as a percent of merchantable volume ranged from 7.5% to 39% per tree.

Relationship Between Decay and Tree and Site Variables

One of the characteristic features of aspen decay is the lack of external indicators of decay. Furthermore, there are many conflicting reports on the relationship between incidence or amount of decay, and indicators such as tree age or diameter. As an example, Maier and Darrah (1989) indicated that tree size (dbh) was more closely related to amount of decay than was tree age. Basham (1987) found that the relationship of decay with age was stronger than with tree size. In a study in B.C., broad age groups (mature vs. immature) were related to decay, but, within these age groups, dbh and risk group¹ were more important indicators of decay (Kumagai and Girvan 1990).

¹ Risk group 1 = no external indicators; risk group 2 = any external indicator (fork, crook, scar, dead or broken top) except conk or blind conk; risk group 3 = conk or blind conk.

Other external indicators, such as scars, are good indicators of sap rot, but the much higher incidence of heart rot that occurs in trees with no external indicators reduces the value of scars and other indicators as predictors of total decay.

Of all the external indicators examined, conks are the most reliable indicators of decay incidence (Basham 1958, 1987) but not of the amount of decay (Hiratsuka and Loman 1984). Maier and Darrah (1989) found no relationship between the number of conks and decay volume. Other than at the site of conks, the distribution of decay within a tree is very unpredictable, making recovery of sound wood difficult and frequently uneconomical (Woodbridge, Reed and Associates 1985).

The lack of good, consistent relationships between external indicators and decay suggests that the decay process is complex and involves other factors such as stand origin, site characteristics, and species composition. A few studies have looked for relationships between site and decay, but no strong relationships developed from this work (e.g., Basham 1958; Paul and Etheridge 1958; Thomas et al. 1960; Kemperman et al. 1976; Hinds 1981).

Fort Nelson District Aspen Decay and Stain Study

A study initiated in 1991 attempted to look more closely at the relationship between decay and site variables. External indicators and tree variables traditionally used to determine cull volumes were also measured to enable a comparison of methods for prediction of decay or stain.

Materials and Methods

The study took place in the BWBS (Boreal White and Black Spruce) mw2 subzone located in the Fort. Nelson Timber Supply Area. To ensure that trees were sampled across a broad range of the factors traditionally used to predict decay, a sampling matrix was constructed that included four age classes, three risk groups, and several diameter classes within each age class (Table 2). An attempt was made to sample six trees in each cell of the matrix, giving a total sample size of 543 trees. To avoid including genotype as a variable, only one tree per clone was sampled. If clones could not be easily distinguished by morphological or phenological characteristics, sample trees were located at least 200 m apart; a distance greater than the diameter of the area occupied by most aspen

Table 2. Sampling matrix. Risk group 1 = no external indicators; risk group 2 = any external indicator (fork, crook, scar, dead or broken top) except conk or blind conk; risk group 3 = conk or blind conk.

Age class	Risk group 1 dbh in 5 cm classes	Risk group 2 dbh in 5 cm classes	Risk group 3 dbh in 5 cm classes
61–80	15 to 40 (six classes)	15 to 40 (six classes)	15 to 40 (six classes)
81–100	15 to 45 (seven classes)	15 to 45 (seven classes)	15 to 45 (seven classes)
101–120	20 to 55 (eight classes)	20 to 55 (eight classes)	20 to 55 (eight classes)
121–140	20 to 55 (eight classes)	20 to 55 (eight classes)	20 to 55 (eight classes)

clones (Weingartner and Basham 1985). Sample trees were selected by walking a predetermined distance into an aspen-dominant stand, then selecting the closest aspen tree that fit within the sampling matrix.

At each sample tree, three “plots” were established: 1) a cruise plot to provide estimates of stand density and net volume using current B.C. Ministry of Forests (MOF) procedures; 2) a decay sampling plot, which involved decay and stain measurements on the felled sample trees using sectioning and measuring procedures in the B.C. MOF Inventory Manual Chapter 9; and 3) a Preharvest Silviculture Prescription survey plot, which involved collection of soil, vegetation, and site information. Table 3 gives a complete list of variables included in the study.

Information from the decay sample was entered and edited for mistakes using a decay analysis program. Merchantable gross volumes were determined for each tree by adding the section volumes. Decay and stain volumes were calculated from the decay length and diameter measurements, and the volume of defect-free wood was calculated as the difference between merchantable gross volume, and stain, and decay volumes. Percent decay, stain, and defect were calculated by dividing stain, decay, and defect volumes by merchantable gross volume. The stand, tree, and site variable information was entered into a databank, edited for mistakes, and transferred into a spreadsheet program.

Scatterplots were generated for each dependent variable (percent decay, percent stain, and percent defect) on the Y axis against each independent variable on the X axis. These were used to identify variables that may have contributed to the variation in decay, stain, or defect.

Several methods were used to test the dependent and independent variables for normality prior to further analysis. First, frequency plots were generated for each

variable by plotting the frequency of occurrence for each class of the variable. The shapes of these plots were compared to normal distributions. Second, frequency distributions of the dependent variables in each class of the independent variable were generated for selected independent variables. These were also compared to a normal distribution. A Poisson distribution best described the dependent variables; therefore, these variables were square root transformed to fit a normal distribution.

To reduce variation within the dependent variable, dependent variable means in each class of selected independent variables were plotted, and regressions were fitted to the plotted lines. Selection of independent variables for this analysis was based on the scatterplots.

Finally, age (the variable most closely related to decay and stain) was combined with other selected site variables in multiple regressions. The variables that showed some relationship in the multiple regressions were examined more closely by creating scatter plots within age stratifications.

Results

Tree, stand, and site variables are summarized in Table 3. None of the scatter plots of dependent variables against each of the independent variables suggested that a useful relationship existed between site or tree variables and decay or stain. The plots showed a high level of variation of decay and stain regardless of the independent variable. Figure 1 shows some examples of the scatterplots.

The most promising variable for predicting percent decay and stain volume was age. The relationship between age and percent decay and stain was partially masked by the large number of zero values for stain and decay. However, even when the zero values were excluded, the relationship

Table 3. Summary statistics of tree, stand, and site variables

Variable	Range	Mean	S.D.
Age	40–175 yrs	102 years	22.7
dbh	13.3–60.7 cm	32.8 cm	11.2
Height	14.1–38.3 m	27.9 m	4.2
Stand density	21.1–2312.6 sph	620.73 sph	
Conk section	0–7	.53	
Aspect ^a	0–8	2.8	2.7
Drainage ^b	1–4	1.9	0.6
Elevation	825–2850 m	1509.4 m	299.6
Moisture regime ^c	2–5.5	3.9	0.5
Nutrient regime ^d	1.5–5.0	3.0	0.5
Rooting depth	10–84 cm	28.5 cm	12.0
Restrictive layer	14–100 cm	41.9 cm	19.8
Slope	0–52%	6.5%	8.5
Slope position ^e	1–7	n/a	n/a
Soil order ^f	1–4	n/a	n/a
Site series ^g	1–6	n/a	n/a
Soil texture ^h	0–3	n/a	n/a

^a Aspect: 0 = flat, 1 = North, 2 = Northwest, 3 = West, 4 = Southwest, etc.

^b Drainage: 1 = well, 2 = moderately well, 3 = imperfect, 4 = poor, 5 = very poor

^c Moisture regime: classes 1 to 7 for xeric to subhydric

^d Nutrient regime: classes 1 to 5 for very poor to very rich

^e Slope position: classes 1 to 7 for crest, upper, mid, lower, toe, depression, or level, respectively

^f Soil order: 1 = brunisol, 2 = luvisol, 3 = gleysol, 4 = podzol

^g Site series: based on edatope, plant species and cover, ten classes

^h Soil texture: 1 = coarse, 2 = medium, 3 = fine

was poor, and the variation in age could explain less than 1% of the variation in percent decay and stain (Figure 2). To reduce variation within the age variable, ages were grouped into 10-year intervals and the mean percent decay and stain were plotted for each age class. These plots showed a much more distinct relationship with age (Figure 3) and explained greater than 95% of the variation in the means for each age class. Figure 3 shows that the age group means of percent decay and stain vary with merchantable volume. When merchantable volume is ignored by using total decay and stain volumes rather than percent decay and stain, the resultant curves are more linear (Figure 4).

Other variables were tested for their significance in predicting decay and stain using two methods. The first was to combine age (unstratified) with other variables in a series of multiple regressions. The other variables were selected from the most promising scatterplots. Age was combined with risk group, and with location variables such as elevation, slope, slope position, and aspect in several different combinations. None of the multiple regressions showed a significant relationship; the largest r^2 was 0.19. The same was true for multiple regressions of age combined with site variables such as moisture, nutrient regime, soil order, drainage, restrictive layer, and rooting depth. None of the r^2 values from these multiple regressions was greater than 0.05. The second method was to look at selected variables within 10-year age classes in the form of scatterplots. This method was used on those variables from the multiple regressions that had shown a hint of a relationship with decay or stain. Age effects were kept to a minimum by using the 10-year age groups. All of the variables examined showed a consistent pattern of greater variation within age groups than the variation among age groups.

Conclusions

The site factors measured in this study do not explain significant levels of the variation in the volume of stain and decay in aspen. The level of variation in the dependent variables was substantial, but none of the tree, stand, or site factors was able to account for sufficient variation of the dependent variables to be useful as predictors of stain or decay.

Two explanations are offered for the lack of significant relationships within this dataset. One is that the sampling design was to sample a large number of trees that were

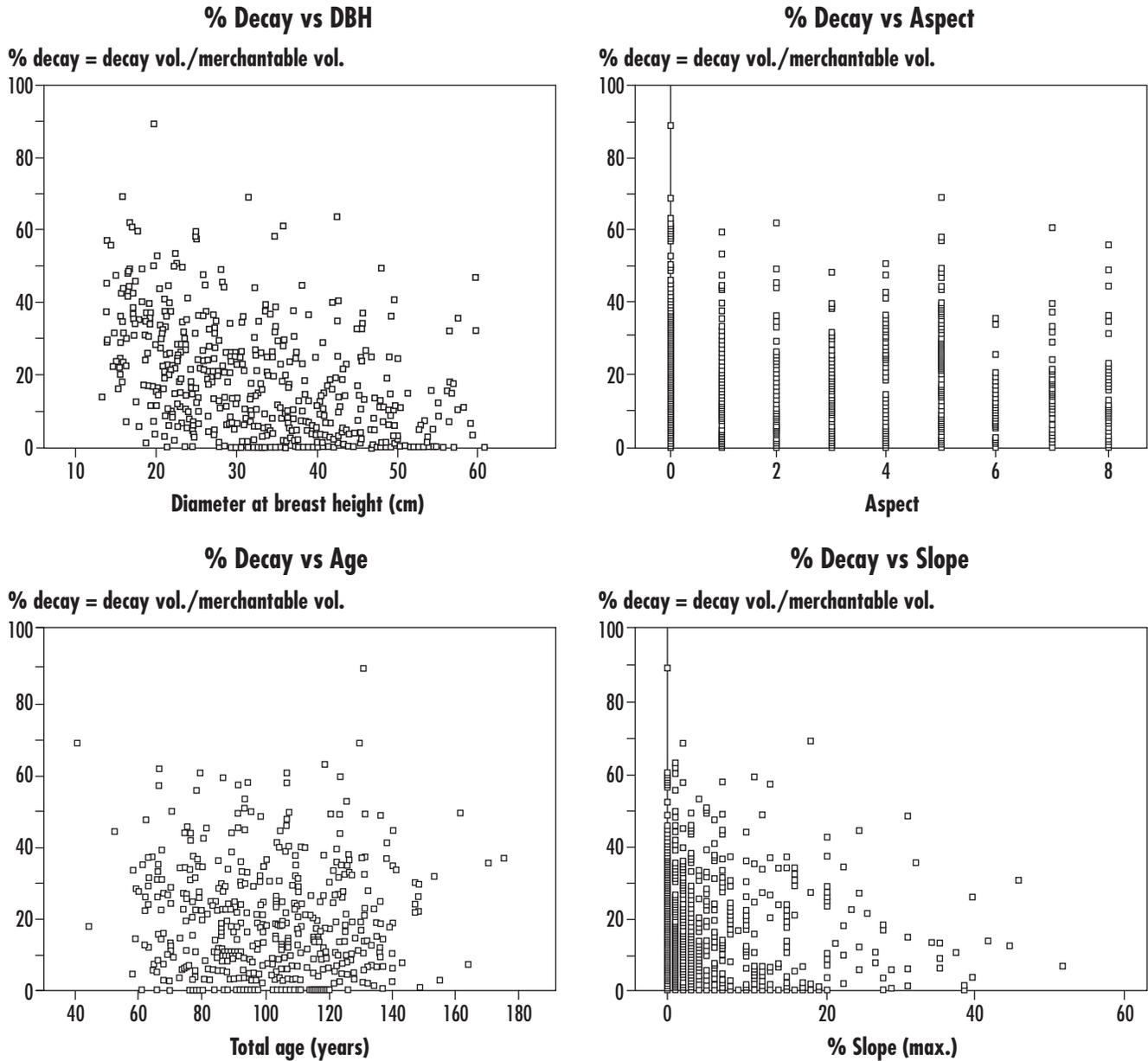


Figure 1. Scatterplots of percent decay volume on selected site and tree variables showing the large amount of variation typical of the data set.

representative of the stand over a large area and therefore a wide variety of site conditions. An equal number of trees was required for each combination of risk group, age, and dbh classes. Early in the collection of the data, selection of trees was determined by access only, because most trees would fit into the required sampling matrix. However, as the data collection continued and the sampling matrix filled, trees were selected to meet the target of six trees per cell of the matrix. Trees that were clearly not representative of the stand as a whole were avoided, but targeted selection of trees for the sampling matrix reduced

the level of randomness of the sample. The second explanation for the lack of significant relationships is that stain and decay in aspen trees are integral components of the ecosystem's function. There are many agents or processes that cause decay and stain, all of which have complex interactions within the ecosystem. A similar ecosystem-level relationship between a pathogen and its host is found in the Interior Cedar-Hemlock zone in southeastern B.C. The root disease fungus *Armillaria ostoyae* is considered as much a part of the ecosystem as are the host trees. Decay fungi, particularly *Phellinus*

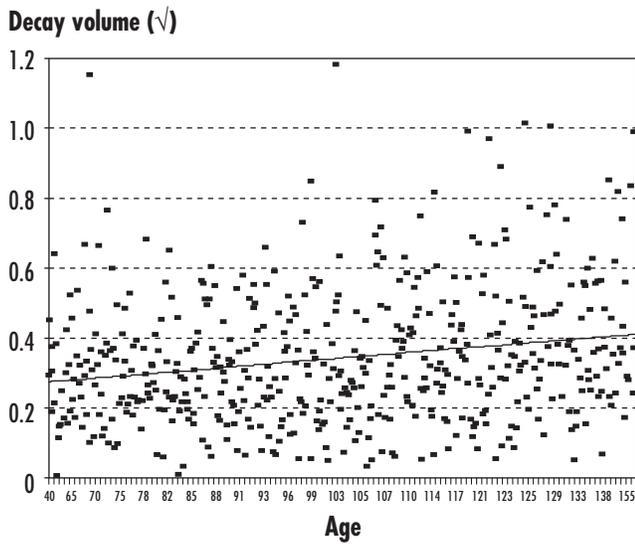


Figure 2. Transformed decay volume data plotted against age, excluding values of zero percent decay.

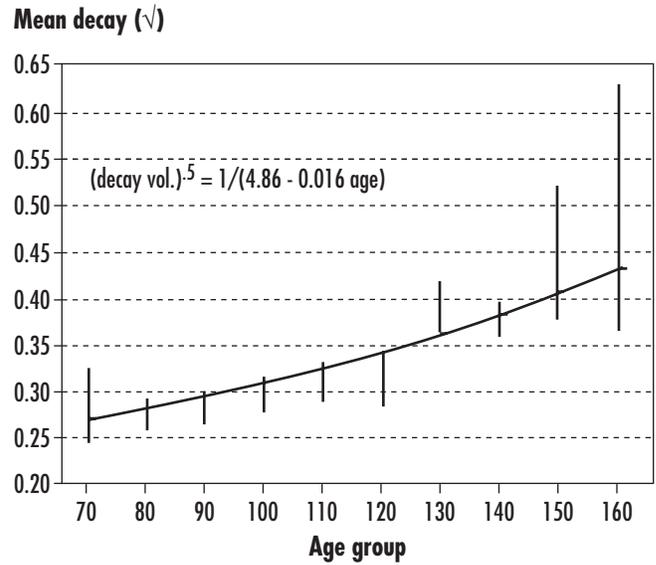


Figure 4. Total mean decay volume plotted against age in 10-year classes. Best fit regression line plotted with error bars around the age group means.

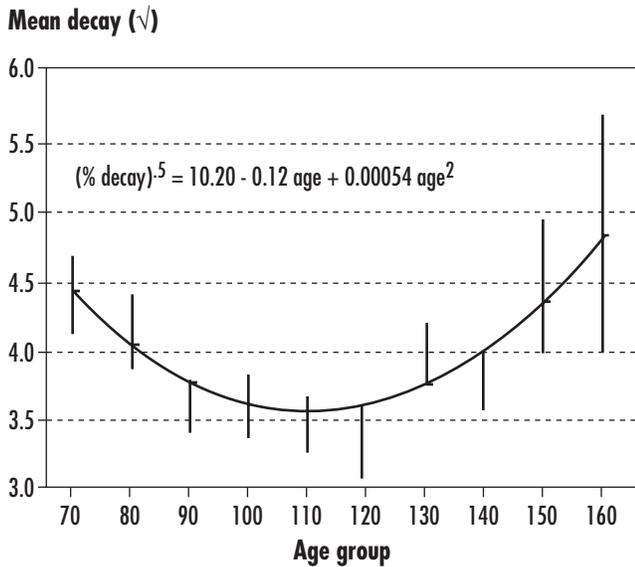


Figure 3. Mean percent decay plotted against age in 10-year classes. Best fit regression line plotted with standard errors around each mean.

tremulae, are as much a part of aspen ecosystems as are the aspen hosts. Therefore, the search for one or a few factors that are strongly correlated with decay and stain is impaired by these interactions and interrelationships. It is suggested that a better understanding of the biology of these decay fungi, their successional pathways, and their role in the ecosystem will provide more useful information for the management of aspen as a timber resource.

Acknowledgements

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Aspen and Poplar Diseases

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Abstract

Increased interest and utilization of both native and hybrid *Populus* species has stimulated research on diseases. Historical Forest Insect and Disease Survey (FIDS) data and collections, plus 3 years of special poplar disease surveys are now giving us an improved picture of the more common and damaging diseases encountered, both in native stands and commercial hybrid plantations.

In native aspen stands, foliar pathogens such as *Venturia macularis* and *Melampsora medusae* are commonly encountered, but usually affect only young stands or suppressed trees. *Phellinus tremulae*, which is discussed in detail in other presentations for this workshop, is the most damaging heart rot with regards to wood quality. *Hypoxyton mammatum*, which is associated with high levels of stand damage elsewhere in North America, is infrequently encountered in B.C. Another canker pathogen, *Encoelia pruinosa*, appears to be widespread at low levels in stands, but until recently has not been well-documented in B.C. *Valsa sordida* is the most common dieback and canker pathogen associated with wounded or stressed trees. Root and butt rot pathogens such as *Armillaria sinapina* and *Bjerkandera adusta* also need further study and documentation as far as distribution and damage.

With regards to native cottonwoods and hybrid poplars, there are several disease problems that appear to be unique to the Pacific Northwest. *Venturia populina* not only causes foliar and shoot blights, but is also associated with cankering and top breakage in damp coastal plantations of hybrids. Septoria leaf spots are commonly encountered on both native and hybrid poplars, and are consistently associated with *S. populicola*. Septoria stem cankers have not been encountered, and, after reviewing herbarium collections and recent survey samples, it appears that the canker-causing *S. musiva* is likely not present in the Pacific Northwest. This is contrary to most current published host-fungus records, which are based on misidentified or immature herbarium specimens. Another leaf blight fungus, *Linospora tetraspora*, is present at damaging levels in some native and hybrid plantations.

Field monitoring for poplar rusts on the lower mainland and Vancouver Island was undertaken by FIDS this year, in anticipation of the first introduction to B.C. of a rust species pathogenic to many of the hybrid poplar clones currently used in commercial plantations. *Melampsora medusae* f.sp. *deltoideae* was first reported in Oregon and Washington on hybrid *P. trichocarpa* × *deltoideae* (T × D) plantations on the lower Columbia River in 1991. Since its discovery, the rust has not only caused severe damage on susceptible hybrids, but has spread rapidly, and in the fall of 1992 was detected close to the Canadian border in Bellingham, Washington.

In October 1993, the rust was first confirmed in B.C. in hybrid poplar plantations in the Fraser Valley, and a week later in a hybrid poplar nursery on Vancouver Island. In the U.S. plantations where the rust has been established for several years, mortality in some of the more susceptible clones has been reported this year. Damage in B.C. plantations so far has been light, due to the fact that initial infections occurred late in the growing season. However, severe defoliation and probable mortality of susceptible T × D clones is likely to occur in the next 2–3 years. Susceptible clones will have to be replaced with the more resistant (i.e., *P. trichocarpa* × *maximowiczii*) hybrids. Another potentially damaging rust recently discovered in the same U.S. plantations, *M. larici-populina*, has not yet spread to Canada.

Introduction

With increased interest in and utilization of native and hybrid *Populus* resources in British Columbia, there is also an increased need for updated, region-specific pathology information.

At the onset of this project, a literature review was conducted to determine the most recent information resource for diseases of *Populus* in B.C. Apart from excerpts from the Forest Insect and Disease Survey's general listing of all pathogens reported from B.C. (Lowe 1977), compiled during the routine monitoring of the health of B.C.'s forests, the last host-fungus list for poplar was an unpublished report produced in 1961 (Ziller). Since then, there has been a change in attitude towards the utilization of native *Populus* for wood and wood products, and an onset of large-scale domestication of hybrid poplar in intensively managed commercial plantations. It is important to have good baseline knowledge of the endemic pathogens that could potentially cause problems in native and hybrid plantations and stool beds (Callan and Ring 1994). We have identified more than 40 new host records for pathogenic and saprophytic fungi on *Populus* in B.C. in just the past 3 years. These pathogens have co-evolved (are in ecological equilibrium) with their native hosts, but may interact differently with large monocultures of non-native hybrid clones. Awareness of *absent* pathogens is just as important; disease organisms that are not presently found in our region require diligent field vigilance to prevent their introduction.

In the Pacific Northwest we are already encountering region-specific disease problems, which are, therefore, not covered in existing diagnostic handbooks aimed at Eastern and Central North American forests. There is also an ominous list of pathogens not encountered to date in western provinces and states. One such pathogen (*Melampsora medusae* f.sp. *deltoidae*) has been introduced to B.C. very recently (1993) and is discussed in this overview.

The following overview is based on:

- a) historical Forest Insect and Disease Survey data, accumulated during the course of routine field surveys over the last 50 years, and deposited in the national FIDS database: Infobase, and
- b) special field surveys of poplar diseases throughout B.C. over the last 3 years.

The majority of these disease data is linked to voucher specimens deposited at Pacific Forestry Centre's Forest Pathology Herbarium (DAVFP), which contains more than 35 000 specimens of all types of forest disease. The herbarium is invaluable in settling doubts regarding anomalous distributions, as in most cases the voucher collection for a distribution record can be examined for confirmation. Several erroneous distribution records have now been corrected or verified via recent examination of herbarium material.

These data were also used to generate disease distribution maps, to better depict the known locations of the more commonly encountered pathogens, and as the basis for an annotated host-fungus checklist for *Populus* species in B.C. (Figure 1). In the future, they will also be used to create a region-specific disease diagnostic handbook.

Poplar Pathology Overview

This overview is divided into sections based on the host tree species, and within each species, further subdivided into basic disease types.

Trembling Aspen: *Populus tr emuloides* Michx.

Trembling aspen is utilized in northern British Columbia for such diverse products as paper, oriented strandboard, plywood, and chopsticks. In the case of the latter three products, a high demand for sound unstained wood frequently results in a large percent of cull. Thus, heart

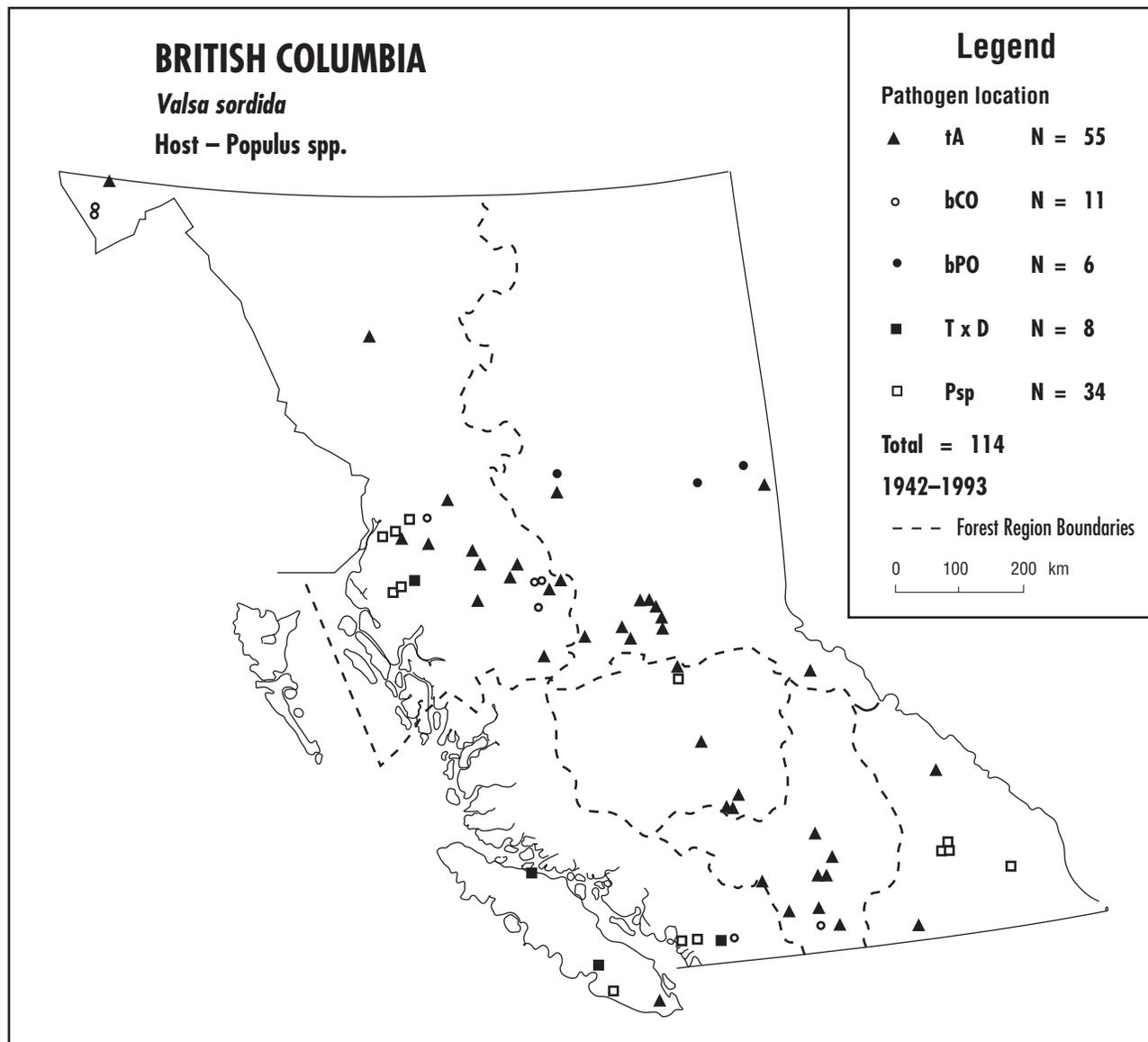


Figure 1. An example of a FIDS disease distribution map; *Valsa sordida* (Cytospora canker) on poplars in B.C. A total of 114 records were found; occasionally distribution points overlap.

Legend:

- tA = trembling aspen
- bCO = black cottonwood
- bPO = balsam poplar
- T x D = hybrids (*P. trichocarpa* × *P. deltoides*)
- Psp = *Populus* sp.

rots and their accompanying stain are well-studied and of great concern. The more important aspen decay fungi are elegantly illustrated in a manual by Hiratsuka (1990). In British Columbia, we have records of 141 fungi associated with trembling aspen. Approximately one-half of these records are for wood decay fungi. For the purpose of this paper, the major and most damaging decay fungus is discussed below, but the majority of fungi considered after *Phellinus tremulae* are pathogens that are recognizable on living trees prior to harvesting (cankers, root rots, foliar diseases).

Decay Fungi

One of the most economically damaging aspen decay fungus is *Phellinus tremulae*, a perennial conk that lowers wood value in the incipient stage of decay by causing a red-brown stain, and that later becomes structurally damaging as a white heart rot (Hiratsuka et al., 1990). Decaying wood often has a sweet, wintergreen-like odour and is laced with black zone lines (Lindsey and Gilbertson 1978). In one study (Thomas et al. 1960), an estimated 38.6% of trunk decay volume was caused by *Phellinus* rot. *Phellinus tremulae* has been documented in mature aspen stands throughout the tree's range in B.C. Within stands, however, decay and stain are extremely difficult to detect in every tree unless the external sign of a conk is present.

Peniophora species have also frequently been associated with decay pockets in aspen. Small, flat, reddish fruiting bodies of this fungus are commonly seen in wounds, on dead branches, and on fallen trees.

Cankers

Hypoxylon canker, caused by the fungus *Hypoxylon mammatum*, can cause widespread severe damage to trembling aspen in many regions of North America. However, it appears to be relatively rare in B.C., with approximately twenty historical records, mostly from areas around Prince George and Kamloops. In the past 2 years only two confirmed collections have been made, from trees in the vicinity of Prince George.

In mature and overmature trembling aspen stands, large diffuse blackened cankers (sooty-bark cankers) caused by *Encoelia pruinosa* (= *Cenangium singulare*) are prevalent in the Prince George, Fort Nelson, and Dawson Creek districts. Although quite different in appearance, sooty-

bark cankers have sometimes been confused with Hypoxylon cankers in field surveys. A quick method of diagnosis is to examine fallen trees in a disease pocket. Blackened areas of exposed wood are frequently covered with the grey cup-like fruiting bodies of this fungus. Stands assumed to be damaged by *H. mammatum* should be rechecked and collections made to confirm identification of the pathogen.

The primary cause of cankers on all wounded and frost- or sun-damaged *Populus* species throughout B.C. is the opportunistic *Valsa sordida* (disease also known as Cytospora canker), which causes a characteristic orange internal discoloration of bark around elongated sunken or cracked lesions (Tao et al. 1984). During damp weather, orange spore tendrils may be exuded from discolored bark. These symptoms differ from commonly encountered damage caused by the poplar borer (*Saperda calcarata*), in which the orange discoloration is a shiny external sap exudate originating from insect entrance holes that are often marked by frass.

Root and Butt Rots

In crowded decadent aspen stands, root decay centres caused by *Armillaria sinapina* have been recently encountered in the Prince George Region. Historical FIDS records are scanty, but have been augmented by culturally confirmed identifications made by Duncan Morrison, root rot pathologist at the Pacific Forestry Centre. The majority of these older records also come from aspen stands around Prince George. Root disease centres usually have fallen or standing dead trees in the centre, and dying trees at the periphery. Advanced decay consists of a yellow stringy root and butt rot (Hiratsuka et al. 1990). *Armillaria* root rot is a potential problem and may contribute to yield declines where it occurs in naturally regenerated stands. Black cottonwood, balsam poplar, and hybrid poplars in natural stands and plantations are also potentially affected by *Armillaria* root rot, but severity and distribution has not yet been well documented.

Ganoderma applanatum (artist's conk) is also frequently encountered as a root and butt rot, as is *Bjerkandera adusta*. Both cause white rots of wood.

All of the above pathogens cause more damage when combined with other factors debilitating the host. Hence, increased incidence of root/butt rots and cankers may be expected in regions where aspen and other *Populus* spp.

have been severely and repeatedly defoliated by insects. Examples of such locations are Williston Lake (4 consecutive years, large aspen tortrix), the Prince George region (9 consecutive years, forest tent caterpillar), and Prince Rupert (northern tent caterpillar).

Foliar Pathogens

Native leaf rusts, primarily *Melampsora albertensis*, frequently cause moderate to high defoliation throughout the range of native *Populus* species. As with most foliar diseases, young trees (regeneration) are most damaged from repeated defoliation. Alternate hosts are conifer species (pine, fir, Douglas-fir, spruce, hemlock). The rust must alternate through the conifer host in order to complete its life cycle and re-infect the *Populus* host the following season.

Venturia species, primarily *V. macularis*, cause leaf blotch and shoot dieback, especially on suppressed trees under conditions of high humidity. The affected tissues take on a blackened appearance, frequently with a olive-green velvety layer, which is in fact a mass of the conidial (*Pollacia*) state. The fungus overwinters on dead tissue, and can be easily overlooked in the resting (*Venturia*) state (Funk 1985, 1981).

Another frequently encountered leaf blight occasionally causing heavy defoliation is caused by species of *Marssonina*. Infected leaves have an orange-brown, speckled appearance and, with a hand lens, the masses of orange spores may be seen on the undersides of the foliage.

Black Cottonwood: *Populus balsamifera* ssp. *trichocarpa* (Torr. & Gray) Brayshaw

Black cottonwood is utilized in B.C. for such products as veneer, pulp, and oriented strandboard. It also hosts a large, diverse array of saprophytic and pathogenic fungi. We have reported a total of 183 species of fungi in the FIDS host-fungus index, 50% of which are decay fungi. With the exception of *Phellinus tremulae*, which is limited to trembling aspen, and other minor decay fungi, the same heart rots affect wood quality. However, some of the canker and foliar fungi are quite different, and are described below.

Cankers

Once again, *Valsa sordida* (*Cytospora*) is most commonly associated with cankering and dieback of stressed or injured

trees. Cankers caused by *Neofabraea populi* are also encountered in the Prince Rupert region and on Vancouver Island, but have not yet been reported from the Lower Mainland. *Neofabraea* cankers look superficially like those associated with *Valsa*. We do not have reliably reported records of *Septoria* canker (caused by *S. musiva*) in British Columbia. This pathogen is responsible for serious canker damage, and also leaf blights in eastern North America, but after critical examination of DAVFP specimens of cankers attributed to *Septoria*, they were all found to be misidentified (usually wounds, or *Valsa* or *Phomopsis* cankers). Microscopic examination of *Septoria* collections on poplar leaves in Pacific Northwest herbaria proved that all specimens labeled as "*Septoria musiva*" were in fact another species, *S. populicola*, which has never been associated with canker symptoms in B.C.

Foliar Pathogens

Septoria populicola leaf blight does, however, cause moderate to severe defoliation on cottonwood, especially during damp cool summers. In the summer of 1993, late-season foliage was strikingly discolored throughout the Pacific Northwest. Infected leaves turn orange or yellow, and minute fruiting bodies will ooze pinkish spore tendrils during wet weather.

Linospora tetraspora causes an easily recognizable foliar blight, which sometimes results in mortality of the infected leaf. Early stages of infection produce blackened blotches with characteristic "feathery" margins, as necrotic areas migrate along leaf veins. Later in the season, the diseased leaf tissue dies and turns a tan colour, upon which small black fruiting bodies develop.

Melampsora occidentalis, the conifer-cottonwood rust, can cause severe defoliation of susceptible trees. The entire underside of the leaves turns orange with urediniospores. Early season infections occur in areas where cottonwoods are in close proximity to conifers.

Hybrid Poplars Currently in Production (*P. trichocarpa* × *P. deltoides* = T × D)

The majority of hybrid poplars currently under production in B.C. are clones of hybrids of our native cottonwood, *P. trichocarpa*, and an eastern species, *P. deltoides* J. Bartram ex Marsh. These hybrids grow twice as fast as our already fast-growing native cottonwoods and are used primarily as a source of pulpwood. We are just beginning to build

up our knowledge of pathogenic fungi on these trees. As most plantations are still quite young, the majority of pathogens are associated with foliar and canker diseases. Compared to records on native poplars, decay fungi comprise approximately 20% of the total of 30 host-fungus records.

Cankers

Interestingly, two species of fungi normally associated with foliar, or (at worst) shoot blights are also linked to stem cankers in stool beds and coastal plantations. *Venturia populina* not only causes characteristic leaf blotching and shoot blight, but, occasionally on susceptible clones, causes dieback to the main stem. Subsequent cankering or breakage occurs. In one Lower Mainland stoolbed, superficial cankers were associated with a species of *Marssonina*.

A disease known as “blackstem” sometimes occurs on newly planted cuttings. Affected tissues darken, and often become pimpled with fungus fruiting bodies, which develop under the bark surface. The fungus primarily involved is *Phomopsis oblonga*, but *Cytospora* canker (*Valsa sordida*) also causes similar symptoms. Sunscald, drought, and other stress factors contribute to blackstem when inoculum, either from contaminated cuttings or nearby diseased trees, is present (Walla and Stack 1980).

Foliar Pathogens

Venturia and *Septoria* leaf blights are two of the most common foliar diseases in hybrid poplar plantations, and have been already discussed above. In addition, yellow leaf blisters caused by *Taphrina populina* and *T. populisalicis* can reach high levels in dense humid plantations. *Linospora tetraspora* can cause severe defoliation on susceptible T × D hybrids, and may be a limiting factor to growth of susceptibles in heavy (cool, wet) disease years, such as the 1993 growing season.

The hybrid poplars used in plantations are generally resistant to endemic rust strains. However, field monitoring for poplar rusts on the Lower Mainland and Vancouver Island has been undertaken this year by FIDS staff, in anticipation of the first introduction to B.C. of a rust species pathogenic to many of the hybrid poplar clones currently used in commercial plantations. *Melampsora medusae* f.sp. *deltoidae* was first reported in Oregon and Washington on hybrid *P. trichocarpa* × *deltoides* (T × D) plantations on the lower Columbia River in 1991

(Newcombe and Chastagner 1993a). Superficial symptoms and signs of this rust are identical to our native *Melampsora*. Microscopic examination is needed to confirm species identification. Since its discovery, the rust has not only caused severe damage on susceptible hybrids, but has spread rapidly and in the fall of 1992 was detected close to the Canadian border in Bellingham, Washington.

In October 1993, the rust was first confirmed in B.C. in hybrid poplar plantations in the Fraser Valley, and a week later in a hybrid poplar nursery on Vancouver Island. In the U.S. plantations where the rust has been established for several years, mortality in some of the more susceptible clones has been reported this year. Damage in B.C. plantations so far has been light, due to the fact that initial infections occurred late in the growing season. However, severe defoliation and probable mortality of susceptible T × D clones is likely to occur in the next 2–3 years. Susceptible clones will have to be replaced with the more resistant (i.e., *P. trichocarpa* × *maximowiczii*) hybrids.

Potential Threats

Septoria musiva appears to be absent from the Pacific Northwest, as discussed above. Care should be taken to avoid its introduction via contaminated (cankered) propagation material.

Rust races and species currently absent from Canada could cause great damage if introduced. Perhaps the most imminent threat is from another rust species recently discovered in the western United States. In the fall of 1991, a second rust was detected in hybrid poplar plantations in Oregon, and its identity as *M. larici-populina* was confirmed in the spring of 1992 (Newcombe and Chastagner 1993b). It is Eurasian in origin and has not been previously detected in North America. To date, *M. larici-populina* is present in two plantations at low levels; it has also overwintered, and was detected again in 1992 and 1993. Both rusts have alternate conifer hosts where they are established elsewhere in the world. However, they have not yet been detected on conifers in the U.S., which indicates that, at least in the United States, they can overwinter on hybrid poplar. Potential damage to conifers is low.

If this rust was to become established in British Columbia, there is no reason to doubt that it would be damaging to hybrid poplar plantations. In fact, *M. larici-populina* is most damaging in countries with cooler climates. Repeated defoliations within a single growing season may occur, but

spread in Oregon plantations has not occurred nearly as rapidly as for *M. medusae* f.sp. *deltoidea* (Newcombe, pers. comm.). Hybrid poplar plantations on Vancouver Island and along the Fraser River are at risk from rust pathogens as the wind-borne rust spores are easily spread over long distances. Rust spores and mycelium can be easily overlooked on imported propagation material, so care should be taken to import material only from rust-free areas.

Bacterial cankers caused by *Xanthomonas populi* cause serious damage in Europe but have never been reported from North America. This bacterium could cause serious disease problems in susceptible (section *Tacamahaca*) poplars if it were introduced (Ostry et al. 1988).

Disease Monitoring in Poplars

Ongoing disease monitoring in both natural stands and plantations is essential to detect problems early. For species determination of foliar diseases, late-season collections are often more valuable because the fungus is more likely to be sporulating. Winter examinations are useful when searching for canker organisms. The Forest Insect and Disease Survey provides identification services; to collect and send in foliar samples, leaves should be pressed between sheets of paper and mailed flat. Wood samples should be also wrapped in paper. Avoid using plastic bags or wrappers, as this encourages development of molds, which obscure symptoms and contaminate cultures.

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