

## The coarse-root system of mature *Populus tremuloides* in declining stands in Alberta, Canada

DesRochers, Annie<sup>1,2</sup> & Lieffers, Victor J.<sup>1</sup>

<sup>1</sup>Department of Renewable Resources, University of Alberta, 4-42 Earth Sciences Building, Edmonton, (Alberta), Canada, T6G 2E3; Fax 7804921767; <sup>2</sup>Current address: Alberta-Pacific Forest Industries Inc., Box 8000, Boyle, Alberta, T0A 0M0 Canada; Fax +17805258423; E-mail desrocan@alpac.ca

**Abstract.** The coarse-root dynamics of ramets of *Populus tremuloides* (aspen) were investigated with respect to persistence of the original root connections (roots of parent trees from which the ramets originated), the time of establishment of new roots at the base of the stem and the fate of the communal root system after death of individual trees. Parts of the root systems of three declining stands of aspen ramets were hydraulically excavated. From each stand, sections of all structural roots were collected at the base of live and dead trees and were analysed using dendrochronology techniques. Parent roots were identified in the root system of every tree. The trees initiated new structural roots shortly after suckering. Live roots were often connected to the stump of dead and decayed trees. Grafting was common, especially at or near the stumps. Death of trees along the parent roots over time did not seem to favour the entry of significant decay, nor promote breakage of the original root connections. Instead of becoming independent of the parent root system the ramets incorporated the parent roots into their own root systems, remaining interconnected.

**Keywords:** Aspen; Clone; Cross-dating; Root age structure; Root connection; Root excavation; Root graft; Tree root.

**Nomenclature:** Moss (1983).

### Introduction

Regeneration of *Populus tremuloides* occurs mostly from root suckering following logging or natural disturbance. Disruption of apical dominance (Farmer 1962) and increased soil temperature, created by removal of the forest canopy, stimulate the production of suckers on the shallow lateral roots of killed or removed trees: parent roots. A parent root may connect several suckers.

Root connections between trees can influence stand dynamics for several reasons; 1. They allow the exchange of assimilates and growth substances between trees (Stone 1974). 2. Roots and the accumulated resources of dead trees may be used by living trees (Eis 1972). 3. Diseases may be transmitted from tree to tree through roots (Epstein 1978).

The persistence over time of the original root connections, as well as the extent of clonal integration among mature aspen trees, however, remains obscure. It was suggested that death of the parent tree and suckers along the parent roots, favours the entry and spread of decay into parental roots, causing the breakage of root connections between remaining suckers (Sandberg 1951; Maini 1960; Barnes 1966). It was thus assumed that suckers are independent early after stand establishment, since young aspen stands usually undergo heavy self-thinning (Brown & DeByle 1989). Parent roots, however, have been observed in 40 (DeByle 1964) and 79-yr old trees of sucker-origin from now-defunct parent trees (Strong & LaRoi 1983), suggesting that root connections with parent roots could remain alive throughout the life of the suckers. Given these inconsistencies further comprehensive studies of root systems in mature *Populus tremuloides* stands are needed to determine if large and old *Populus tremuloides* clones, as noted by Kemperman & Barnes (1976), could remain functionally interconnected.

Due to its clonal structure, the study of the communal root system of *Populus tremuloides* requires excavations of areas large enough to include several ramets of a clone. Tree ring analysis and dendrochronological reconstruction of the stem and root system can be used to examine the persistence of parent roots and the time of initiation of new roots at the base of the sucker as it develops into a tree. Consequently, construction of root age structures was used to verify the nature of the roots (parent or new) composing the root system of mature *Populus tremuloides* stands displaying some decline and, at the same time, determination of the time of new root production. Examination of the roots during an episode of stand decline (death of large trees) allows determination of both the persistence of root connections with old age and how stem mortality affects the root system of this clonal species. The time of stand decline/break-up is difficult to consistently estimate but can occur any time after the normal rotation age of *Populus tremuloides* (ca. 45-60 yr) (Peterson & Peterson 1992).

To our knowledge, this study is the first large-scale study using cross-dating techniques to study root dynamics of mature/post mature *Populus tremuloides* trees. Previous root studies of mature *Populus tremuloides* were based on single-tree (Sandberg 1951; Maini 1965; Gifford 1966) or partial excavations (Strong & LaRoi 1983; Shepperd & Smith 1993). Some studies used injections of dyes, phytocides or radioactive tracers into the root system (DeByle 1964; Gifford 1966; Tew et al. 1969; Shepperd 1993) but these methods gave inconsistent results depending on the tracer used, distance between trees and translocation efficiency of the trees at the time of the study (Bormann & Graham 1959; DeByle 1964; Tew et al. 1969).

## Methods

### Study area

Three study sites were located in north central Alberta, Canada, near the localities of Devon (53° 23' N, 113° 45' W), Lodgepole (53° 04' N, 115° 20' W) and Lac La Biche (55° 00' N, 111° 40' W). They have, respectively, been classified in the Aspen Parkland, Lower Boreal-Cordilleran and Mid Boreal Mixed-wood ecoregions of Alberta (Strong & Leggat 1992). The study sites were chosen in different ecoregions of Alberta, to avoid observing localized or site-specific patterns.

The three ecoregions receive similar annual precipitation, with a mean value of 424 mm. Mean summer and winter temperatures are 14.4 °C and – 8.7 °C for Devon, 12.8 °C and – 7.8 °C for Lodgepole and 13.5 °C and – 13.2 °C for Lac La Biche (Strong & Leggat 1992). The general areas are undulating terrain, with mean elevations of 682 m a.s.l. at Devon, 924 m a.s.l. at Lodgepole and 583 m a.s.l. at Lac La Biche. Soil types are a Podzolic sandy loam at Devon (Bowser et al. 1962), a silty clay Orthic Gray Luvisol at Lodgepole (Knapik et al. 1981) and a loamy sand Degraded Dystric Brunisol at Lac La Biche (Kocaoglu & Brunelle 1975).

In addition to the ecoregion, criteria for site selection were pure aspen of natural sucker origin after a stand-replacing disturbance (no surviving parent tree), > 50 yr old, and in decline, i.e. with some standing dead dominant stems and little recent suckering. The sites also needed to have a nearby water source and a gentle slope, to allow for hydraulic excavation. Presence of charcoal and even-aged structure of the stands suggested fire origin for all three stands, in 1945 for the Devon and Lodgepole sites and 1920 for the Lac La Biche site. The three study sites had similar understorey species composition, mainly *Alnus crispa*, *Rosa acicularis* and *Calamagrostis canadensis*.

### Sampling

Root systems were exposed hydraulically in the summer of 1997 using a high-pressure water spray from a WAJAX™ forest fire pump. Excavation depth in the mineral horizons varied from ca. 30 cm to 60 cm. One area was excavated at each location. The excavated area included most of the root system of at least three live and three dead trees and was ca. 30 m<sup>2</sup> at each of the three sites. Stem and root maps of the excavated areas were produced. Due to a shortage of water, only the surface roots of the Lac La Biche site were collected and analysed. The data collected from this site were not discarded altogether, since the extent of the excavation was sufficient to indicate similar root dynamics between this site and the others.

Since it was important to accurately age the trees cross sectional disks of stems were collected at breast height and at ground level for every tree included in the excavation, to avoid locally missing growth rings. The use of more than one cross-sectional disk per tree combined with cross-dating between trees of a same site, lessens the risk of underestimating age due to locally missing rings (Schweingruber 1989). Cross sections from each coarse root (diameter > 2 cm) were sawn adjacent to the stump. Dead roots were distinguished from live roots by colour; bright yellowish-white for live roots *versus* brown for dead roots.

### Dendrochronological analysis

The cross sections were dried and sanded with a 350 grade grit paper. The visibility of very small growth rings was improved by cutting the surface with a sharp razor blade and filling the wood cells with white chalk. Ring width was measured with a Parker Instruments micrometer, with a precision of 1 µm. Roots commonly have eccentric radial growth, and locally missing growth rings are more frequent in the areas having least radial growth (Fayle 1968; Krause & Eckstein 1993). Therefore, ring number and width were measured only on the longest radius from the primary tissue of the root. Growth ring patterns were compared (cross-dated) visually (Swetnam et al. 1985), then verified and corrected with the program COFECHA (Holmes 1983).

The presence of missing/false rings in the stem cross-sections (breast height and ground level) was first verified by cross-dating all stems from the same site. In traditional dendrochronological studies a 'master chronology' would then be constructed, which is a graphical representation of the annual ring width over the years, calculated from dated trees of a same location (Schweingruber 1989). This master chronology

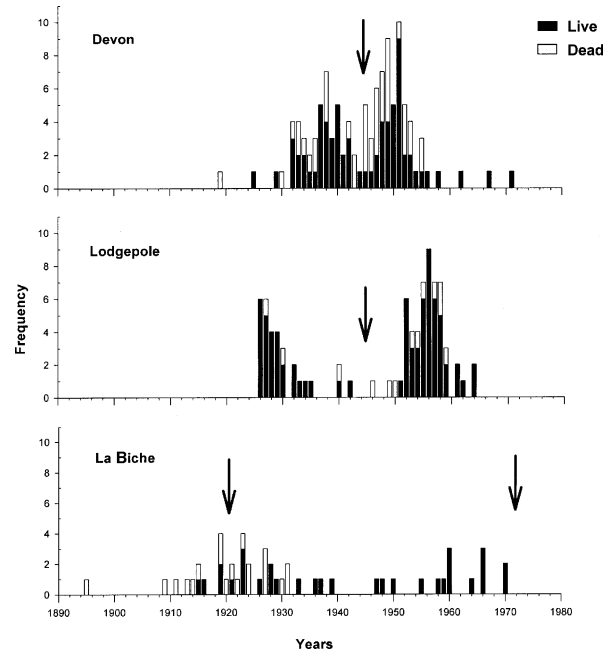
can then be utilized to compare with undated material from the same climatic region, in order to corroborate age of the undated material and to locate missing rings. In this study, however, the preliminary visual cross-dating, aided with the verification program COFECHA (Holmes 1983), showed that root radial growth was less related to the site master chronology than to the radial growth pattern of its own corresponding stem. Consequently, to facilitate determination of root age, the root cross sections were cross-dated with their corresponding and corrected stem chronology. Since parent roots are older than trees of sucker origin, the ring width pattern of the older portion of these roots could not be compared with stem chronologies and the presence of missing rings in these older portions was verified by cross-dating parent roots with other parent roots from the same site.

Difference in root size of the parent and new roots from each tree was statistically tested with paired *t* tests. Differences in the proportion of dead roots in the parent and new roots cohorts were tested with  $\chi^2$  analyses.

**Results**

A total of 112, 88 and 51 roots were cross-dated for Devon, Lodgepole and Lac La Biche, respectively. The coarse roots arising from the tree stumps in these *Populus tremuloides* stands were composed of two distinct cohorts of roots (Fig. 1); roots older than the trees (parent roots), and roots younger than the trees (new roots). At Devon and Lodgepole, there were nearly equal numbers of parent and new roots (Fig. 1). The Lac La Biche site differed in that it was 25 yr older and a second suckering event occurred in 1972. Interestingly, the coarse-root system of this second cohort of trees was exclusively parent roots (roots older than 1972; Fig. 1).

Production of new roots at the base of developing suckers at Devon started immediately after stand initiation, while it appeared to be delayed by about 5 yr after the period of suckering at the Lodgepole site (Fig. 1). Parent roots at Lodgepole had larger diameters at the time of suckering than at the Devon site (Table 1;  $p < 0.001$ ). Near the tree stumps, where the roots were collected, there was no difference in the mean diameter of parent and new roots at the time of the excavation at any of the three sites (Table 1;  $p > 0.10$ ). However, parent roots tapered little and maintained a similar diameter throughout their length while new roots usually tapered down and were highly branched. The oldest live roots dated from 1925 at Devon, 1926 at Lodgepole and 1915 at Lac La Biche. There was a



**Fig. 1.** Age structures of roots at point of connection to the trees (former suckers). The arrows indicate the year of the suckering events.

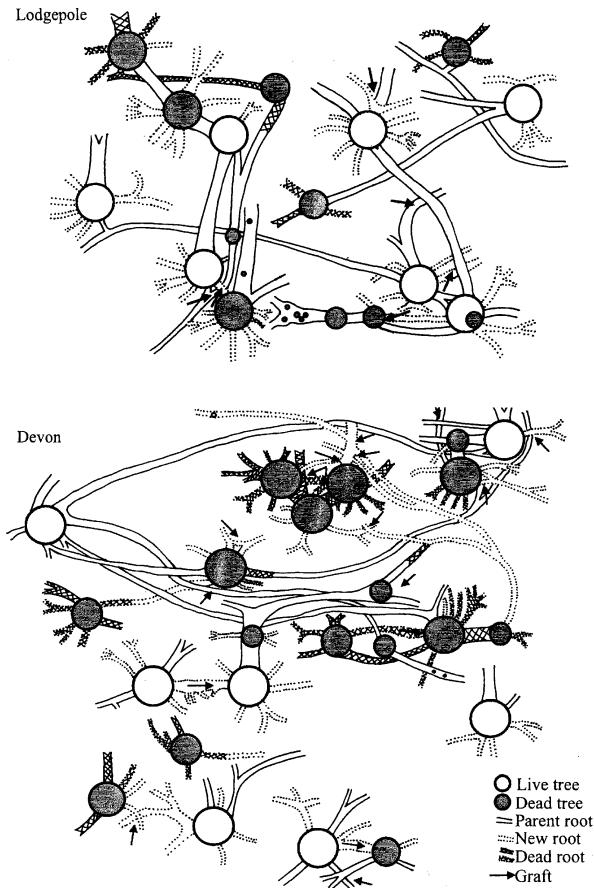
trend of a higher proportion of dead new roots than parent roots at both the Devon ( $p = 0.086$ ) and Lodgepole ( $p = 0.052$ ) sites.

A notable variability in root radial growth was observed; 26 missing rings were identified in the roots at Devon, 57 at Lodgepole and 69 at Lac Labiche site. At Devon, Lodgepole and Lac Labiche, at least one growth ring was missing in 7 %, 39 % and 53 % of the analysed roots while 5 %, 16 % and 35 % missed more than one growth ring, respectively.

At the Devon and Lodgepole sites, parent roots were found in the root systems of all trees (Fig. 2). Because of the incomplete excavation at Lac La Biche site only root maps for Devon and Lodgepole are reported. Only one tree was not connected to at least one other tree within the excavated area. Root grafts were identified at 17 locations at the Devon site and six at Lodgepole (Fig. 2). Virtually

**Table 1.** Mean root diameter (cm) of the excavated aspen coarse roots (standard deviations are given in parentheses).

	Devon	Lodgepole	Lac La Biche
Parent root at the time of suckering	0.41 (0.34)	0.87 (0.40)	0.24 (0.71)
Parent root at the time of excavation	5.74 (0.46)	6.53 (0.77)	5.85 (1.04)
New root at the time of excavation	5.75 (0.39)	7.29 (0.53)	5.20 (0.74)



**Fig. 2.** Stem and root maps of the excavated areas at the Lodgepole and Devon sites (with approximate scale). The roots were drawn in their entire length only if connected to other trees or roots within the excavated area.

all root grafts were located directly underneath or within 30 cm from the stumps. Living roots were commonly observed on trees that had been dead for several years before the excavation. These roots were connected to the roots of live trees by grafting of the new roots, or by the original root connection (parent root). For smaller trees that died some decades ago even if stumps had completely rotted away often making a hole in the parent root, the root connections were usually maintained by a band of healthy root tissue passing under and across the decayed area. The rot from dead trees rarely spread far into the parent root system. Dead trees that could still be aged died between 1977 and 1995 at Devon, 1975 and 1994 at Lodgepole and between 1980 and 1995 at Lac La Biche.

## Discussion

Dendrochronological analysis of the root systems showed that nearly half of the coarse roots sampled were parent roots (Figs. 1 and 2). There were no surviving parent trees in the studied sites, which indicates that the parent roots remained an integral part of the root system of the stands, even after the trees had matured and developed roots of their own. These results showed that turnover of *Populus tremuloides* coarse roots (replacement of parent roots by new roots) did not occur during the life of the stands. This contrasts with results from Shepperd & Smith (1993) for *Populus tremuloides* in western United States. There, large diameter roots were rare and had numerous wounds caused by burrowing rodents (W.D. Shepperd 1999, pers. comm.), which could increase mortality. In our study, despite their older age and large diameters, the parent roots were healthy and there were approximately equal numbers of dead parent roots and new roots (Fig. 1). Nonetheless, we speculate that old parent roots similar to those observed in this study would probably not survive after the next stand disturbance since suckering typically occurs on roots less than 2 cm diameter (Table 1; Schier & Campbell 1978; Shepperd & Smith 1993; DesRochers & Lieffers 2001), and there was no evidence of parent roots surviving without being supported by a live tree.

The fact that parent roots had large diameters in this study (Table 1) indicates significant growth of the parent root after the time of suckering, which contrasts with reports by Maini (1960) and Sandberg (1951), who observed negligible radial growth of the parent roots after suckering. Brown (1935) explained that high initial sucker density can produce parent roots of larger diameter, because when two suckers arise in close proximity on the same parent root, roots are enlarged in both acropetal and basipetal directions.

The trees were also connected by many root grafts (Fig. 2). The grafts were usually located near or directly on the stumps, despite the frequent intertwining of the roots elsewhere. Grafting could be facilitated by friction of the bark between roots near the stumps caused by wind swaying of the stems (LaRue 1934; Cook & Welch 1957). The sandy soil, and its possible greater abrasiveness, at the Devon site could explain the greater number of grafts there compared to the clay soil at the Lodgepole site. Others, however, have questioned the hypothesis that friction leads to greater grafting (Kozłowski & Cooley 1961; Graham & Bormann 1966) because it could also prevent root fusion by disrupting the delicate processes involved in the establishment of vascular continuity.

Grafting in *Populus tremuloides* was rarely observed in previous studies (Maini 1965; Barnes 1966). Grafts

could possibly have been missed simply because the stump itself was not excavated or because there is less grafting in younger stands, as observed for *Dacryodes excelsa* trees (Basnet et al. 1993). Moreover, grafts could have been missed because they were mistaken for original root connections. Although root grafts can easily be distinguished from original root connections if they occur away from the stump, age determination of the root is necessary to positively distinguish between a parent root (original root connection) and grafted new roots.

We cannot guarantee that grafting occurred only between trees of the same clone, since we did not verify that the excavated area contained only one genotype. However, since most trees were also connected through original root connections (parent roots), they must be part of the same clone. The trees for which an original root connection was not directly observed in the excavated area (Fig. 2) could, potentially, belong to different clones. Grafting is possibly a mechanism which aids maintenance of functional root connections in very old clones.

The five year delay in production of new roots at Lodgepole (Fig. 1) could be related to clonal differences between the two stands (Schier 1982) or because this stand originated from bigger roots than at Devon (Table 1). One could argue that initiation of new roots was not needed immediately after suckering at Lodgepole as the roots were large enough for water and nutrient requirements as well as structural support of the suckers. Also, since the respiration demands of these larger parent roots had to be supported by the suckers, we speculate that less energy remained for the immediate production of new structural roots.

Our data indicate that death of a *Populus tremuloides* stem does not necessarily mean that its root system will die. The ability of the trees to 'capture' part of the root system of a dead neighbour also provides evidence that the root connections and grafts were functional. Connections to living trees often kept the root system of dead trees alive (Fig. 2). This was also observed in *Populus grandidentata* Michx. (DeByle 1964). Maintenance of root connections and formation of root grafts throughout the lives of aspen trees can have a major impact on stand dynamics. As stems die during stand development, the remaining trees of the clone have access to their roots. Acquiring roots left by dead trees can have a positive effect on growth of a residual tree, because it inherits a functioning and established root system, giving access to an increased resource area. However, the respiration needs of such newly acquired roots also have to be supplied. Therefore, capturing roots from a dead tree via parent roots or root grafts will have a positive impact on growth only if the respiration

costs of that root biomass is balanced by increased photosynthetic capacity (Eis 1972). Given the large size of roots left by dead trees, large amounts of photosynthates would be needed to maintain respiration, possibly causing a strain on connected residual trees and further decline of the stands. At the sites examined aspen trees rarely became independent and, with the formation of root grafts, the level of interdependence between trees may even increase with time. Because even roots belonging to dead trees were still alive and healthy, decline of the studied stands was not due to root dieback. This is also in accordance with Lavertu et al. (1994), who demonstrated that a few remaining aspen trees in overmature stands could maintain enough healthy roots to support vegetative regeneration after complete removal of the overstorey. Translocation of substances between trees through parent roots and grafts probably have a role in stand dynamics, and should be accounted for in the management of aspen stands.

**Acknowledgements.** This study was supported by Ainsworth Lumber Inc., Alberta-Pacific Forest Industries Inc., Daishowa Marubeni International Ltd., Millar Western Industries Ltd., Slave Lake Pulp Corporation, Weyerhaeuser Canada Ltd. and Natural Sciences and Engineering Research Council of Canada. We also wish to thank C. Protz and R. Man for field work.

## References

- Barnes, B.V. 1966. The clonal growth habit of American aspens. *Ecology* 47: 439-447.
- Basnet, K., Scatena, F.N., Likens, G.E. & Lugo, A.E. 1993. Ecological consequences of root grafting in Tabonuco (*Dacryodes excelsa*) trees in the Luquillo experimental forest, Puerto Rico. *Biotropica* 25: 28-35.
- Bormann, F.H. & Graham, F., Jr. 1959. *The occurrence of natural root grafting in eastern white pine, Pinus strobus L., and its ecological implications*. Ph. D. Thesis, Bot. Dep., Duke University, Durham, NC.
- Bowser, W.E., Kjearsgaard, A.A., Peters, T.W. & Wells, R.E. 1962. *Soil survey of Edmonton (83-H)*. Alberta Soil Survey Report no. 21, University of Alberta (Bull. SS-4).
- Brown, A.B. 1935. Cambial activity, root habit and sucker shoot development in two species of poplar. *New Phytol.* 34: 163-179.
- Brown, J.K. & DeByle, N.V. 1989. *Effects of prescribed fire on biomass and plant succession in western aspen*. USDA Forest Service, Research Paper INT-412. Intermountain Research Centre, Ogden, UT.
- Cook, D.B. & Welch, D.S. 1957. Backflash damage to residual stands incident to chemi-peeling. *J. For.* 55: 265-267.
- DeByle, N.V. 1964. Detection of functional intraclonal root connections by tracers and excavation. *For. Sci.* 10: 386-396.
- DesRochers, A. & Lieffers, V.J. 2001. Root biomass of regen-

- erating aspen (*Populus tremuloides*) stands of different densities in Alberta. *Can. J. For. Res.* 31: 1012-1018.
- Eis, S. 1972. Root grafts and their silvicultural implications. *Can. J. For. Res.* 2: 111-120.
- Epstein, A.H. 1978. Root graft transmission of tree pathogens. *Annu. Rev. Phytopathol.* 16: 181-192.
- Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. *For. Sci.* 8: 403-410.
- Fayle, D.C.F. 1968. *Radial growth in tree roots; distribution, timing, anatomy.* Faculty of Forestry, University of Toronto, Tech. Rep. 9.
- Gifford, G.F. 1966. Aspen root studies on three sites in northern Utah. *Am. Midl. Nat.* 75: 132-141.
- Graham, B.F., Jr. & Bormann, F.H. 1966. Natural root grafts. *Bot. Rev.* 32: 255-292.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43: 69-78.
- Kemperman, J.A. & Barnes, B.V. 1976. Clone size in American aspen. *Can. J. Bot.* 54: 2603-2607.
- Knapik, L.J., Pettapiece, W.W. & Peters, T.W. 1981. *Reconnaissance soil survey of the Brazeau Dam area.* Pedology Consultants, Land Resource Research Institute, Research Branch Agriculture Canada, Alberta Soil Survey Report no. 40. Edmonton, Alberta.
- Kocaoglu, S.S. & Brunelle, A. 1975. *Soil survey of the Sand River area (73L).* Alberta Institute of Pedology Bull SS-15, Alberta Soil Survey Report no. 34.
- Kozlowski, T.T. & Cooley, J.H. 1961. Natural root grafting in Northern Wisconsin. *J. For.* 59: 105-107.
- Krause, C. & Eckstein, D. 1993. Dendrochronology of roots. *Dendrochronologia* 11: 9-23.
- LaRue, C.D. 1934. Root grafting in trees. *Am. J. Bot.* 21: 121-126.
- Lavertu, D., Mauffette, Y. & Bergeron, Y. 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. *J. Veg. Sci.* 5: 561-568.
- Maini, J.S. 1960. *Invasion of grassland by Populus tremuloides in the northern Great Plains.* Ph. D. Thesis, University of Saskatchewan, Saskatoon.
- Maini, J.S. 1965. *On the organization and growth of aspen roots. II. Rapidly-tapering and cord-like roots.* Department of Forestry Canada, Forest Research Branch, Preliminary report project 0-24.
- Moss, E.H. 1983. *Flora of Alberta.* 2nd ed. University of Toronto Press, Toronto.
- Sandberg, D. 1951. *The regeneration of quaking aspen by root suckering.* M. Sc. Thesis, School of Forestry, University of Minnesota, MN.
- Schier, G.A. 1975. *Deterioration of aspen clones in the middle Rocky Mountains.* USDA Forest Service, Res. Pap. INT-170. Int. For. Range Exp. Sta., Ogden, Utah.
- Schier, G.A. 1982. Sucker regeneration in some deteriorating Utah aspen stands: development of independent root systems. *Can. J. For. Res.* 12: 1032-1035.
- Schier, G.A. & Campbell, R.B. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. *For. Sci.* 24: 303-308.
- Schweingruber, F.H. 1989. *Tree rings: Basics and applications of dendrochronology.* Kluwer Academic Publishers, Dordrecht.
- Shepperd, W.D. 1993. *Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains.* USDA Forest Service, Res Pap RM-312. Rocky Mtn For. Range Exp. Sta., Fort Collins, CO.
- Shepperd, W.D. & 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.
- Stone, E.L. 1974. The communal root system of red pine: growth of girdled trees. *For. Sci.* 20: 294-305.
- Strong, W.L. & La Roi, G.H. 1983. Root-system morphology of common boreal forest trees in Alberta, Canada. *Can. J. For. Res.* 13: 1164-1173.
- Strong, W.L. & Leggat, K.R. 1992. *Ecoregions of Alberta.* Alberta Forestry, Lands and Wildlife, Edmonton, Alberta.
- Swetnam, T.W., Thompson, M.A. & Kennedy Sutherland, E. 1985. *Using dendrochronology to measure radial growth of defoliated trees.* USDA Forest Service, Agriculture Handbook 639: 1-39.
- Tew, R.K., Debyle, N.V. & Schultz, J.D. 1969. Intraclonal root connections among quaking aspen trees. *Ecology* 50: 920-921.

Received 20 April 1999;  
 Revision received 15 May 2000;  
 Accepted 4 January 2001.  
 Coordinating Editor: G. Rapson.