Is the Wide Distribution of Aspen a Result of Its Stress Tolerance?

V. J. Lieffers[1], **S. M. Landhäusser**[1], **and E. H. Hogg**[2]

Abstract—Populus tremuloides *is distributed from drought-prone fringes of the Great Plains to extremely cold sites at arctic treeline. To occupy these conditions aspen appears to be more tolerant of stress than the other North American species of the genus* Populus. *Cold winters, cold soil conditions during the growing season, periodic drought, insect defoliation, and competition from conifers are typical stresses faced by aspen. Aspen is capable of high photosynthetic rates but has conservative use of water during high vapor pressure deficits. This paper examines photosynthesis, water relations, morphological characteristics and root growth, and carbon allocation strategies in relation to the above stresses.*

Introduction

By most accounts, poplars are considered to be competitors (Grime 1979) that are adapted for rapid growth in high resource environments (Stettler et al. 1996). Poplars grow most successfully in fertile and moist sites; indeed, high-resource, short-rotation forest plantations have used poplars to achieve very high rates of productivity (Heilman et al. 1996). Poplars are well known for their rapid juvenile growth rates, rapid expansion of leaf area, and high productivity (Heilman et al. 1996). They are generally considered to be fast growing colonizers and intolerant of stresses such as low moisture conditions or shaded environments. In contrast, stress-tolerating species often have slower growth rates but are able to withstand environments that are deficient in nutrients, water, or light (Grime 1979). Slower growth rates are often correlated with greater tolerance to stress (Lambers et al. 1998).

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed poplar in North America ranging from Alaska, to scattered locations in Mexico, and east to New Brunswick (Perala 1990). It is most abundant in the boreal forest zone but it can survive at both the arctic treeline and at the drought-prone fringes of the Great Plains. A large proportion of the genus *Populus* grows almost exclusively on riparian and moist sites (Braatne et al. 1996). Trembling aspen, however, is very widespread and can form extensive stands in upland sites, as indicated by its dominance of the well to imperfectly drained sites in the boreal forests (Peterson and Peterson 1992) To occupy this wide geographic range of harsh climatic conditions, trembling aspen has to be able to tolerate a wide range of stresses, from extreme cold to drought. Aspen, therefore, seems to be different from most other poplars in that it is able to withstand significant stresses. While it may not have the drought tolerance of some of the conifers such as jack pine or the tolerance to the stresses of alpine treeline such as lodgepole pine or subalpine fir, it seems to be well adapted to tolerate stress, especially compared to other poplars.

The objectives of this paper are to examine some of the morphological and physiological characteristics of aspen compared to other species, particularly the other poplars.

[1]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada.
[2]Canadian Forest Service, Edmonton, Alberta, Canada.

Clonal Root System

Trembling aspen is noted for its extensive clonal root system (Kemperman and Barnes 1976) with many shallow, widely spreading horizontal roots with occasional sinker roots (Strong and LaRoi 1983). When the aboveground trees die following a stand-replacing disturbance, these shallow roots are the main source of suckers that re-establish the next stand. The section of large roots originating near the stump of this dead tree usually die within a few years. Distal ends, however, remain alive if they sucker (figure 1). Thus, each of the major branches of the parent root becomes separated. There is some controversy in the literature regarding the persistence of root connections between suckers on these major branches. They may break down early (from Colorado, Shepperd and Smith 1993), live as long as 40–50 years (from Michigan, Debyle 1964), or remain as persistent connections between mature trees (from Alberta, DesRochers and Lieffers 2000), even if some intermediate ramets on the parent root system died (figure 2). The different observations recorded above may relate to the degree of root damage sustained from burrowing animals during the life of the stand (Shepperd, personal communication). With the next disturbance event, however, the original connecting roots between trees will likely die as these roots are usually untapered and greater than 5 cm in diameter, which makes them very unlikely to sucker (DesRochers 2000). Root grafting may occur near or under the stumps of trees (figure 3). Thus, even though there is partial loss of the original connectivity of root of the parent generation at the time of each disturbance, the roots systems of the clone may reconnect physiologically by grafts. Separated individual trees could, therefore, potentially share resources and hormones with their neighbors both within, and perhaps between clones. The degree of interconnectivity is difficult to assess without extensive physiological testing or excavation. Connectivity of the clone, however, may have ecological significance as discussed below. Other poplars are capable of stump sprouting and sucker regeneration (Pregitzer and Friend 1996) but it appears that aspen relies upon suckering for regeneration more than the rest of the poplars.

The root systems of mature trembling aspen stands in Alberta were recorded at 23 t/ha (Peterson and Peterson 1992) with the highest values ranging up to 41 t/ha. A significant percentage of this root system could potentially be passed on to the next generation of trees after stand-replacing disturbance. This could be from both incorporation of the parent roots into the structural roots of the suckers and transfer of nonstructural carbohydrates (TNC) to sucker development; TNC of coarse roots from maturing aspen stands are about 15% of dry weight (DesRochers 2000). DesRochers (2000) recorded an average of 8.7 t/ha of roots from 12 regenerating stands in Alberta (values ranged up to 18 t/ha). Given the initially small biomass of the regenerating suckers, regenerating stands have a high root:shoot ratio (Shepperd 1993; Shepperd and Smith 1993). If the suckers can eventually meet the respiration costs of a large root system (summer

Figure 1—Parental root and suckers. Large roots and original stump of the parent tree (shaded) die shortly after logging or disturbance. Thus, lines of suckers are connected on a root but not necessarily connected to other parent roots.
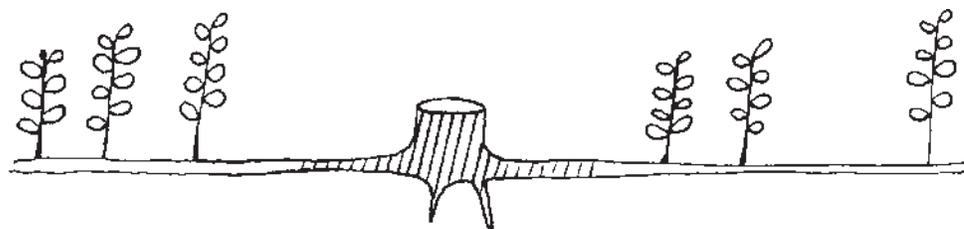
Figure 2—Root system of aspen in a declining stand. The two trees in the foreground are dead trees with portions of their root system still alive (part of the study by DesRochers and Lieffers 2000).

Figure 3—Grafting of aspen roots. The root in the bottom center, remains alive through a root graft.

rates for coarse roots were recorded at 181 mmol CO_2 m^{-3} s^{-1}, at 15 ºC [DesRochers 2000]), they should be in a good position to capture water and nutrients from the site. The legacy of the root biomass from the previous stand and the resulting high root:shoot ratio of juvenile stands might allow them to survive a stress (especially drought stress) that might have killed the parent trees or a seedling. Along the dry, northern fringe of the Canadian prairies, aspen stands that die off above ground following drought and/or repeated insect defoliation can simply resucker and reestablish (Peterson and Peterson 1992; Hogg 1994). Regeneration from an established root system seems to be a much more reliable means of reproduction in water stressed environments than from

Lieffers, Landhäusser, and Hogg

Is the Wide Distribution of Aspen a Result of Its Stress Tolerance?

seed. In riparian cottonwoods, Rood et al. (1994) found that 52% of the regeneration of *P. angustifolia*, *P. balsamifera*, and *P. deltoides* was from seedlings, 30% through root suckers, and 18% as resprouts. Seedlings occupied microsites closer to the river while suckers were generally produced in areas away from the river.
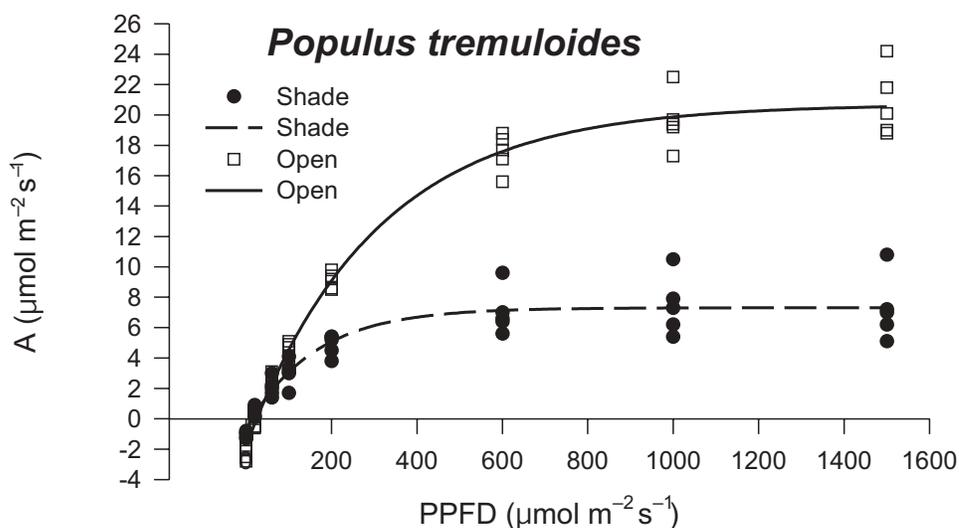
Photosynthesis

Photosynthesis rates for trembling aspen range up to 22 µmol m^{-2} s^{-1} (Ceulemans and Isebrand 1996; Landhäusser, unpublished data). These rates are in the same range as most of the high yield poplar clones used in plantations (Ceulmans and Isebrand 1996). Like the hybrid poplars (Ceulmans and Isebrand 1996), aspen produces shade leaves in low light environments (Landhäusser, unpublished data) with a light compensation point of about 25 µmol m^{-2} s^{-1} (figure 4). Leaf dark respiration rates were 1.0 in the understory environment and 2.2 µmol m^{-2} s^{-1} in the open. These values were within the range of other poplars (Ceulemans and Isebrands 1996). Indeed, aspen foliage must have relatively good capability for photosynthesis at low light conditions, as lower foliage in dense stands with high leaf area index would rarely be exposed to high light. Aspen doubles its photosynthetic rates from 5 to 25 °C (Lawrence and Oechel 1983) and photosynthesis declines at temperatures greater than 25 °C. Aspen bark is capable of sufficient photosynthesis to offset the respiration losses from the stem (Foote and Schaedle 1976). While some other poplars have photosynthetic bark in juvenile stages, the fact that aspen bark is usually green and nonthickened even late in life may offer it an advantage over species with thickened bark.

Water Relations

Given trembling aspen's ability to survive on the edge of the drought-prone Great Plains of North America, aspen must have significant abilities to withstand water stress. Aspen appears to react conservatively to both the low soil moisture and high vapor pressure deficit (VPD) typical of drought-prone areas. Stomatal

Figure 4—Photosynthetic light response of 2-year-old aspen from seedlings grown in open and understory environments (trembling aspen-balsam poplar stand). Photosynthesis was measured at 20 °C and 40% RH (Landhäusser, unpublished data).

conductance tends to decrease with soil drying (Iacobelli and McCaughey 1993) but also varies inversely with VPD. This leads to reduced photosynthesis on hot days with low humidity (Dang et al. 1997), even when soils are moist (Hogg et al. 2000). An intriguing result of aspen stomatal responses is that daytime transpiration rates remain remarkably constant over a wide range of VPD, from 1.0 to 4.8 kPa (Hogg and Hurdle 1997), thus demonstrating the ability of this species to conserve moisture during periods of high atmospheric demand. At the same time, aspen withstands leaf water potentials of –2 to –3 MPa on most summer days without any apparent impact on photosynthesis rates (Hogg et al. 2000).

In contrast, some of the hybrid poplars have little change in stomatal conductance until there is a large change in leaf water potential (Blake et al. 1984) and there are some clones where stomata are insensitive to VPD, soil moisture, and light levels (Schulte and Hinkley 1987; Ceulemans et al. 1988; Furukawa et al. 1990). Aspen stomatal responses to soil moisture and VPD stresses appear to be operating to maintain water potential above a critical level in an environment where water is frequently limiting, compared to most other poplars that evolved in riparian areas where water supply is usually plentiful and heavy water loss through transpiration is not a critical factor. Given the strongly clonal nature of aspen (Kemperman and Barnes 1976), conservation of soil water may be a critical component of the clone's survival and might have been an evolutionary selection force. With increasing clone size, we speculate that a single aspen clone would exert greater control over stand hydrology so that the rate of soil water depletion might become more strongly coupled with clone-specific transpiration rates. Thus, it could be postulated that during drought, a large clone with high stomatal conductance would deplete its own soil water reserves more rapidly, therefore increasing the risk of mortality of the entire clone.

Under extreme water stress, xylem cavitation may result in vaporization of water, which causes embolism within the conducting elements of the xylem. This prevents water uptake (Tyree and Sperry 1988). Measurements on stem sections of various species show that aspen is far less vulnerable to xylem cavitation than most of the other native poplars in western North America (*Populus balsamifera*, *P. fremontii*, *P. deltoides*, and *P. angustifolia*), which are usually restricted to river floodplains or moist sites (Tyree et al. 1994; Blake et al. 1996). *Populus trichocarpa* is similar to aspen in terms of cavitation resistance, but at least some populations and hybrids of this species are nevertheless vulnerable to cavitation because stomata do not respond to decreases in leaf water potential (Bassman and Zwier 1991), even at values of –4 MPa (Ceulemans et al. 1988).

A few poplar species, including trembling aspen, have strongly flattened petioles, which cause leaves to flutter even in a slight breeze. Fluttering reduces boundary layer resistance to heat transfer, which can cause a cooling of leaf temperature up to 2–4 °C, thus promoting CO_2 uptake on hot days (Roden and Pearcy 1993). Such an adaptation, coupled with the small size of aspen leaves relative to other poplars, might be especially important in preventing overheating of leaves as stomata close to avoid water stress during periods of drought. In boreal forests, aspen is usually confined to the warmest positions on the landscape (Van Cleve et al. 1983). There is virtually no root growth of aspen until soil temperatures are greater than 6 °C while large amounts of roots are produced at 20 °C (Landhäusser and Lieffers 1998). As lignified roots have minimal water uptake and hydraulic conductivity compared to when new non-lignified roots develop (Wan et al. 1999), cold soils will limit water relations.

Cold soils also limit water uptake of roots by reduced activity of water channel (aquaporin) proteins in the membranes (Wan and Zwiazek 1999). Since these proteins require energy to function and cold soils limit respiration, there appears to be insufficient ATP available to allow them to function properly in cold soils (Wan and Zwiazek 1999). These proteins may also be limited by anaerobic conditions, but this needs more work to verify this hypothesis. In contrast, Lawrence and Oechel (1983) found relatively little difference in photosynthetic rates between warm and cold soils; however, in this case, the aspen seedlings were grown in warm conditions and moved to cold soils.

Carbon Allocation

There is developing evidence that differences in photosynthetic rates and water relations among plant species from different ecological niches may often be relatively small. (Reich et al. 1998). Other factors such as C allocation to leaves versus other organs are often the important components for determining growth rates among species or genotypes (Landhäusser, unpublished data). Differences in foliar morphology may also be important in this context (e.g., Niinemets et al. 1998). Leaf area development in aspen is driven by both leaf size and leaf number. Both preformed leaves (flushed from an overwintered bud) and neoformed (initiated during the growing season) are smaller when aspen is grown in cold soils (Landhäusser and Lieffers 1998). Cold soils also result in early bud set on long shoots, greatly inhibiting the production of neoformed leaves (Landhäusser and Lieffers 1998). Thus, in the second half of the growing season, aspen in cold soils appears to horde C in reserves instead of attempting to capture more C by building more leaves. This switch to C storage instead of shoot growth appears to be analogous to the switch that occurs in hybrid poplars in the fall, away from shoot growth to C storage in preparation for winter (Isebrands and Nelson 1983). In other poplars species, smaller leaves are also characteristic of drought and flooding stress (Van Volkenburgh and Taylor 1996). It is likely that cold soils, drought, and flooding all produce water stress and inhibit the leaf expansion rates. Thus, while there may be clonal differences in leaf size, size can be a good indicator of site conditions and the ability of the tree to take up water.

Aspen stands typically develop maximum leaf area at a very early age (Johnstone and Peterson 1980). Leaf area indices (LAI) of 2-year-old stands may be 2 and climb to 4 or 5 by 14–20 years of age (Shepperd 1993; B. Pinno, unpublished data). Based upon light transmission values (Constabel and Lieffers 1996) and litter fall estimations (DeLong et al. 1996), LAI of older stands decline, sometimes to less than 2. It is not clear why LAI declines with age but may relate to increased hydraulic resistance from tall stems, crown abrasion, and/ or decreased nutrient supply (Ryan et al. 1997). As older stands have greater biomass to sustain with a smaller leaf area, they are likely more vulnerable to sustained stress. On a stand basis, the LAI of aspen is relatively low compared to hybrid poplars, where values of up to 10 or more have been reported (Heilman et al. 1996). Because these leaves may be positioned more vertically, however, they tend to transmit more light to lower layers than aspen with its more random leaf distribution (Stadt and Lieffers 2000).

Landhäusser (unpublished data) found that in low light conditions, aspen and balsam poplar carbon allocation was opposite to what one would anticipate in a plant growing in an understory. Seedlings of both species grown in shade

Is the Wide Distribution of Aspen a Result of Its Stress Tolerance?

Lieffers, Landhäusser, and Hogg

produced less leaf area, while root:shoot ratio (RSR) was higher compared to open grown conditions. An increase in allocation to roots at the expense of leaf growth is not likely to be adaptive in a light-limited environment. Decreased RSR as a result of increases in leaf area ratio (LAR, $cm^2_{leaf} g^{-1}_{plant}$) and leaf mass ratio (LMR, $g_{leaf} g^{-1}_{plant}$) are thought to be advantageous to a life in an understory environment (Givnish 1988; Lambers et al. 1998; Reich et al. 1998).

Response of Aspen to Various Stressful Environments

Growth in Extremely Cold Air and Soil Temperatures

Aspen appears to be able to withstand severely cold air temperatures, unlike many other hardwood species that have a cold hardiness limit near –40 °C, corresponding to the freezing point of supercooled water within ray parenchyma (Waring and Schlesinger 1985). In aspen and other boreal species, ray parenchyma cells allow water movement out of cells during cooling, which prevents ice crystal development (Burke et al. 1976), so that dormant twigs can even survive immersion in liquid nitrogen with a temperature of –196 °C (Sakai and Weisner 1973). During the growing season, aspen is relatively frost-tolerant, although foliage does not survive experimental exposure to severe summer frost (–6 °C) (Lamontagne et al. 1998).

Aspen is capable of photosynthesis at relatively low air temperatures of 5 °C or less (Lawrence and Oechel 1983). In contrast, aspen does not perform well under cool soil temperatures (Landhäusser and Lieffers 1998, and see above). Most regeneration of aspen stands in boreal forest regions would have occurred naturally after fire (Rowe and Scotter 1973). Fires reduce insulating litter layers and blackened the soil surface increasing soil temperatures. Hungerford (1988) and Maini (1967) suggest a threshold soil temperature of 15 °C is necessary for successful aspen sucker regeneration. Currently minimal soil disturbance is recommended on northern boreal forest sites after clear-cutting to promote aspen suckering (Navratil and Bella 1990; Bates et al. 1993); however, there have been numerous examples in Northern Alberta where this technique has resulted in sparse and sporadic sucker initiation (Darrah 1991; Landhäusser and Lieffers, personal observation).

Competition From Growth With Other Trees (Notably Spruce)

As noted above, aspen leaves are capable of photosynthesis in low light. This concept is reenforced by the fact that young aspen stands are capable of carrying a large leaf area and the leaves on the lowest parts of the canopy are presumably contributing positively to the carbon balance. In low light conditions, however, aspen allocates resources to root growth at the expense of leaves (Landhäusser, unpublished data). This appears to be an inappropriate strategy for growth in understories. Aspen, like the other species classed as shade-intolerant northern species, has a higher probability of mortality when its growth rates decline than species considered shade tolerant (Wright et al. 1998). In boreal mixed-wood forests, aspen is an early colonizer but usually it is eventually replaced by white spruce (*Picea glauca* [Moench] Voss) (Lieffers et al. 1996). As aspen stands age, there is a gradual decline in aspen leaf area (Lieffers and Stadt 1994), increase

in stem decay (Peterson and Peterson 1992), and gradual or episodic mortality of stems (Hogg and Schwarz 1999). In mixed-wood stands this is usually accompanied by development of spruce. As spruce is more shade tolerant and capable of growth in cold soils (Van Cleve et al. 1983), the gradual buildup of insulating forest floor litter with aging of the stand and the shift from warm soils with ample nutrients to colder soils with lower mineralization rates could be important in understanding the decline of aspen with concurrent development of spruce.

Drought and Insect Defoliation

One of the responses of aspen to dry soil conditions is reduced height growth and reduced maximum height growth. This may be seen by a striking reduction in maximum height moving from boreal forest where precipitation is greater than evaporation to the drought-prone parklands of the Canadian prairie provinces (Maini 1972; Hogg and Hurdle 1995). In the extreme examples of this phenomenon, especially in windy areas, krummholz-type forests of aspen develop (figure 5). These stunted forests are subject to widespread dieback following years with severe prairie drought (Bailey and Wroe 1974; Hogg and Lieffers , personal observation).

In the boreal forest, moisture is a significant factor affecting interannual variation in aspen radial growth (Hogg and Schwarz 1999), but under the present climate at least, drought is rarely severe enough to cause aspen dieback except in combination with other stresses. One of the major stresses on aspen is defoliation by insects such as the forest tent caterpillar (*Malacosoma disstria* Hbn.), which can affect vast areas of the landscape (>500 x 300 km) during major outbreak years such as in 1988 (Emond and Cerezke 1989). Severe defoliation causes dramatic reductions in stem growth (figure 6), but its impact on stem mortality is often not evident until several years following major outbreaks (Churchill et al. 1964). Thus, the causes of dieback can be difficult to determine.

Figure 5—Stunted aspen growing in windy open sites in the West Castle Valley, Alberta.
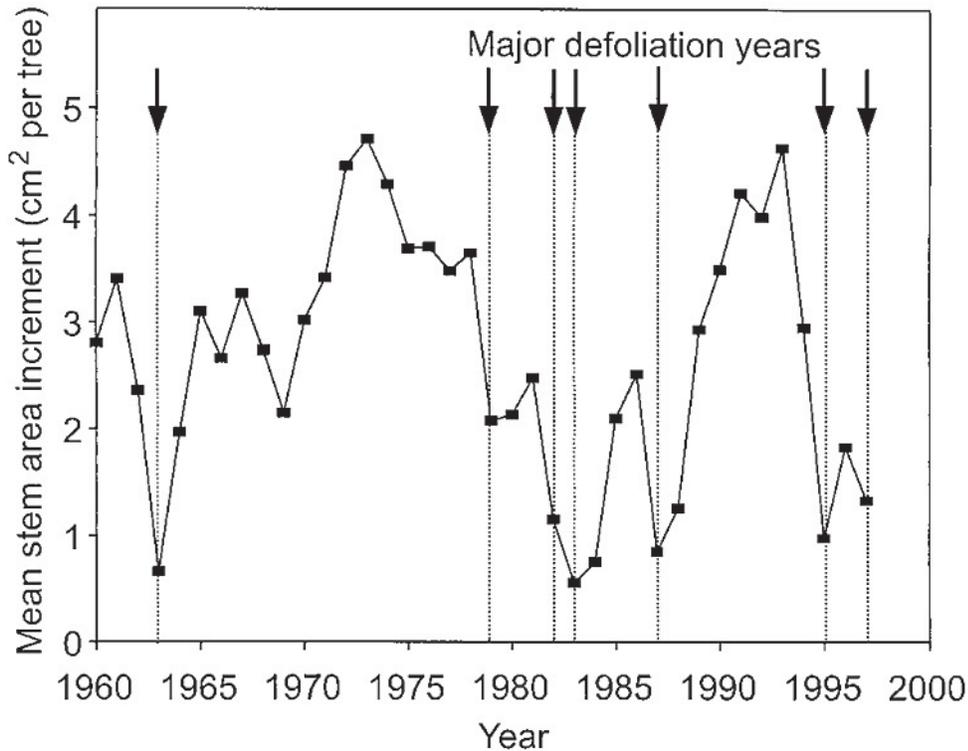
Figure 6—Growth of aspen in relation to defoliation by forest tent caterpillar in a 53-year-old stand in northwestern Alberta, Canada (55° 28'N, 118°23'W). Growth is expressed as mean stem area increment of 10 trees, based on tree rings in disks collected at 1.3 m height). Major defoliation years are shown (1963, 1979, 1982, 1983, 1987, 1995, and 1997). The stand showed significant crown dieback and was affected by three fungal pathogens (*Armillaria, Venturia,* and *Phellinus*) when sampling was conducted in 1997 (part of study by E.H. Hogg, J.P. Brandt, and B. Kochtubajda, unpublished).

Since the early 1990s, extensive dieback of aspen stands has been noted in some areas of the western Canadian boreal forest and adjacent parkland. A recent retrospective analysis using dendrochronology indicated that the dieback was caused primarily by insect defoliation during several consecutive years throughout the 1980s, in combination with drought (Hogg and Schwarz 1999). However, aspen stands showing dieback also usually exhibit symptoms of subsequent damage by fungal pathogens and wood-boring insects (Churchill et al. 1964; Hiratsuka 1987; Ives and Wong 1988). Thaw-freeze events during winter and spring can also lead to crown dieback (Cayford et al. 1959; Cox and Malcolm 1997); such events are especially common near the Rocky Mountains where chinook winds are most intense. Thus, there is a wide variety of stresses, both biotic and abiotic, that aspen, through its continued persistence over much of North America, has demonstrated that it can withstand.

Conclusions and Needs for Further Research

Because of its clonal nature and persistent interconnections through retention of parent roots or reestablishment of connections through root grafts, many aspects of the physiology of natural stands of aspen are extremely difficult to study, particularly C allocation strategies. Aspen clones occupy large areas in drought-prone upland sites. Because of the increased occurrence of drought, aspen appears to have more conservative water use during periods of high VPD. This response may have developed to maintain soil water reserves during periods of extended drought.

Relative to white spruce and other boreal forest conifers, aspen does not grow well in cold soils. This appears to be driven by reduced respiration slowing the activity of root water channel proteins. As aspen is more tolerant to extremely

cold air temperatures than other poplars, however, it is likely that it also has better adaptations to cold soils than other poplars (except perhaps for *Populus balsamifera*), but this would need to be studied further by comparative studies.

Understanding aspen's response to competition from conifers is complex. Aspen has high photosynthetic rates in strong light and low VPD. Aspen is capable of producing shade leaves that have a low light compensation point, but saplings may actually decrease their leaf area in shaded conditions, which negates the benefits of a low compensation point. As stands age and the coniferous component increases, there is a buildup of forest floor litter and more interception of solar radiation, especially in winter and early spring. This likely causes a net cooling of soils and decreases in root activity or mineralization rates, which may in turn inhibit the aspen growth. These components need more study.

There is a vast literature on hybrid poplars and a large literature on aspen, but there has not been a comprehensive comparison of aspen with other poplars in responding to the wide variety of stresses mentioned above. While it would be useful to compare aspen with other poplars, particularly hybrids, it is possible that comparisons in block plantings may give unrealistic results because the benefits of conserving moisture may not be apparent when many clones are drawing from the same limited water resource.

Acknowledgments

References

Bailey, A.W. and Wroe, R.A. 1974. Aspen invasion in a portion of the Alberta parklands. J. Range Manage. 27: 263-266.

Bassman, J.H. and Zwier, J.C. 1991. Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa x P. deltoides* clones. Tree physiology 8: 145-159.

Bates, P.C., Blinn, C.R., and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. Can. J. For. Res. 23: 2403-2412.

Blake, T.J., Sperry, J.S., Tschaplinski, T.J., and Wang, S.S. 1996. Water relations. *In* Biology of *Populus* and its implications for management and conservation. Part II Chapter 16 *Edited by* R. F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman and T.M. Hinckley. NRC Research Press. National Research Council of Canada, Ottawa, ON: 401-422.

Blake, T.J., Tschaplinski, T.J., and Eastham, A. 1984. Stomatal control of water use efficiency in poplar clones and hybrids. Can. J. Bot. 61: 1344-1351.

Braatne, J.H., Rood, S.B., and Heilman, P.E. 1996. Life history, ecology and conservation of riparian cottonwoods in North America. *In* Biology of *Populus* and its implications for management and conservation. Part I Chapter 3 *Edited by* R. F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press. National Research Council of Canada, Ottawa, ON: 57-85.

Burke, M.J., Gusta, L.V., Auamme, H.A., Weiser, C.J., Li, P.H. 1976. Freezing and injury in plants. Ann. Rev. Plant Physiol. 27: 507-528.

Cayford, J.H., Hildahl, V., Nairn, L.D., and Wheaton, P.H. 1959. Injury to trees from winter drying and frost in Manitoba and Saskatchewan in 1958. Forestry Chronicle 35: 282-290.

Ceulemans, R., Impens, I., and Imler, R. 1988. Stomatal conductance and stomatal behavior in *Populus* clones and hybrids. Can. J. Bot. 66: 1404-1414.

Ceulemans, R. and Isebrands, J.G. 1996. Carbon acquisition and allocation. *In* Biology of *Populus* and its implications for management and conservation. Part II Chapter 15 *Edited by* R. F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press. National Research Council of Canada, Ottawa, ON: 355-399.

Churchill, G.B., John, H.H., Duncan, D.P., and Hodson, A.C. 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. Ecology 45: 630-633.

Constabel, A.J. and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26: 1008-1014.

Cox, R.M., and Malcolm, J.W. 1997. Effects of duration of a simulated winter thaw on dieback and xylem conductivity of *Betula papyrifera*. Tree Physiol. 17: 389-396.

Dang, Q.-L., Margolis, H., Coyea, M.R., Sy, M., and Collatz, G.J. 1997. Regulation of branch level gas exchange of boreal forest trees: roles of shoot water potential and vapor pressure differences. Tree Physiol. 17: 521-535.

Darrah, D.W. 1991. Aspen harvesting: a government perspective. *In* Navratil, S. and P.B. Chapman (eds.). Aspen management for the 21st century. Forestry Canada and Poplar Council of Canada. Edmonton, Alberta: 61-66.

DeByle, N.V. 1964. Detection of functional intraclonal root connections by tracers and excavation. For. Sci. 10: 386-396.

DeLong, H.B., Lieffers, V.J., Blenis, P.V. 1997. Microsite effects on first year establishment and over-winter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27: 1452-1457.

DesRochers, A. Clonal root connections and respiration in aspen. Ph.D. Thesis. University of Alberta, Edmonton, AB.

DesRochers, A. and Lieffers, V.J. 2000. Structural root system of mature aspen (*Populus tremuloides*) in declining stands of Alberta, Canada. J. Veg. Sci. Accepted.

Emond, F.J. and Cerezke, H.F. 1989. Forest insect and disease conditions in Alberta, Saskatchewan, Manitoba, and the Northwest Territories in 1988 and predictions for 1989. For. Can., North. For. Cent., Edmonton, AB. Info. Rep. NOR-X-303.

Foote, K.C. and Schaedle, M. 1976. The contribution of aspen bark photosynthesis and respiration in stems of *Populus tremuloides*. Plant Physiol. 58: 91-94.

Furukawa, A., Park, S.-Y., and Fujinuma, Y. 1990. Hybrid poplar stomata unresponsive to changes in environmental conditions. Trees 4: 191-197.

Givnish, T.J. 1988. Adaptation to sun and shade: a whole plant perspective. Aust. J. Plant Physiol. 15: 63-92.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, New York. 222 p.

Heilman, P.E., Hinckley, T.M., Roberts, Da.A., and Ceulemans, R. 1996. Production physiology. *In* Biology of *Populus* and its implications for management and conservation. Part II Chapter 18 *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press. National Research Council of Canada, Ottawa, ON: 459-489.

Hiratsuka, Y. 1987. Forest tree diseases of the prairie provinces. Canadian Forestry Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-286.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Can. J. For. Res. 24: 1835-1845.

Hogg, E.H. and Hurdle, P.A. 1995. The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? Water, Air and Soil Pollution 82: 391-400.

Hogg, E.H. and Hurdle, P.A. 1997. Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. Tree Physiology. 17: 501-509.

Hogg, E.H., Saugier, B., Pontailler, J.-Y., Black, T.A., Chen, W., Hurdle, P.A., and Wu, A. 2000. Reponses of trembling aspen and hazelnut to vapor pressure deficit in a boreal deciduous forest. Tree Physiology 20: 725-734.

Hogg, E.H. and Schwarz, A.G. 1999. Tree-ring analysis of declining aspen stands in west-central Saskatchewan. Nat. Resour. Can., Canadian Forestry Service, Northern Forestry Centre, Edmonton, AB. Info. Rep. NOR-X-359.

Hungerford, R.D. 1988. Soil temperature and suckering in burned and unburned aspen stands in Idaho. USDA For. Serv. Res. Note INT-378.

Iacobelli, A. and McCaughey, J.H. 1993. Stomatal conductance in a northern temperate deciduous forest: temporal and spatial patterns. Can. J. For. Res. 2: 245-252.

Isebrands, J.G. and Nelson, N.D. 1983. Distribution of 14C-labeled photosynthates within intensively cultured Populus cloned during the establishment year. Physiol. Plant. 59: 9-18.

Ives, W.G.H. and Wong, H.R. 1988. Tree and shrub insects of the prairie provinces. Canadian Forestry Service, Northern Forestry Centre, Edmonton, AB. Info. Rep. NOR-X-292.

Johnstone, W.D. and Peterson, E.B. 1980. Above-ground component weights in Alberta Populus stands. Environ. Can., Canadian Forestry Service. Info. Rep. NOR-X-226.

Kemperman, J.A. and Barnes, B.V. 1976. Clone size in American aspen. Can. J. Bot. 54: 2603-2607.

Lambers, H., Chapin, F.S., III, Pons, T.L. 1998. Physiological ecology. Springer, New York. 540 p.

Lamontagne, M., Margolis, H., and Bigras, F. 1998. Photosynthesis of black spruce, jack pine, and trembling aspen after artificially induced frost during the growing season. Can. J. For. Res. 28: 1-12.

Landhäusser, S.M. and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Can. J. For. Res. 28: 396-401.

Lawrence, W.T. and Oechel, W.C. 1983. Effects of soil temperature on the carbon exchange of taiga seedlings. II. Photosynthesis, respiration, and conductance. Can. J. For. Res. 13: 850-859.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter K., and Stewart, J.D. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72: 286-292.

Lieffers, V.J. and K. Stadt. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24: 1193-1198.

Maini, J.S. 1967. Variation in the vegetative propagation of Populus in natural populations. Bull. Ecol. Soc. 48: 75-76.

Maini, J.S. 1972. Silvics and ecology in Canada. Aspen symposium proceedings. USDA Forest Service Gen. Tech. Rep. NC-1: 67-73.

Navratil, S. and Bella, I.E. 1990. Regeneration, development and density management in aspen stands. *In* Management and utilization of Alberta's poplar. Proceedings Poplar Council of Canada 10th Annual Meeting, Edmonton, Alberta October 1988. Forestry Canada, North. For. Cent., Edm. Alberta and Alberta Dept. For. Lands and Wildlife, Edmonton, Alberta: 19-37.

Niinemets, U., Kull, O., and Tenhunen, J.D. 1998. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous species of contrast-ing shade tolerance. Tree Physiol. 18: 681-696.

Peterson, E.B and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Forest Region., Northern For. Cent. Edmonton, Alberta. Spec. Rep. 1.

Perala, D.A. 1990. *Populus tremuloides* Michx.: quaking aspen. *In* Silvics of North America. Vol 2 Hardwoods. *Edited by* R.M Burns and B.H. Honkala. USDA Forest Service Ag. Handbook 654. Washington, DC: 555-569.

Pregitzer, K.S. and Friend, A.L. 1996. The structure and function of Populus root systems. *In* Biology of *Populus* and its implications for management and conservation. Part II Chapter 14 *Edited by* R. F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press. National Research Council of Canada, Ottawa, ON: 331-354.

Reich, P.B., Tjoelker, J.G., Walters, J.B., Vanderklein, D.W., and Buschena, C. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal trees species grown in high and low light. Funct. Ecology 12: 327-338.

Roden, J.S. and Pearcy, R.W. 1993. The effect of flutter on the temperature of poplar leaves and its implication for carbon gain. Plant Cell Environ. 16: 571-577.

Rood, S.B., Mahoney, J.M., Reid, D.E., and Zilm, L. 1994. Instream flows and the decline of riparian cottonwood along the St. Mary River, Alberta. Can. J. Bot. 73: 1250-1260.

Rowe, J.S. and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. 3: 444-464.

Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27: 213-262.

Sakai, A. and Weisner, C.J. 1973. Freezing resistance of trees in North America with reference to tree regions. Ecology 54: 118-126.

Schulte, P.J. and Hinckley, T.M. 1987. The relationship between guard cell water potential and the aperature of stomata of *Populus*. Plant Cell Environ. 10:313-318.

Shepperd, W.D. 1993. Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains. USDA Forest Service Res. Pap. RM-312.

Shepperd, W.D. and Smith, F.W. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. For. Ecol. Manage. 61: 157-170.

Stadt, K.J. and Lieffers, V.J. 2000. MIXLIGHT: A flexible light transmission model for mixed species forest stands. Ag. For. Meteor. 102: 235-252.

Stettler, R.F., Bradshaw, H.D., Jr., Heilman, P.E., and Hinckley, T.M. 1996. Biology of *Populus* and its implications for management and conservation. NRC Research Press. National Research Council of Canada, Ottawa.

Strong, W.L. and La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. 13: 1164-1173.

Tyree, M.T., Kolb, K.J., Rood, S.B., and Patiño, S. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? Tree Physiol. 14: 455-466.

Tyree, M.T. and Sperry, J.S. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. Plant Physiol. 88: 574-580.

Van Cleve, K., Oliver, L., Schlentner, R., Viereck, L.A., and Dyrness, C.T. 1983. Productivity and nutrient cycling in taiga forest ecosystems: vegetation, soils and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. 13: 747-766.

Van Volkenburgh, E. and Taylor G. 1996. Leaf growth physiology. *In* Biology of *Populus* and its implications for management and conservation. Part II Chapter 12 *Edited by* R. F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press. National Research Council of Canada, Ottawa, ON: 283-299.

Wan, X., Landhäusser, S.M., Zwiazek, J.J., and Lieffers, V.J. 1999. Root water flow and growth of aspen (*Populus tremuloides*) at low root temperatures. Tree Physiol. 19: 879-884.

Wan, X. and Zwiazek, J.J. 1999. Mercuric chloride effects on root water transport in aspen seedlings. Plant Physiol. 121: 1-8.

Waring, R.H. and Schlesinger, W.H. 1985. Forest Ecosystems: concepts and applications. Academic Press. NY.

Wright, E.F., Coates, K.D., Canham, C.D., and Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28: 871-886.