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Aspen (*Populus tremuloides* Michx.) Clonal Root Dynamics and Respiration

By

Annie DesRochers

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Department of Renewable Resources

In

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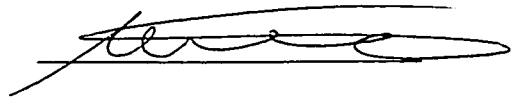

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Victor J. Lieffers

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John R. Spence

Ken C.J. Van Rees

Janusz J. Zwiazek

April 11th, 2000

DEDICATION

To my husband Chris
To all who believed in me

ABSTRACT

In this dissertation, mechanisms involved in the decline of aspen (*Populus tremuloides* Michx.) stands were investigated. The persistence of the original root connections (parent roots), the establishment time of independent root systems (new roots), and the fate of the communal root system after death of individual trees were examined by hydraulic excavation and dendrochronological analysis of roots from declining stands. The parent roots were maintained throughout the life of the trees and interconnected most of the trees within each excavated area. Live roots were observed on dead and decayed stumps, which demonstrated that the death of trees along parent roots did not necessarily cause the breakage of the original root connections and death of the parent roots.

After harvesting, the subsistence of the parent roots depends on carbohydrates provided by the suckers. The effects of low suckering densities were then investigated in juvenile stands, on the survival of the parental root system, on the formation of new roots and on the growth of suckers. Root systems were excavated from 5-10 year-old stands of different suckering densities. It was found that young sucker stands could support a considerable biomass of roots in relation to their shoot biomass, due to very high leaf area index (LAI), comparable to mature stands. Live root biomass was proportional to sucker density and leaf area index. Stands with low sucker densities had high proportions of dead roots. This loss of parental root biomass seemed to be detrimental to the growth of the suckers, since plots with more parental root biomass / sucker had greater sucker height

growth. The amount of new roots was not affected by stand density, but increased with basal area of suckers and decreased with increasing mean parental root diameter.

Lastly, aspen root longevity and the carbon cost of maintaining root biomass were investigated by measuring respiration rates of coarse and fine roots were measured at 5, 15 and 25 °C. Fine roots respired at much higher rates than coarse roots, with an average rate at 15 °C of 1289.04 μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$ during the growing period (growth + maintenance respiration), compared to 662.64 μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$ during the dormant period (maintenance respiration). The temperature response of fine root respiration was not linear, with an average $Q_{10} = 3.90$ between the 5-15°C increase, and an average $Q_{10} = 2.19$ between the 15-25 °C increase. Surprisingly, coarse root respiration rates measured in late fall (dormant season) were higher than rates from the coarse roots collected at leaf flush and early summer. Rates at 15 °C were 372.83 μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$ in the fall and averaged 204.82 μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$ in spring and early summer. These higher respiration rates in the fall were accompanied by lower total non-structural carbohydrate (TNC) levels, suggesting that rates comprised growth expenditures, reflecting recent radial growth. Bud flush and shoot growth of the trees did not cause an increase in coarse root respiration or a decrease of TNC levels, suggesting a limited role of the coarse roots as reserve storage organs for spring growth.

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CHAPTER I

GENERAL INTRODUCTION

Aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Perala 1990). With the changes in wood handling and manufacturing occurring in the Canadian Forest Industry, it has become increasingly valuable (Peterson and Peterson 1992). Management of aspen stands has traditionally depended on its regenerative capacity by root suckering.

ROOT SUCKERING

Aspen will regenerate readily and abundantly by root suckering, after a stand-replacing disturbance. The suckers are produced from dormant or newly formed buds on shallow lateral roots of the killed or removed trees (Day 1944; Schier 1973; Schier and Campbell 1978). Suckering is stimulated by the increased heat absorption of the forest floor, created by the removal of the forest canopy (Shirley 1931; Zehngraff 1949; Maini and Horton 1966; Steneker and Walters 1971). Also, it is believed that apical dominance, the translocation of auxins produced in the shoots to the roots where it inhibits sucker formation, must be broken to initiate the regenerative processes (Farmer 1962; Steneker 1974; Schier 1975). Sucker production is usually completed within two years following stand disturbance. Further suckering is inhibited by the stabilization of hormonal levels

(Perala 1990) and a return to cooler soil temperatures with developing leaf area (Hungerford 1988). The increase in soil temperature seems to play a larger role on suckering than the disturbance of hormonal levels, because suckering can sometimes be found in the understory of intact trees (Maini and Horton 1966; Schier and Smith 1979; Betters and Woods 1981; Jones and DeByle 1985).

Because they carry the same genetic material, trees originating from the same parental root system form a clone (Day 1944). Clones up to 81 hectares in size have been recorded (Kemperman and Barnes 1976). More than being genetically identical, members of a clone that are growing on an interconnected parental root system can share growth substances through these root connections. The exact nature and circulation patterns of the substances travelling from tree to tree are mostly unknown to date, although they could potentially have a major impact in inter-tree relationships and stand dynamics.

PERSISTENCE OF THE PARENTAL ROOT SYSTEM

The regeneration of aspen by root suckering has often been qualitatively described and may even seem banal. However, the suckering process is rather spectacular, because the roots of a tree, a clone, or an entire stand in which trees have been killed or harvested, remain alive and are used by the next generation of ramets. These roots, from which the suckers originate and which initially belonged to the previous generation of trees, will be referred to in this dissertation as 'parent roots' or 'original root connections'. The persistence over time and importance of the parental root system for the growth of the suckers has often been discussed. Some of the early root studies attributed a relatively

minor role to the parental root system; Sandberg (1951) observed negligible radial growth of the parent roots after suckering. Gifford (1966) reported that the root connections of clones growing on poorly aerated soils had deteriorated through decay, but these results were not confirmed by the work of Tew *et al.* (1969). According to Maini (1960) and Sandberg (1951), the root connections between suckers would only persist until the death of one of the two connected trees. Since young aspen stands usually have a heavy self-thinning phase in the first five years (Brown and Debyle 1989) it would be logical to assume that the trees are independent of each other early after stand establishment. However, peridermal scar tissues marking the positions of former suckers can be observed on living parent roots (Tappeiner 1982; Strong and LaRoi 1983), indicating that parent roots do not necessarily deteriorate with the death of suckers. Other studies have suggested longer persistence of the parent roots; the original root connections have been reported to remain functional for at least 14 (Shepperd 1993) or 50 years (the latter in bigtooth aspen [*Populus grandidentata* Michx.]) (DeByle.1964). The term 'functional' as used in these studies, means that injected substances, like dyes or herbicides, traveled from tree to tree. In Alberta, Strong and LaRoi (1983) observed a live root connection between 79-year-old trees, suggesting that root connections could remain functional throughout the life span of the trees.

FORMATION OF NEW ROOTS

As the suckers grow into trees, adventitious roots are produced at the base of the stem and along the parent roots. These roots will be referred to in this dissertation as 'new roots'. Compared to younger or older stands, Shepperd and Smith (1993) measured lower root volumes in stands 20-80 years old, suggesting a change from a root system dominated by old large roots (parent roots) to one dominated by new and smaller roots. This suggests that as the trees develop, the new roots progressively replace the parent roots. Strong and LaRoi (1983) also reported the production of a secondary root system that supplements the parental root system. It is not clear, however, whether this means that the parent roots eventually die and are replaced by new roots, or if they remain in the root system and simply loose some of their importance because of their relative proportion to the new roots.

Some of these fundamental questions could be answered by investigating the dynamics of the root system in mature trees for the type of roots they are composed of (parent *vs* new roots) and the pattern of root production and death over time. It is difficult to conduct extensive root excavations in multiple stands along a chronological sequence from young to mature stands, which is most probably why such studies are lacking. However, one way to overcome this problem is to carry out a dendrochronological reconstruction of the root system of mature stands. The new roots are produced by the suckers, therefore they are younger in age than the suckers themselves. The new roots are also younger than the parent roots, which were produced by the previous generation of trees, hence before suckering occurred. This difference in

age between the parent roots and the new roots, delimited by the year at which suckering occurred, can be used in differentiating between the two types of roots using dendrochronology techniques. These techniques can also be used to determine the year at which roots were produced and the time at which they died.

The time of new root production is critical for the suckers, because with development, the suckers become less dependent on the parental root system (Zahner and Debyle 1965). Schier (1982) investigated the time of new root production in different clones. He found that there was no apparent relationship between sucker age, mean annual shoot growth or mean size of parent root and the capacity of suckers to initiate new roots. Further research is needed to address this issue.

IMPACT OF LOW SUCKERING DENSITY ON THE ROOT SYSTEM

Aspen stands regenerated by root suckering are usually well stocked, followed by a rapid mortality phase in the first decade after stand establishment (Stoeckeler and Macon 1956; Brown and DeByle 1989). Sucker numbers in the first two growing seasons can, in extreme cases, exceed up to a million per hectare (Peterson and Peterson 1992). The number of suckers then decreases precipitously in stands of high sucker density (Shepperd 1993). The more poorly regenerated stands do not show these substantial decreases in initial density (Garret and Zahner 1964; Sorensen 1968). Poor sucker regeneration can occur if soils do not reach a critical temperature, such as when basal area of the residual stand is too high after harvesting (Stoeckeler and Macon 1956). In Alberta, the invasive bluejoint grass (*Calamagrostis canadensis* [Michx.] Beauv.) keeps soil temperatures low

and is a problem for aspen establishment and early growth (Landhäusser and Lieffers 1998).

Suckers depend on the parent roots for water and nutrients absorption and for structural support until they have developed sufficient new roots (Zahner and Debyle 1965). Nevertheless, the survival of the parental root system also depends on the suckers; roots are composed of non-photosynthetic tissues, hence they need to be supplied with carbohydrates to compensate for their carbon lost through respiration. In an early study, Barnes (1966) had suggested that the numerous ephemeral suckers growing after a major disturbance probably played a significant role in carbohydrate replenishment of the root system, which presumably occurs at the end of each growing season (FitzGerald and Hoddinott 1983). Aspen suckers are thus at first importers of carbohydrates from the parental root system, but as the shoots develop leaf area, replenishment of root carbohydrate commences. Root/shoot ratios are very high in young sucker stands (Shepperd and Smith 1993), and if sucker density is low, the amount of carbohydrates produced by these few suckers might be insufficient to replenish root carbohydrates and support the respiration of the parental root system. Consequently, parent roots might start deteriorating, which may in turn, affect sucker growth; Shepperd (1993) reported that suckers growing in low-density stands were smaller and had shorter leaders than suckers growing in well-stocked stands. The effects of low density suckering on the parental root system and on the growth of the suckers still remain mostly unexplored.

Suckers are usually produced on small lateral roots, ranging from 2-20 mm in diameter (Sandberg 1951; Schier and Campbell 1978; Schier 1982). It thus seems reasonable to assume that large roots are more likely to deteriorate in the rotation from

one generation of trees to the next; large roots are located further away from the suckers, thus from a carbohydrate source necessary to compensate for the carbon lost through respiration. Debyle (1964) explained that the lack of connections among all trees in a certain clone was caused, in part, by the death and decay of the large roots about the base of the stump of the now dead parent trees. Stumps with live and healthy roots systems functionally connected to living trees have, however, been observed (Brown 1935; DeByle 1964). For the same reason, it can be assumed that parent root segments not immediately supporting suckers are more likely to deteriorate if carbohydrates are limiting, causing the breakage of root connections between distant ramets (Brown 1935). A parental root system divided in many little sections may be detrimental to the growth of the suckers, because a given section may be disconnected from the feeder roots of the end sections (Strong and LaRoi 1983). Deterioration of the parental root system would hence be less damaging for suckers that have rapidly developed new roots, and may on the other hand, stimulate production of new roots. By pruning both ends of the parent roots, Zahner and DeByle (1965) indeed found that the ramets that survived the treatment had already developed their own roots.

Schier (1982) observed that the absence of developed independent root systems (new roots) early in the life of the ramets suggests that the strategy of the clone is first to expand and maintain the parental root system by developing the suckers and their leaf area before the formation of new roots. The way that the suckers are attached to the parent root also suggests expansion of the clone. The cambium and secondary vascular system of the suckers align with the portion of the parent root immediately on the distal side of the sucker, the portion of the parent root going away from the original location of the

parent tree (Brown 1935). Consequently, the parent root has faster radial growth on the distal side of the sucker (DeByle 1961; Gifford 1966), suggesting that most of the photosynthates are directed toward the distal side of the parent root. There also is, however, secondary xylem formation on the proximal side of the parent root, indicating that polarity of photosynthate translocation is not complete and that proximal translocation does occurs (Brown 1935; Debyle 1964; Gifford 1966). As a result of photosynthate translocation in both directions, when two suckers arise close to each other on the same root, the acropetal and basipetal cambial activity along the parent roots results in roots of larger diameter (Brown 1935; Gifford 1966). Hence, if sucker density is high, the entire parental root system is more likely to be maintained by the suckers. Regeneration with low suckering densities might jeopardize the maintenance of the parent roots, and because of their interdependence, the growth of the suckers.

ROOT RESPIRATION

Root respiration plays a major role in the carbon balance of trees (Ericsson *et al.* 1996), and respiration rate measurements are essential to evaluate the energy required to sustain root biomass.

Respiration rates are usually divided into two or three components: maintenance respiration represents the energy required in keeping cells alive and growth respiration represents the energy required for building new tissue (Lambers *et al.* 1983; Amthor 1984). The third respiration component, related to the energy required in the active uptake of ions by roots, is often included in the maintenance component. Maintenance

respiration rates are higher for roots than for shoots, because the roots are involved in active ion uptake (Johnson 1983; Amthor 1984). Most of the maintenance cost for plant cells is related to protein turnover, more active plants having higher maintenance respiration rates due to increased protein turnover and ion fluxes. Maintenance respiration is temperature dependent (Szaniawski and Kielkiewicz 1982); temperature response curves of respiration are thus necessary if annual carbon balances are to be estimated. It is expected that respiration rates are limited by carbohydrate concentration at high respiration rates, since the affinity of enzymes for their substrate is usually affected by temperature and substrate concentration (Hunt and Loomis 1979). Ryan (1990) suggested that lower maintenance rates probably occur with mistletoe-infected conifers because the mistletoe lowers the carbohydrate levels and lessens the need for enzymes to convert starch to sugars. Because of the regeneration mode of aspen by root suckering, a large part of the discussion revolves around the maintenance of the parental root system and the root connections between trees. Maintenance respiration rates of aspen roots should therefore be estimated.

In the next three chapters, a different aspect of the root dynamics of aspen discussed in this general introduction has been investigated. Mechanisms involved in the decline of aspen stands have been investigated. The root system of mature declining stands has been dendrochronologically analyzed, to identify its root dynamics, the origin of its structural roots (parent or new), and how this might influence aspen decline. In this study I also examined the time at which roots were produced and died, and the extent of root connections between mature trees. Since parent roots were found to be maintained

in the root system of sucker-origin trees throughout their lifetime, the effects of low suckering density on parent root survival and subsequent sucker growth was investigated in a series of young stands with different sucker densities. I examined root/shoot ratios, the production of new roots, maintenance of the parental root system and growth of the suckers.

Lastly, root respiration rates of aspen coarse and fine roots were measured. Root respiration can consume large proportions of net primary productivity. It can thus have a great importance in stand dynamics, especially in young aspen stands with high root/shoot ratios or in mature declining stands with interconnected root systems. The temperature response of respiration as well as the relationships between respiration and *N* and *TNC* were examined.

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CHAPTER II

STRUCTURAL ROOT SYSTEM OF MATURE ASPEN (*POPULUS TREMULOIDES*) IN DECLINING STANDS IN ALBERTA, CANADA*

INTRODUCTION

Regeneration of aspen (*Populus tremuloides* Michx.) occurs mostly from root suckering following logging or natural disturbance. This regeneration mechanism creates stands in which trees are part of a clone, sharing a common root system (Barnes 1966). The size of aspen clones can range from individual trees to stands greater than 81 hectares (Kemperman and Barnes 1976). Due to its clonal structure, the study of aspen's communal root system requires excavations large enough to include several ramets of a clone. Although, in the past, the root systems of young aspen stands have been described from large-scale excavations (Day 1944; Sandberg 1951; Gifford 1966; Barnes 1966), there has been little work on the root systems of mature aspen. The information available on the root systems of mature stands is mostly based on studies of young stands, or from partial excavations in mature stands; Sandberg (1951) excavated the roots of a single 35 year-old tree, Maini (1965) of a single 41 year-old bigtooth aspen (*Populus grandidentata* Michx), and Gifford (1966) of a 52 year-old aspen tree. In Alberta, Strong and LaRoi (1983) partially excavated the roots of 5 aspen trees ranging from 19 to 79 years of age.

More recently, Shepperd and Smith (1993) sampled aspen roots using 3 m-long trenches, in 47 clones up to 122 years of age. This latter study is of larger scale than the previous ones, but still did not allow for the observation of roots as part of a communal root system.

To avoid large-scale excavations, some researchers have injected dyes, phytocides or radioactive tracers into the root system, to investigate root connections between trees (Debyle 1961, 1964; Gifford 1966; Tew *et al.* 1969; Shepperd 1993). It was demonstrated, however, that these methods are inefficient in tracing all root connections, depending on the type of tracer used, the distance between trees and the translocation efficiency of the trees at the time of the study (Bormann and Graham 1959; Debyle 1964; Tew *et al.* 1969).

Zahner and Debyle (1965) demonstrated the importance of the original root connections (parent roots) for the growth of bigtooth aspen suckers. It was initially suggested that the death of suckers along the parent roots favors the entry and spread of decay into the root system, causing the breakage of these root connections between remaining suckers and resulting in fewer interconnections over time (Sandberg 1951; Maini 1960; Barnes 1966). However, in bigtooth aspen, Debyle (1964) found that old parent roots remained alive and functioning for at least 40-50 years. Strong and LaRoi (1983) also found live root connections between 79-year-old aspen trees, suggesting that parent roots were maintained throughout the life of the trees. More recent work showed that the parent roots remained functional for a certain time after stand establishment

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(Shepperd 1993), but that renewal of the structural root system, i.e. the replacement of parent roots by new roots formed by the suckers, seemed to occur between 20-80 years of stand age (Shepperd and Smith 1993). Given these inconsistencies, further comprehensive and larger-scale studies of root systems in mature aspen stands are needed. Because they connect trees together, the persistence of functional parent roots throughout the life of aspen stands can have a major impact on stand dynamics, since they could allow the exchange of assimilates and growth substances (Stone 1974), the use of roots and resources left by dead trees (Eis 1972), and transmission of diseases (Epstein 1978).

Apart from Day (1944) and Maini (1965) who aged some aspen roots to estimate root elongation rates, other studies have not consistently used dendrochronological techniques to describe structural root dynamics of aspen. Construction of root age-structures in mature aspen stands would indicate if there actually is a replacement of the parent roots by new roots after stand reinitiation, or if the parent roots are maintained throughout the life of the stand. Knowledge of root age-structures would also indicate the time of production of independent (new) roots by the suckers (Schier 1982).

The objectives of this study were to describe the root dynamics of aspen from mature stands, with regard to the persistence of the original root connections (parent roots) and the time of establishment of independent roots. The root systems of declining stands were chosen to further observe the communal root system after death of individual mature trees. To our knowledge, this study is the first large-scale study using cross-dating techniques to study root dynamics of mature aspen stands.

METHODS

STUDY AREA

The three study sites were located in north central Alberta, near the localities of Devon (53°23'N, 113°45'W), Lodgepole (53°04'N, 115°20'W) and Lac LaBiche (55°00'N, 111°40'W). They have respectively been classified in the Aspen Parkland, Lower Boreal-Cordilleran and Mid Boreal Mixewood ecoregions of Alberta (Strong and Leggat 1992). The three ecoregions receive similar annual precipitation, averaging 424 mm. Average 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 LaBiche (Strong and Leggat 1992). The general areas are undulating terrain, with average elevations of 682 m for Devon, 924 m for Lodgepole and 583 m for Lac LaBiche. 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 Eluviated Dystric Brunisol at Lac LaBiche (Kocaoglu and Brunelle 1975).

Criteria for site selection were pure aspen, >50 years old, and in decline, i.e. with some standing dead dominant stems and little suckering. Presence of charcoal and even-aged stand structure of the trees suggested fire origin of the 3 stands, in 1945 for the Devon and Lodgepole sites, and in 1920 for the Lac LaBiche site. The sites also needed to have a nearby water source and at least a gentle slope, to allow for hydraulic

excavation. The major understory species were green alder (*Alnus crispa* [Ait.] Pursh), wild rose (*Rosa acicularis* Lindl.) and bluejoint grass (*Calamagrostis canadensis* [Michx.] Beauv).

SAMPLING

Root systems were exposed hydraulically in summer 1997 using a high-pressure water spray from a WAJAX™ forest fire pump. Excavation depth varied from about 30 cm to 60 cm in the mineral horizons. The excavated areas included at least three live and three dead trees and averaged 30 m^2. Stem and root maps of the excavated areas were produced (only the Devon and Lodgepole are presented here). Cross sectional disks of stems were collected at breast height and at ground level for every tree included in the excavation. Cross sections from each structural root (diameter >2 cm) were collected adjacent to the stump. Dead roots were distinguished from live roots by color, bright yellowish-white for live roots, versus brown for dead roots.

DENDROCHRONOLOGICAL ANALYSIS

The cross sections were dried and sanded up to a 350-grid paper, and then further prepared with a razor blade. White chalk was rubbed on the cut surface to increase ring visibility. Ring width was measured with a Parker Instruments micrometer, with a precision of 1 μm. Because of eccentric growth of the roots (Fayle 1968; Krause and Eckstein 1993), ring width was measured on a path with the greatest diameter, to obtain the maximum number of growth rings.

The presence of missing / false rings was first determined by graphically cross-dating all stems of the same site, from the cross sections collected at breast height and ground level. This analysis revealed the age of the trees, thus the time at which suckering occurred. To facilitate determination of root age, the root cross sections were cross-dated with their corresponding and corrected stem chronology rather than using a master chronology of the sites. The older part of the parent roots chronologies (not present on the stem chronologies) was verified with other parent roots of the same site. The visual cross dating was subsequently verified and corrected with the program COFECHA (Holmes 1983).

Differences in root sizes from the parent and new roots were statistically tested with one-way ANOVA using the PROC GLM in SAS statistical package (SAS Institute Inc. 1996). Differences in the proportion of dead roots in the parent and new roots cohorts were tested with $\chi 2$ analyses. The chosen level of significance was $p \leq 0.05$.

RESULTS

A total of 112 structural roots were cross-dated for the Devon site, 88 at Lodgepole and 51 at Lac LaBiche. Due to a shortage of water, only the surface roots (approx. to a depth of 20 cm) of the Lac LaBiche site were collected and analyzed. All stands had roots that were older than the stems (parent roots) (Fig. 2.1). At Devon and Lodgepole, the structural root systems were composed of nearly equal numbers of parent roots and roots younger than stand age (new roots) (Fig. 2.1). The Lac LaBiche site

differed from the other sites in that it showed some suckering, a second cohort of trees originating from 1972, now growing on the new roots of the stand initiated in 1920. Therefore, the roots located in between the two suckering events constitute new roots for the trees established in 1920, and at the same time are parent roots for the trees established in 1972. This second generation of trees did not have any new roots larger than 2 cm in diameter at the time of the excavation.

The production of new roots at Devon started immediately after stand initiation, while it appeared to be delayed by about 5 years after stand initiation at the Lodgepole site (Fig. 2.1). Coincidentally, the parent roots at the Lodgepole site had larger diameters at the time of suckering ($P < 0.001$; Table 2.1). Near the stump, there was no difference in the average size of the parent roots and new roots at the time of the excavation ($P > 0.05$; Table 2.1). However, the parent roots tapered little and maintained about the same diameter throughout their length while the 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 LaBiche site. The proportion of dead parent roots did not differ significantly from the proportion of dead new roots at any of the three sites, but a trend showed increased mortality of the new roots at the Devon ($P = 0.09$) and Lodgepole ($P = 0.05$) sites.

A notable plasticity in root growth ring formation was observed; the graphical cross-dating and verification with the program COFECHA allowed us to retrace 26 missing rings at Devon, 57 at Lodgepole and 69 at the Lac Labiche. At Devon, Lodgepole and Lac Labiche, at least one growth ring was missing in 7%, 39% and 53% of

the analyzed 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. 2.2). Because of the incomplete excavation of the Lac LaBiche site, only the root maps for Devon and Lodgepole were reported. All trees but one were connected to at least one other tree inside the excavated area. Root grafts were identified at 17 locations at the Devon site and 6 at Lodgepole (Fig. 2.2). All grafts were located directly on the stump of live or dead trees or within 30 cm of the stumps. On dead trees, it was common to find living roots connected to live trees through grafts or through original root connections (parent roots), despite decayed or completely rooted away stumps. The rot, however, had 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 LaBiche.

DISCUSSION

The root age structures of Devon and Lodgepole (Fig. 2.1) show that most trees never became "independent" of the roots from which they originated; the parent roots were incorporated into their structural root systems. These roots were the largest and relatively untapered, and on this basis and by their direct connection to other trees, could be easily identified as parent roots in the field. Brown (1935) explained that photosynthate translocation and cambial activity in both directions along the parent root

result in roots of larger diameter, when suckers arise close to each other on the same parent root. This suggests that our study stands were previously densely stocked with suckers growing close to each other, thus producing parent roots of large diameter. This contrasts to what was reported by Maini (1960) and Sandberg (1951), who observed only negligible radial growth of the parent roots after suckering.

It does not appear that there was or will be a replacement of the parent roots by new roots during the life of the stands, unlike what was suggested for aspen in the western United Stated by Shepperd and Smith (1993). The parent roots remained part of the root system of the mature trees, even after they developed new roots. Moreover, even as the stands were breaking up, there was a trend for higher mortality in new roots than in parent roots (Fig. 2.1). Differences in the longevity of parent roots could be site-specific throughout the range of aspen; besides scars left by dead suckers, the large parent roots in our study showed little wounding. In contrast, in the western United States, roots of large diameter were rare and roots exhibited numerous wounds caused by burrowing rodents (Shepperd 1999, pers. comm.). This damaging of roots by rodents could explain the loss of the large parent roots during stand life in the western United States (Shepperd and Smith 1993). Nonetheless, we speculate that the old parent roots in our sites will probably not survive after the next stand disturbance, since suckering typically occurred on roots smaller than 2 cm in diameter in our study and others (Schier and Campbell 1978; Shepperd and Smith 1993). The analyzed roots, over 2 cm in diameter, will probably not sucker and will die because of lack of support from living suckers (Debyle 1964).

Besides being interconnected through original root connections, the trees were also connected by many root grafts (Fig. 2.2). 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 and Welch 1957). The sandy soil, and its possible greater abrasion, at the Devon site could explain the greater number of grafts there compared to the fewer grafts in the clay soil of the Lodgepole site. Others, however, have questioned the hypothesis that friction leads to greater grafting (Kozlowski and Cooley 1961; Graham and Bormann 1966), because it could also prevent root fusion by disrupting the delicate processes involved in the establishment of vascular continuity.

We cannot assure that grafting occurred only between trees of the same clone, since we did not verify that the excavated area comprised only one genotype. However, since most of the trees were also connected through original root connections (parent roots), most of the trees were part of the same clone.

Grafting in aspen was rarely observed in previous studies (Maini 1965; Barnes 1966). The 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 Tabonuco (*Dacryodes excelsa*) trees (Basnet *et al.* 1993). Moreover, the grafts could have been missed because they were mistaken for original root connections. In our study, dendrochronological analysis was sometimes necessary to distinguish between a root graft and a parent root connection, when the grafts occurred directly on or under a stump.

The five year delay in production of new roots by the trees at the Lodgepole site (Fig. 2.1) could be related to clonal differences between the two stands (Schier 1982), or to the fact that this stand originated from bigger roots than at Devon. One could argue that production of new roots was not needed immediately after suckering at Lodgepole,

since the roots were large enough for water and nutrient transport requirements as well as for structural support of the suckers. Also, since the respiration demands of the large parent roots had to be supported by the suckers, we speculate that less energy was left for the immediate production of new structural roots.

Our data indicate that death of an aspen stem does not necessarily entail that its root system will die. In bigtooth aspen, Debyle (1964) also observed dead stumps with healthy root systems. The maintenance of root connections and formation of root grafts throughout the life of aspen can constitute a major advantage for the species; as stems die during stand development, the remaining trees of the clone can have access to the roots left by dead trees. Acquiring roots left by dead trees can be beneficial for the residual trees, because they inherit a functioning and established root system. It is noteworthy that the respiration needs of such newly acquired roots also have to be supplied. Capturing roots from a dead tree via root connections and grafts will, therefore, be beneficial for a tree only if the respiration costs of that root biomass can be balanced by increased photosynthetic capacity (Eis 1972). Given the large 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. This ability of the trees to "capture" part of the root system of a dead neighbor also provides good evidence that the root connections and grafts were functional.

In the sites examined, aspen trees rarely became independent of each other, and with the formation of root grafts, the level of interdependence between trees may even increase with time. Because even dead trees still had live and healthy root systems, the decline of the studied stands was not due to root dieback. Our results support the

hypothesis of Schier (1975), that the absence of suckering in declining stands may be due to the persistence of the root connections between the trees, rather than because of unhealthy root systems: Even though the death of mature trees likely increases soil temperatures by opening the canopy, apical dominance is probably maintained in the roots of the dead trees by root connections with living trees. This is also in accordance with Lavertu *et al.* (1994), who demonstrated that a few remaining aspen trees in overmature stands can maintain some healthy roots which support vegetative regeneration after complete removal of the overstory

Translocation of substances between trees through parent roots and grafts likely plays a role in stand dynamics, and should be accounted for in the management of aspen stands. For example, root connections between trees may constitute high-speed networks for diseases to spread in a forest stand. Forest managers might consider digging trenches around infected groups of trees to prevent further spreading of the disease. Herbicides can also be transmitted from tree to tree by root connections (Shepperd 1993) and should thus be applied carefully to prevent killing non-target trees.

In summary, it was demonstrated that parent roots are integral part of the root system of mature sucker-origin trees. The level of interconnection between mature trees remain high as they age because the original root connections (trees connected through their parent root) persist, but also because of the formation of numerous root grafts. Finally, death of trees along the parental root system does not seem to favour the entry of decay into the communal root system, or cause breakage of root connections.

Table 2.1: Average root diameter of the excavated aspen coarse roots.

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

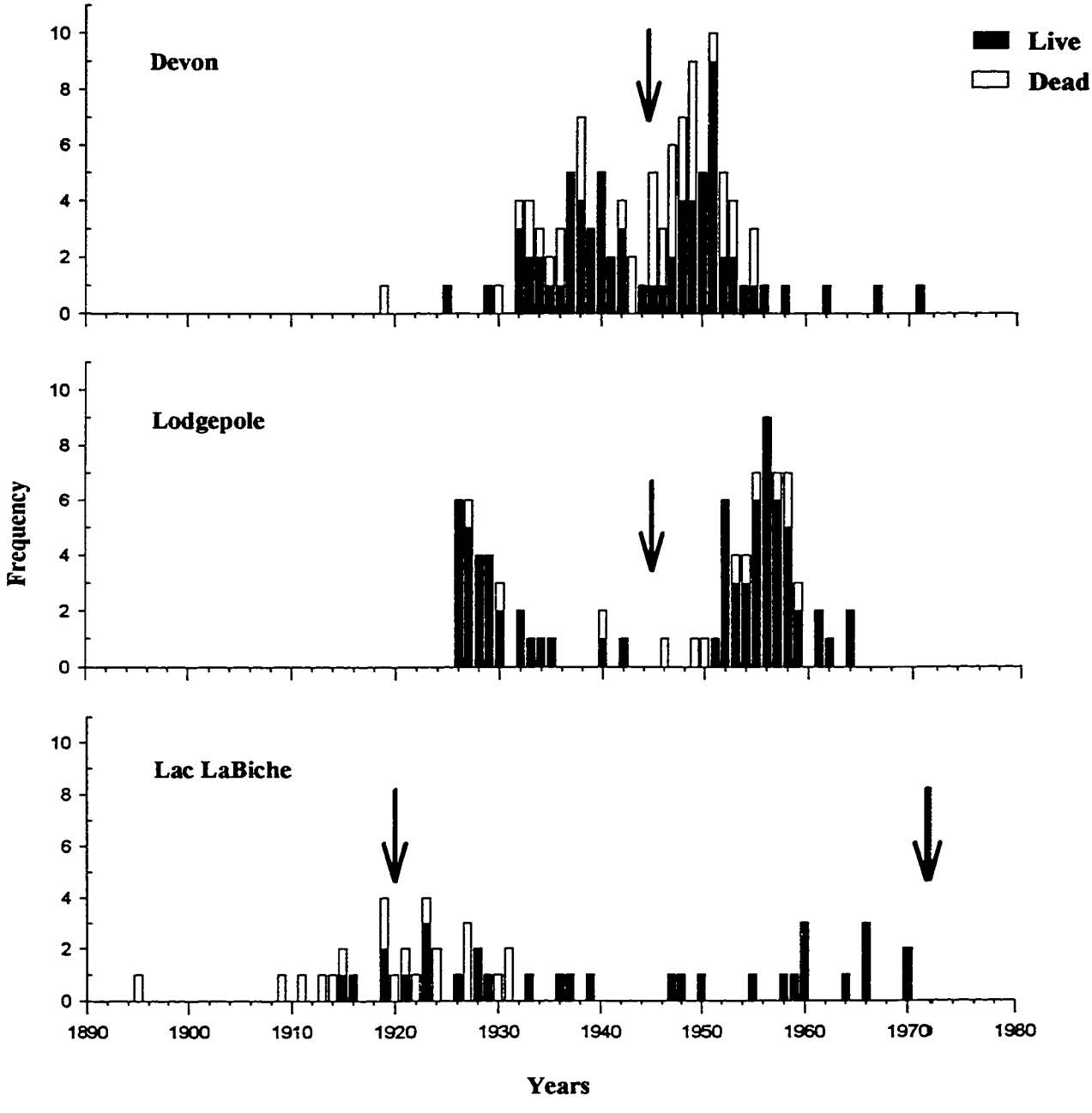

Figure 2.1: Frequency distribution of root age for the three excavated sites. The arrows indicate the year at which suckering occurred. Stacked bars are not additive.

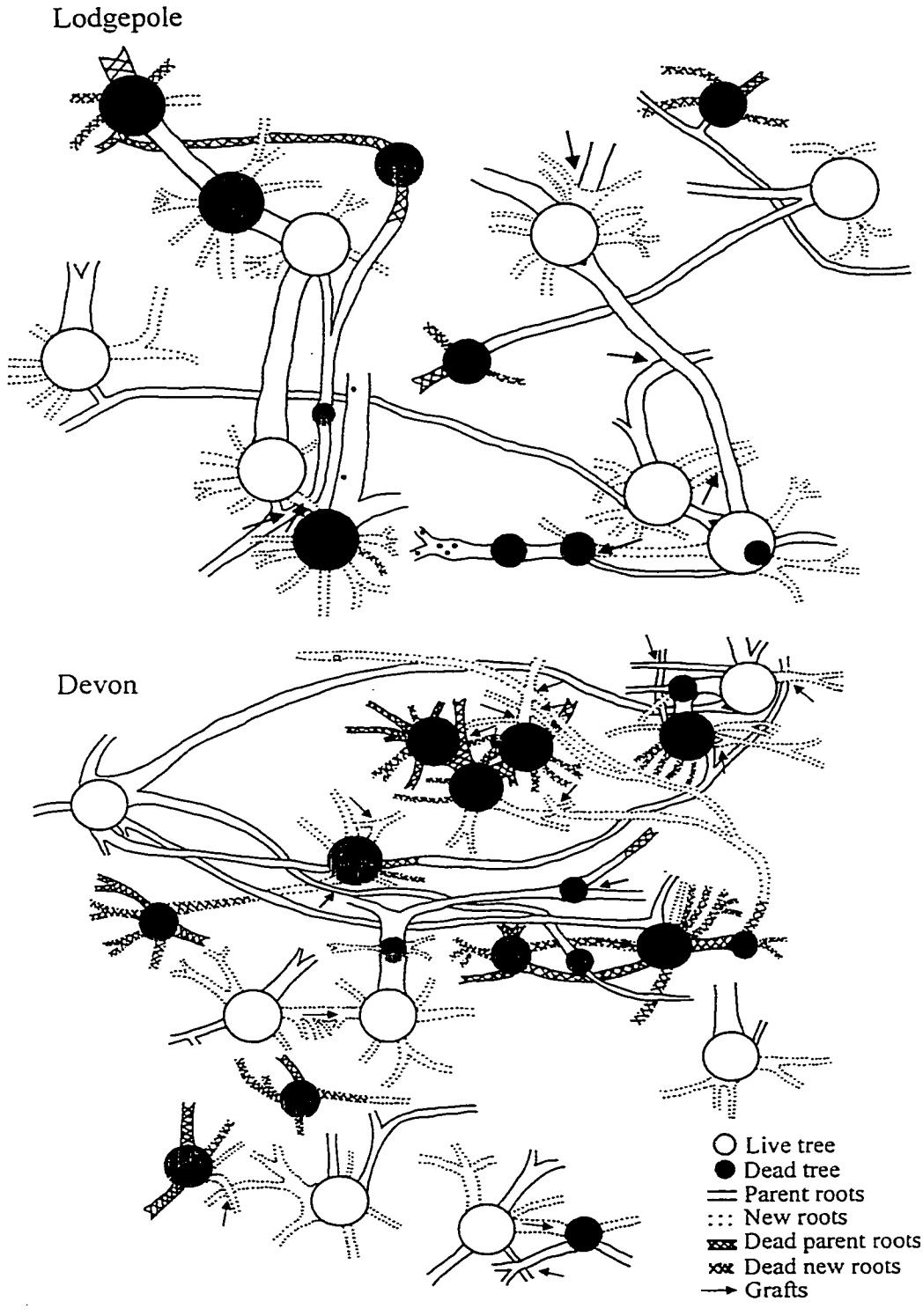

Figure 2.2: Stem and root maps of the excavated areas (not to scale). The roots were drawn in their entire length only if connected to other trees or roots inside the excavated area.

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CHAPTER III

ROOT BIOMASS OF REGENERATING ASPEN (*POPULUS TREMULOIDES*) STANDS OF DIFFERENT DENSITIES IN ALBERTA

INTRODUCTION

Regeneration of aspen (*Populus tremuloides* Michx.), following natural disturbances or logging, mostly occurs through root suckering. Because of the importance of this mode of regeneration, there have been several studies assessing the structure and development of the clonal root system in young aspen stands (Day 1944; Sandberg 1951; Barnes 1966; Gifford 1966; Schier 1982; Shepperd and Smith 1993). However, none of these studies have addressed the possible impacts of suckering density on the parental root system. The latter is important, not only because parent roots are the origin of the suckers, but also because the suckers rely on this root system for their initial growth (Zahner and Debyle 1965) until they have developed 'independent' roots (Schier 1982). Until then, the suckers entirely depend on the parental root system for water and nutrients uptake. Moreover, since parent roots are also found in the root system of mature trees (Strong and LaRoi 1983; DesRochers and Lieffers *in press),* they continue to play an important role throughout the life of the stands.

Although root suckering depends on the condition of the parent roots, low suckering density is not necessarily a result of diseased root systems. Suckering may be suppressed by soil compaction during logging (Shepperd 1993a; Corns 1998), by low densities of roots capable of suckering or by suppression of suckering through hormonal control from residual trees (apical dominance) (Farmer 1962; Schier 1975). Low suckering density may also result from insufficient increases in soil temperatures after harvesting (Maini and Horton 1966; Schier and Zasada 1973; Hungerford 1988), such as in locations where basal area of the residual stand is too high (Stoeckeler and Macon 1956), where large amounts of slash or chipped residue cover the ground (Corns 1998) or where cut blocks are quickly invaded by grass (Landhäusser and Lieffers 1998). Low initial densities of suckers might be detrimental to the clonal root system of aspen. Stands less than 10 years old have extremely high root/shoot ratios (Shepperd and Smith 1993), and few suckers may not be sufficient to maintain the entire parental root system. Portions of the parental root system are thus likely to deteriorate and die. Loss of certain portions of the parental root system may in turn affect growth of suckers and timing of establishment of new roots.

The objectives of this study were to quantify and characterize the root biomass supported by young sucker-origin stands of different densities, and to evaluate the effects of sucker density on the parent root system, on the formation of new roots (independent roots) and on the growth of the suckers. Age and size of parent roots at the time of suckering were also determined, because these data are lacking (*Chapter II*) and most of the data describing diameters of parent roots come from warmer sites in aspen forests of the United States (Sandberg 1951; Farmer 1962; Schier and Campbell 1978; Schier 1982).

METHODS

STUDY AREA

Twelve study plots were chosen in five regions of north central Alberta, Canada. Three were established near the locality of Peace River (56°14'N, 117°18'W), three near Drayton Valley (53°23'N, 113°45'W), two near Slave Lake (55°15'N, 114°45'W), 2 near Lac Labiche (54°46'N, 111°54' E) and two in the Whitecourt area (54°8'N, 115°40'W). These areas belong to the Low- and High-Boreal Mixewood and Lower Boreal-Cordilleran ecoregions of Alberta (Strong and Leggat 1992). Mean summer temperatures (May through August) range from a minimum of 6.9 °C to a maximum of 20.4 °C, and from –18.6 °C to –2.1 °C in winter (December through February). Average annual precipitation is 414 mm, with over 60% falling during summer (Strong and Leggat 1992).

The plots were randomly selected from stands originated following commercial harvesting of mature aspen stands, between 5 and 10 years previously. These stands are categorized as aspen-dominated low-bush cranberry ecosites (Beckingham and Archibald 1996), on moderately well-drained mesic sites with medium to rich nutrient regimes. Plots were all located near sufficient water supply for excavation. The regenerating stands were mostly pure aspen, with occasional white spruce (*Picea glauca* (Moench.) Voss), balsam poplar (*Populus balsamifera* L.) or white birch (*Betula papyrifera* Marsh.). Dominant shrubs, forb and grass species were green alder (*Alnus crispa* [Ait.] Pursh), wild rose

(*Rosa acicularis* Lindl.), fireweed (*Epilobium angustifolium* L.), and bluejoint grass (*Calamagrostis canadensis* [Michx.] Beauv.).

SAMPLING

Throughout the summer of 1998, after leaf expansion was completed, a 3 × 3 m plot within each chosen stand was hydraulically excavated using a high-pressure spray from a WAJAX™ fire pump. Sites were thus selected only if they had a water source nearby and at least a gentle slope to allow for the water to run off the excavated plot. The sample plots were established in areas representing the average sucker distribution and density of the stand.

The hydraulic excavation method allowed collection of roots down to a diameter of about 1 mm. Roots smaller than 1 mm usually broke off the root systems under the high pressure spray, preventing them from being collected. Excavation was to a depth of about 70 cm, exposing the entire root system. Roots were divided into dead parental roots, live parental roots, and new roots originated since suckering. The new root category was restricted to the adventitious roots growing on the sucker stem, or those growing directly below or beside the stem on the parent root; new roots could also have been produced further away on the parent roots, but they were impossible to distinguish from parent roots without a complete dendrochronological analysis. The roots were oven-dried to constant weight at 75 °C. A cross section of the parent root, for each sucker, was collected for dendrochronological analysis of its size (without bark) and age at suckering. For each sucker included in the plot, height (H) and basal diameter (D_b) were measured,

and leaves were collected for leaf area determination. To estimate shoot biomass (without leaves) from D_b and H measurements, 35 aspen stems (leaf off) were collected over the same range of sizes found in the 12 plots from a 80 km-long transect in west central Alberta. These were dried at constant weight at 75 °C, and used to develop allometric equations to predict biomass (B). For trees under 2 m height we obtained the equation:

$$B = 0.9979 + D_b^2H \quad (R^2 = 0.968;\ n = 12;\ P < 0.001)$$

And for trees from 2 m to 5 m tall we obtained:

$$B = 663.28 - 936.85\ D_b + 389.52\ D_b^2 - 59.93\ D_b^3 + 30.37\ D_b^2H$$

$$(R^2 = 0.971;\ n = 23;\ P < 0.001)$$

Where B = biomass in g , Db = basal diameter in cm and H = height in m.

SAS statistical package (SAS Institute Inc. 1996) was used for statistical analysis of the data, using REG and CORR procedures. PROC GLM with the MEANS and LSD statements were used to examine plot differences in parent root size and age. A significance level of $P \leq 0.05$ was chosen.

RESULTS

Sucker density of plots varied from 15,554 to 61,105 suckers/ha (Table 3.1), and was not correlated with the age of the stands ($P = 0.14$). Leaf Area Index (LAI = surface area of foliage per unit area of ground) ranged from 0.27 to nearly 4 (Table 3.1) and also was not correlated with stand age ($P = 0.31$). Mean dry weights of leaves for all plots was 1.37 t/ha (min.: 0.28 t/ha, max.: 2.73 t/ha). There was increasing LAI with stand density ($r^2 = 0.37$; $P = 0.01$). The amount of live root biomass (including new roots biomass)

increased with stand density ($r^2 = 0.68$; $P < 0.001$; Fig. 3.1) and LAI ($r^2 = 0.62$; $P = 0.002$; Fig. 3.2). In contrast, the proportion of dead roots decreased with stand density ($r^2 = 0.36$; $P = 0.04$) (Fig. 3.3). It appears that parent roots cannot survive on their food reserves alone for extended periods of time, since we found no evidence of parent roots surviving without being connected to a live sucker in close proximity. Root/shoot biomass ratios ranged from 0.46-3.52, but were not correlated with stand age ($P = 0.48$) or density ($P = 0.14$). Annual height increment estimates was well correlated with parental root biomass / sucker ($r^2 = 0.51$; $P = 0.01$) (Fig. 3.4), however it was not correlated to stand density ($P = 0.51$) or root/shoot biomass ratios ($P = 0.28$).

The average parent root diameter at the time of suckering, for all plots, was 8.60 mm (Figure 3.5a). There was a positive correlation between age and diameter of parent roots ($r^2 = 0.80$; $P = 0.002$). Although there were differences between plots ($P < 0.001$) in the average size and age of parental roots (Fig. 3.5a, b), size of suckering roots and their age did not explain differences in stand density; there was no correlation between stand density and mean parental root diameter ($P = 0.34$) or mean parental root age ($P = 0.16$).

There was a trend to have greater biomass of new roots in stands with smaller mean parent root diameter ($r^2 = 0.31$; $P = 0.07$), which is consistent with the results from Chapter II. The biomass of new roots was not correlated with stand density ($P = 0.59$) or to stand age ($P = 0.80$). Basal area of the suckers, however, explained nearly 74% of the variation in biomass of new roots ($r^2 = 0.74$; $P < 0.001$) (Fig. 3.6).

DISCUSSION

Young sucker stands support massive underground biomass (Table 3.1), representing on average about 38% (and up to 80% for site 3) of the root biomass of mature stands in Alberta (~23 t/ha; Peterson and Peterson 1992). The average root biomass of regenerating stands measured in our study (8.73 t/ha, Table 3.1) is considerably higher than the biomass estimations from unpublished data (ENFOR Project P-205), reported in Peterson and Peterson (1992) (4.39 t/ha). They also report very little biomass from roots larger than 0.5 cm until stands reach 10 years old, which suggests that their sampling ('stump-pulling' method) excluded larger roots. Indeed, it is the presence of large parent roots that explains the high root/shoot ratios measured in stands younger than 10 years old (Table 3.1; Shepperd and Smith 1993). Our results are comparable to the large root biomass estimates from a 10 year-old aspen stand in Wisconsin (Ruark and Bockheim 1987), which had nearly 16 t/ha of roots from 3 to 30 mm in diameter.

Extensive leaf area and its photosynthesis is needed to support the respiration demand of such a large underground biomass. Six of the 12 study plots had LAI greater than 2, with a maximum value of 3.87 (Table 3.1). These LAIs are comparable and even higher than levels of LAI from healthy mature stands (Pollard 1972; Johnstone and Peterson 1980; DeLong *et al.* 1997). Although it may seem that young aspen stands have large leaf areas relative to the amount of respiring stem biomass, they also support a

tremendously large underground biomass. As noted by Barnes (1966), it appears that large numbers of suckers (and presumably their high leaf area) is necessary for carbohydrate replenishment of the parent root system. Fast sucker growth and leaf area development allows the clone to sustain a larger portion of the previous generation of roots, as is suggested by the reduced proportion of dead roots with increasing stand density (Fig. 3.3).

Nevertheless, even in the highest density stands, at least 20% of parent root biomass was lost in the transition from one generation to the next (Fig. 3.3). These dead roots were often large parent roots located near the parent stump (Debyle 1964); these roots are much larger than the usual suckering root (Fig. 3.5a). Also, these roots are likely lost because they are located proximally (closer to the parent stump) from the suckers, while photosynthate translocation along the parent root is mostly directed distally from the suckers (Brown 1935). The sampled dead root biomass was somewhat underestimated in our study. Firstly, the sampling method did not allow for biomass estimation of dead fine roots, because they were nearly impossible to recover from the mud created by the hydraulic excavation. Secondly, because of decomposition in the 5 to 10 year period after logging, mass was lost and some of the more decayed roots disintegrated under the water pressure. The relationship between the proportion of dead root biomass and stand density may be stronger than our results reflected, because it appeared that not all the same proportion of dead roots was missed in each plot.

It was not our objective to determine the causes of low suckering densities. Whether roots died as a result of low suckering densities, or whether low densities are a

result of damage to roots during harvest, the end result does not change; low-density stands have less live root biomass and a higher proportion of dead roots (Figs. 3.1, 3.3). This suggests that the parental roots do not live for extensive periods on their food reserves alone. The relations between live root biomass and stand density or LAI (Figs. 3.1, 3.2) show that parent roots need to be supported by suckers to remain alive, beyond five years after the parent trees have been harvested.

Our results suggest that retaining high proportions of the parental root system was beneficial for growth of the suckers (Fig. 3.4). However, the amount of parental root biomass/suckers doesn't exactly reflect the parental root biomass originally captured by the suckers, because a proportion of this biomass is, in fact, wood that was laid down on the parent roots by the suckers during their 5 to 10 years of growth. Figure 3.4 nevertheless suggests that the parental root system is being used by the suckers for rapid growth. In Colorado, Shepperd (1993b) found that suckers in poorly stocked stands were shorter and had shorter leaders than suckers growing in densely stocked stands. There was no correlation between annual increment and stand density in our study, however plots with lowest densities (4 and 10) had the smallest mean annual height increment (Table 3.1). Differences in height growth could be site-specific or due to clonal differences. Height growth could also be affected by the condition of the parental root system. Also, death of large proportions of the parental root system, in low-density stands, could cause the remaining portions of the parental root system to become non-functional, slowing height growth of the suckers.

The biomass of new roots produced at the base of the suckers increased with basal area of suckers (Fig. 3.6). Since they are located at the base of the stem, these new roots certainly play a role in structural support of the stem. It is also logical that new roots be produced earlier and in greater quantities when the parent root system is or becomes too small to provide suckers with water and nutrients, as suggested by the trend for greater biomass of new roots with smaller mean parent root diameter. Data from Schier and Campbell (1978), Schier (1982) and results reported in Chapter II also show that stands which have originated from smaller parental roots form new roots at an earlier stage than stands with large parental roots.

The analysis of the parent roots showed that, although relatively small on average (8.6 mm), they could be quite old, up to 70 years old (Fig. 3.5 a, b). Dendrochronological examination of the parent roots, showed that suckers quickly enlarged the diameter of parent roots on the distal side of the suckers, but also to a lesser extent, on the proximal side. Brown (1935) explains that although the enlargement of the proximal side is usually less than on the distal side, it increases with stand density; since photosynthate translocation occurs in both direction of the parent root (Debyle 1964). When suckers arise close to each other, portions of parent root located in between 2 suckers get enlarged by both distal and proximal photosynthate translocation, causing a greater enlargement of the proximal side of the parent root. Thus, one must not assume that the proximal side of the parent root is a good estimate of the diameter of the root at the time of suckering. The mean diameter of parent roots across all of our sites was 30-50% smaller than the mean diameters estimated by Schier and Campbell (1978) and Schier

(1982) for 1-6 year-old aspen stands in Utah, based on measurements of the proximal side of the parent roots.

In summary, it has been demonstrated that young sucker-origin aspen stands support a large underground biomass, and that high sucker densities and LAI are required to prevent loss of parental root biomass. The maintenance of large proportions of the parental root biomass seems to be beneficial for growth of the suckers. It was also observed that the production of new roots do not depend on stand age or density, but rather on the size of the parent roots and on the basal diameter of the sucker. Traditionally, young sucker stands have been viewed as dependent upon their parent root system. This study develops a different perspective, by demonstrating that the parent roots also depend on the suckers for survival.

Table 3.1: Mean plot characteristics of regenerating aspen stands where roots were excavated.

Site	Age (years)	Stand density (suckers/ha)	Average sucker height (m)	Average basal diameter suckers (cm)	LAI (m^2/m^2)	Live roots (t/ha)	New roots (kg/ha)	Dead roots (t/ha)	Estimated shoot biomass (t/ha)	Root/shoot ratio
1	5	27775	2.47	2.30	1.57	11.11	254	3.15	8.78	1.27
2	5	44440	2.98	2.36	2.98	15.37	350	4.81	19.43	0.79
3	7	57772	1.43	1.37	2.47	18.12	206	3.17	5.14	3.52
4	7	16665	1.00	1.94	0.39	2.93	23	1.84	1.86	1.57
5	7	36663	2.30	2.42	3.87	12.31	328	8.48	11.85	1.04
6	7	61105	2.14	2.14	2.79	12.92	1192	3.59	14.83	0.87
7	6	37774	1.77	2.02	1.38	6.76	398	6.85	7.21	0.94
8	7	27775	1.41	1.90	0.76	5.37	n.a.*	16.43	3.49	1.54
9	9	21109	1.96	2.26	0.98	2.25	181	6.71	4.88	0.46
10	10	15554	1.05	1.50	0.27	1.02	79	0.69	1.31	0.78
11	8	28886	2.58	2.84	3.29	9.74	1331	15.47	14.46	0.67
12	8	21109	3.80	3.29	2.07	6.81	1418	8.14	21.22	0.32

*n.a.: not available

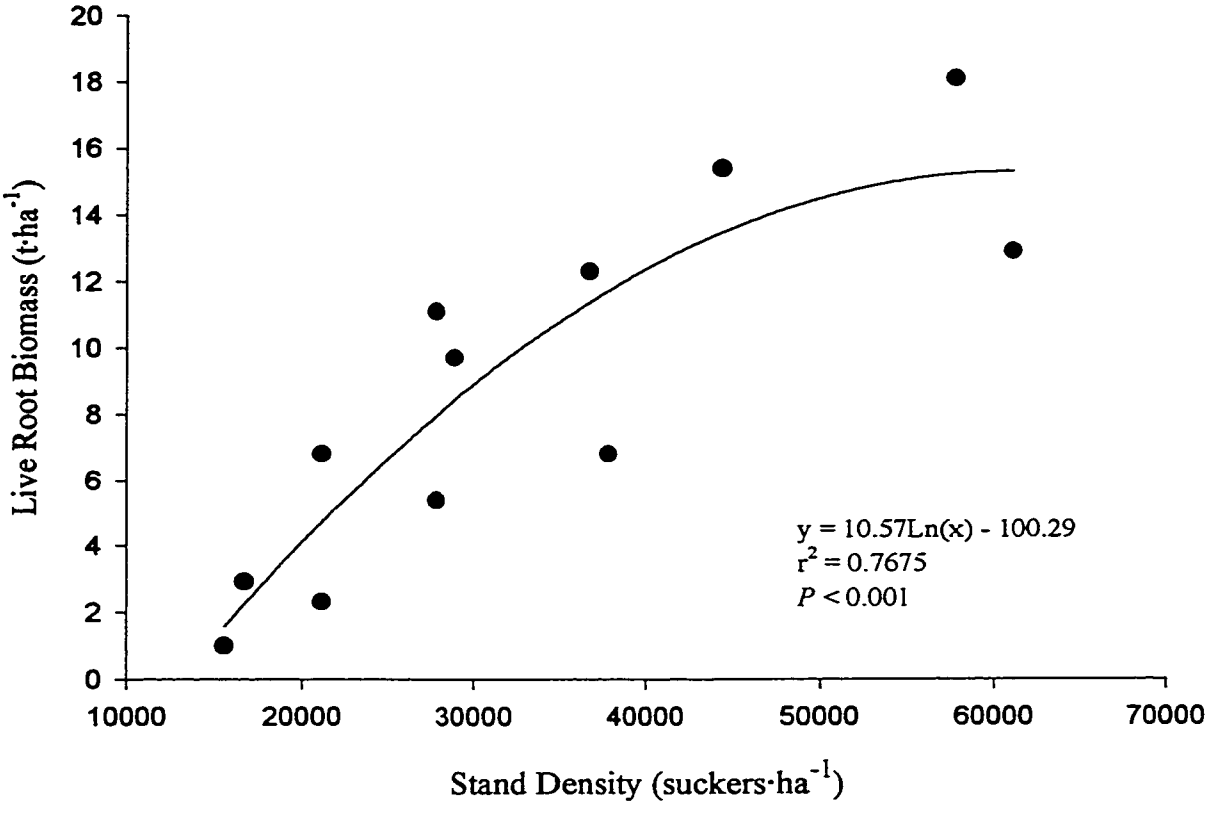

Figure 3.1: Live root biomass as a function of stand density.

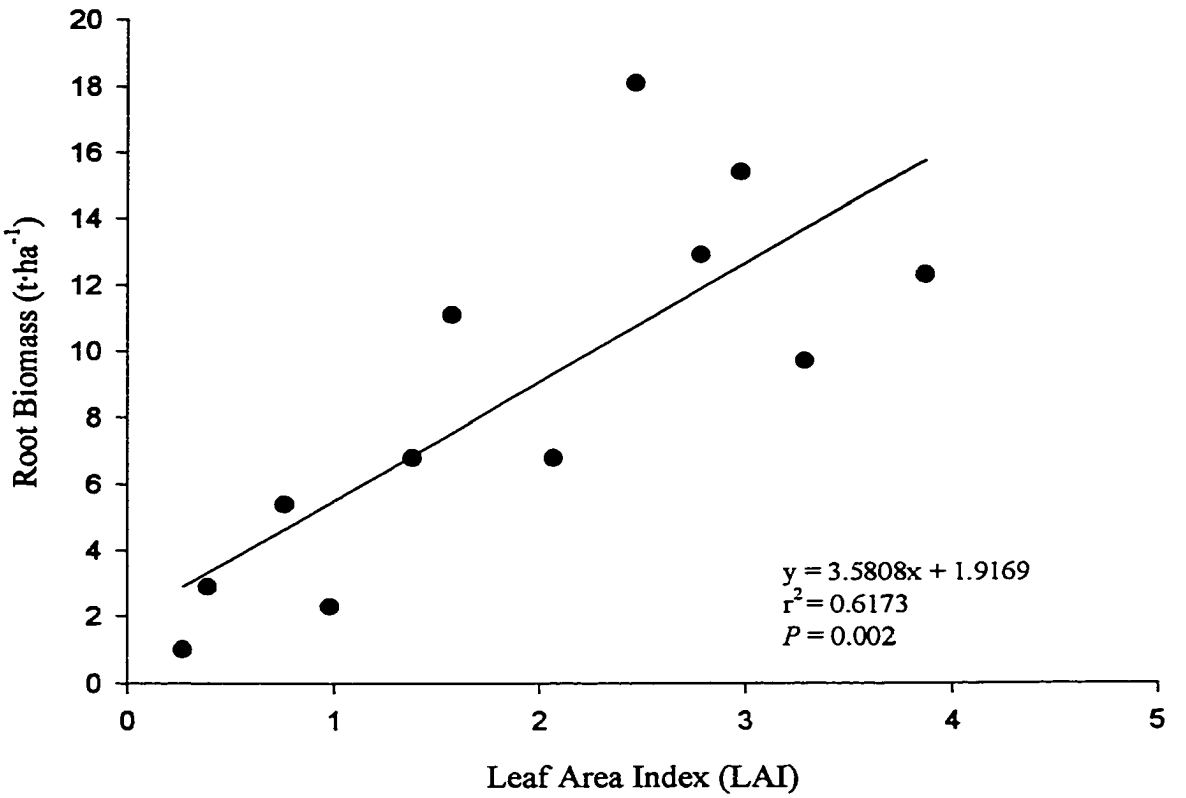

Figure 3.2: Live root biomass as a function of leaf area index.

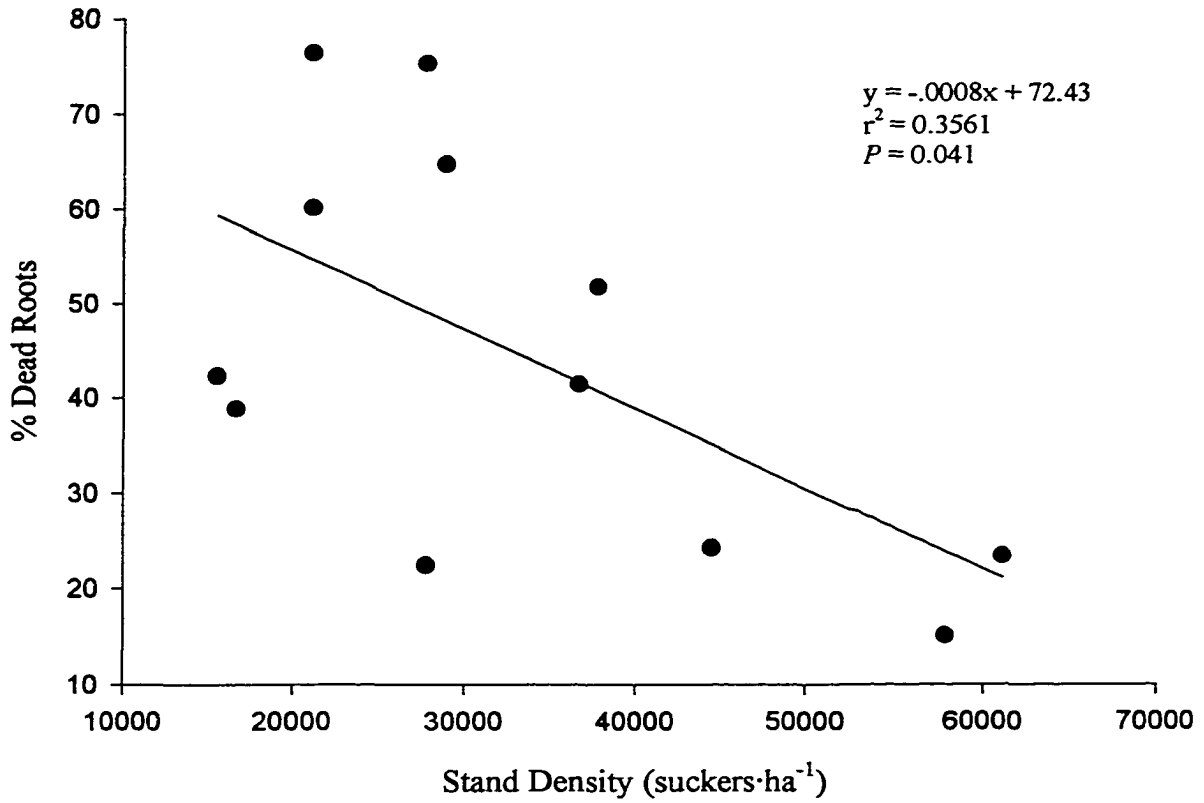

Figure 3.3: Proportion of dead roots (dead root biomass / total root biomass) in relation to stand density.

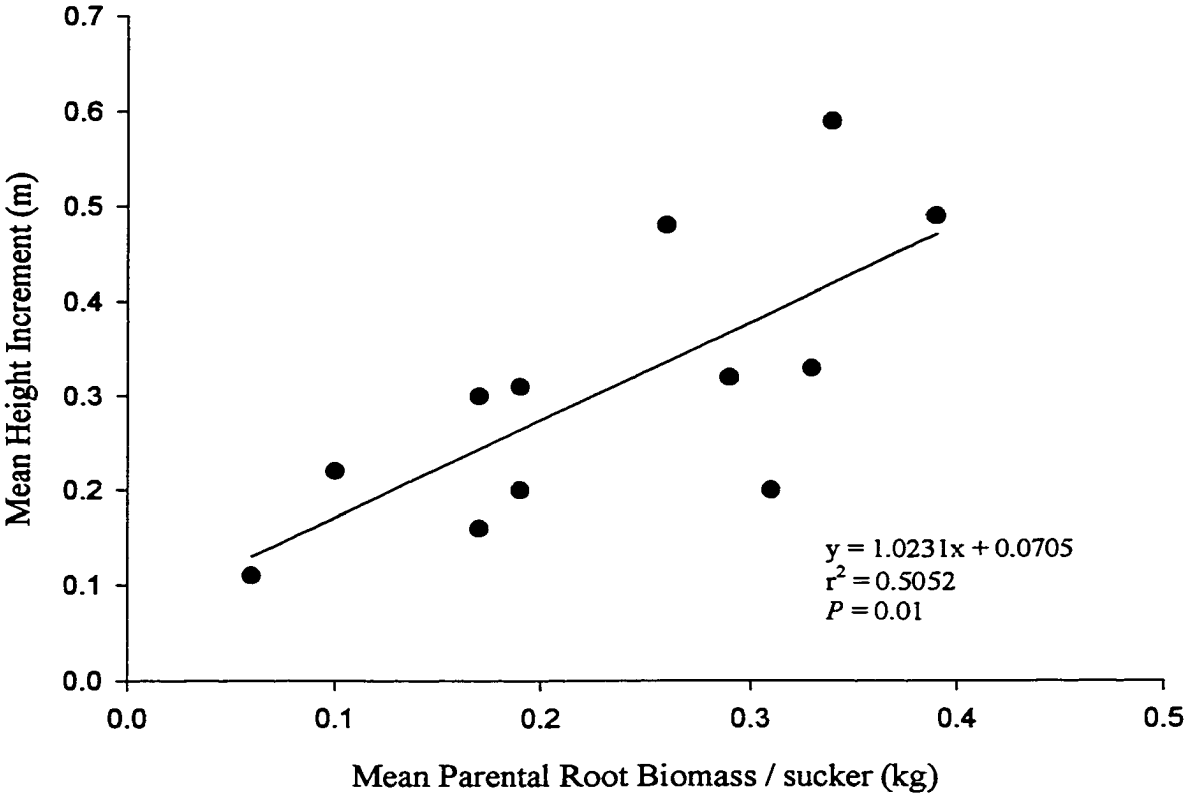

Figure 3.4: Mean annual height increment in relation to the biomass of parental roots per sucker.

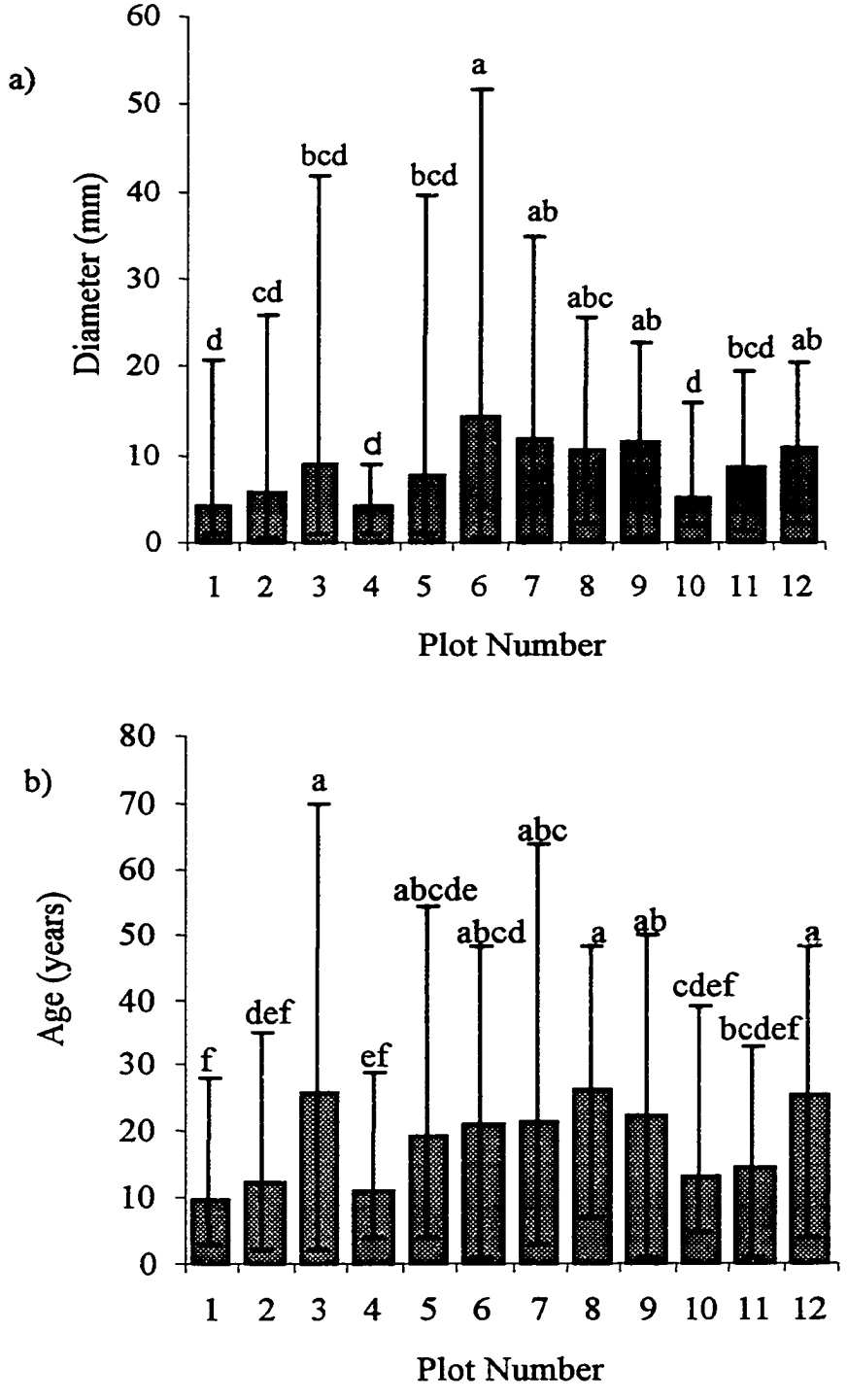

Figure 3.5: Average and range of a) diameter and b) age of parent roots, at the time suckering occurred. Bars represent the range. Plots with the same lowercase letters are not significantly different ($P > 0.05$; LSD multiple comparison of means).

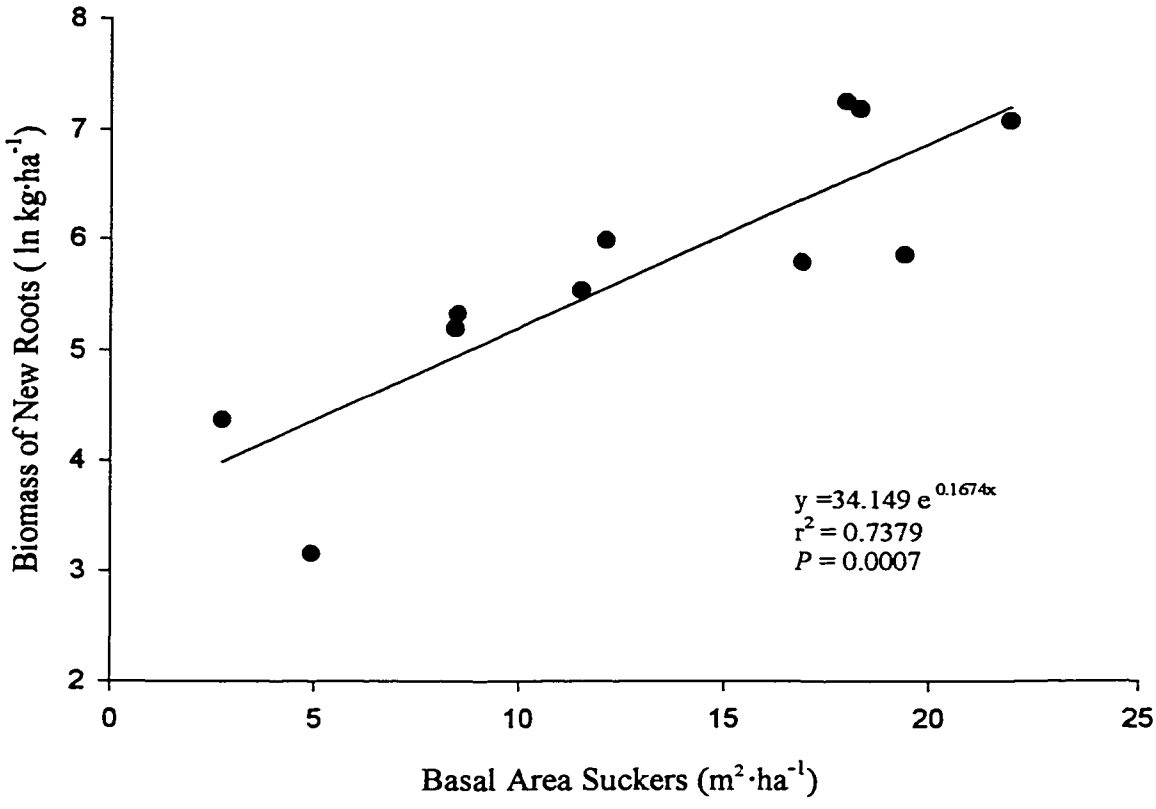

Figure 3.6: Relationship between biomass of new roots (log-transformed data) and basal area of suckers.

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CHAPTER IV

ASPEN COARSE AND FINE ROOT RESPIRATION

INTRODUCTION

Aspen (*Populus tremuloides* Michx.) usually regenerates by root suckering after a stand-replacing disturbance. Juvenile stands are characterized by high root/shoot ratios, reflecting the persistence of a large mass of parental roots in comparison to a small mass of suckers (Shepperd 1993; Chapter III). Since root respiration can consume large proportions of net primary productivity (Ericsson *et al.* 1996), the high sucker densities commonly observed in regenerated stands (Peterson and Peterson 1992), are probably necessary to support the respiration needs of this large root biomass. Also, in mature stands, the increasing burden of supporting the respiration of a large communal root system (DesRochers and Lieffers *in press*) could explain their rapid decline, once they have started to break up.

Respiration rates are usually separated into maintenance and growth components. Maintenance respiration represents the energy required to keep root cells and tissues alive, while growth respiration relates to the building of new tissue (Amthor 1984). The energy required in ion uptake is sometimes isolated as a third component of respiration (Veen 1980; Lambers *et al.* 1983). To separate maintenance from growth respiration, rates are

commonly measured at the end of the growing season, or after seedlings have set bud in laboratory experiments (Sprugel 1990; Ryan 1990; Ryan *et al.* 1995; Ryan *et al.* 1996). However respiration rates measured at the end of the growing season may not represent only maintenance respiration, because root growth can occur even if shoots are deep into dormancy (Lyr and Hoffmann 1967; Vogt *et al.* 1980). In experimental conditions, no root growth was observed at soil temperatures of 5 °C for boreal forest aspen (Landhäusser and Lieffers 1998; Wan *et al.* 1999). Low soil temperature could therefore be used as an indicator of the absence of root growth, if the maintenance component of respiration is to be estimated.

The objectives of this study were to estimate the seasonal variation in respiration rates of aspen coarse and fine roots. For coarse roots, we hypothesize that respiration rates measured on roots collected in late fall, when soil temperatures are below 5 °C, will be lower than root respiration rates measured during leaf flush, even if soil temperatures are still under 5 °C (no root growth), reflecting the additional energy required in the mobilization and translocation of reserve carbohydrates toward the developing leaves (Sprugel 1990). Respiration rates measured in the summer, when trees are actively growing and soil temperatures are above 5 °C should be higher than rates from the fall- and spring-collected roots. For fine roots, respiration rates were measured on actively growing (with leaves and soil temperature of 15 °C) and dormant (abscised leaves and soil temperatures < 5 °C) seedlings. Because the maintenance component of respiration is temperature dependent (Sprugel and Benecke 1991), the temperature response of the respiration rates was characterized. Additionally, relationships between respiration rate and total nonstructural carbohydrates (*TNC*) and nitrogen content (*N*) were examined;

total nonstructural carbohydrates (*TNC*) constitute the substrate for respiration (Kramer and Kozlowski 1979), and maintenance respiration in used for repair and replacement of proteins, to which most *N* is associated (Lexander et al 1970).

METHODS

COARSE ROOTS SAMPLING

Coarse roots were collected from a 55-year-old pure aspen stand near Devon (53°23'N, 113°45'W), Alberta, Canada, within an area of 50 × 50 m. This stand is categorized as an aspen-dominated low-bush cranberry ecosite (Beckingham and Archibald 1996), which occurs on moderately well-drained mesic sites with medium to rich nutrient regimes. Average elevation is 682 m, with undulating terrain and podzolic sandy loam soil (Bowser *et al.* 1962). Average summer and winter air temperatures are 14.4 °C and –8.7 °C, respectively, and average annual precipitation is 424 mm (Strong and Leggat 1992).

Roots were collected twice while soil temperatures at 20 cm depth were below 5 °C; in early December 1998 for the fall measurements, and in the spring during leaf flush (May 1999), to estimate the increase in respiration rates created by mobilization and translocation of carbohydrates to the flushing and developing leaves. The fall of 1998 was unusually warm; it can be expected that soil temperatures normally be below 5 °C earlier in the season during a more typical year. A third root collection was done one month after leaf flush, in early June 1999, when soil temperatures ranged from 6-8°C, to estimate the

growth component of respiration. On each collection date, 50cm-long sections of roots ranging from 0.5 to 5 cm in diameter were hand-excavated with care to avoid any wounding. A large circle was excavated from which sections of presumably different roots were collected. The roots were gently cleaned with a low concentration bleach solution (1 ml of 5% hypochlorate per liter of deionized water). Roots were stored in moistened sphagnum moss at 2 °C for a maximum of four days until respiration was measured. New collections were made after four days, in the same aspen stand but presumably from different trees (further from the previous collection location). A total of 4 collections were made for each season, over a period of approximately 2 weeks.

FINE ROOTS SAMPLING

For fine root respiration measurements, dormant one year-old container-grown aspen seedlings (6-15 plugs) were obtained from a commercial grower using a local seed source. Prior to planting in sand, the roots systems of 18 seedlings were carefully washed under running distilled water to remove all soil. After planting, pots were placed in a water bath system to provide a constant soil temperature of 15 °C (Landhäusser and Lieffers 1998). The pots were 15 cm across and 18 cm deep, self-watering, with a drainage area (false bottom). A hose was inserted into the drainage area, to allow excess water to be suctioned out after each watering. The seedlings were grown for a period of 6 weeks in a growth chamber with 18 h light and 6 h dark cycle, and with day air temperatures of 18 °C and night temperature of 16 °C. Relative humidity was maintained at 60%. Light intensity was 350-400 μmol photons $m^{-2} \cdot s^{-1}$ at pot level. The pots were

watered as needed and fertilized twice a week with full-strength Hoagland's solution (Epstein 1972), and later with a solution (2 $g \cdot l^{-1}$) of 20-20-20 (N-P-K) commercial fertilizer with chelated micronutrients. During the growing period, the pots were moved weekly to different positions to compensate for differences in growth chamber conditions. Respiration rates were measured on half of the seedlings after 6 weeks. Dormancy was induced on the other half of the plants by shortening day length to 6 hours, lowering air temperatures to 11 °C during day and 8 °C at night, and by lowering soil temperature to 5 °C for a period of 2 weeks. Watering and fertilization regimes were also reduced. The plants were then placed in a dark refrigerator at a temperature of 2 °C for another 2 weeks, before root respiration rates were measured on the dormant seedlings.

RESPIRATION MEASUREMENTS

Recent studies have shown that respiration is artificially increased by low levels of CO_2 (Qi *et al.* 1994; Burton *et al.* 1997; Clinton and Vose 1999). To avoid overestimation of the respiration rates, soil CO_2 concentrations were measured at a depth of 20 cm by slowly drawing 20 ml of soil air with a syringe connected to an aluminum probe. The air was injected in Vacutainers™ (Fisher Scientific cat. #02-683-54) tubes and the CO_2 concentrations measured with a gas chromatograph (GC). Soil concentrations at 5 °C were 3,233 ± 609 ppm (n=16). We therefore used a concentration of 3000 ppm of CO_2 for the air circulated through the respiration chamber during measurement.

A clamp-on respiration chamber was built out of ABS pipe to accommodate both the coarse and fine roots. It included a small fan for air circulation and a set of fine-gage

copper-constantan thermocouple wires inserted in the xylem (coarse roots) or root mass (fine roots) for monitoring root temperature inside the chamber. The respiration chamber was sealed from outside air with non-toxic, non-drying putty, and put inside a dark cooling chamber to measure respiration at 5, 15 and 25 °C (Landhäusser *et al.* 1996). Respiration was measured with an open-system infrared gas analyzer (IRGA, CIRAS I, PP Systems, Haverhill, Mass.). Bottled gas with 3000 ppm of CO_2 was supplied to a 9.6 L mixing chamber to maintain stable concentrations CO_2 in the supplied air. CO_2 concentration of the air coming from the mixing chamber (reference air) was monitored constantly with an IRGA just before it was supplied to the respiration chamber, and re-measured when coming from the respiration chamber. Roots were allowed to acclimate to the measurement temperature for 45 to 90 minutes, and respiration was allowed to stabilize for about 20 minutes before the rate was recorded. Air humidity inside the respiration chamber was kept at maximum with the IRGA to avoid drying of the roots, and ranged from 40-90% relative humidity.

Each coarse root was randomly assigned a temperature measurement of 5, 15 or 25 °C, and to ensure a good range in root sizes for each temperature measurement, the largest range in sizes was chosen from the available roots for each temperature run. To avoid wound respiration caused by cutting the roots (Müller 1924), the respiration chamber was clamped around the middle section (10 cm long) of the 50 cm long coarse root segments, thereby excluding the cut parts of the root. Root volume that was included in the respiration chamber was calculated as representing a cylinder shape.

For the fine roots, the sand was gently washed away from the root mass by rinsing it away submerged in distilled water. Excess water was absorbed with a paper towel. The

whole root system was put into the respiration chamber, with the above ground portion of the tree still intact, and sealed outside the respiration chamber with putty. Respiration was measured, for each seedling, at 5, 15 and 25 °C (repeated measures). Root volume was calculated immediately after respiration was measured, by water displacement.

TISSUE ANALYSIS

After respiration rates were measured, the age of each coarse root was determined by counting the number of annual growth rings. A section of root was soaked for 24 hours in a solution of 1% triphenyl-tretazolium chloride, to identify sapwood area. Another section was oven-dried at 68 °C to constant weight and ground in a Wiley mill through a 40 mesh-screen. For the seedlings, the entire fine root system was dried and ground. For total nitrogen (N) analysis, samples were digested using the Kjeldhal method (Kalra and Maynard 1991), and total nitrogen was quantified with a Technicon AutoAnalyzerII (Tarrytown, NY). For total non-structural carbohydrates (TNC), samples were digested for an hour in 0.2N H_2SO_4 in a 115 °C-bath (Shepperd and Smith 1993), and the concentration determined by a colorimetric reaction to phenolsulfuric acid (Smith *et al.* 1964).

Respiration rates of the coarse roots were analyzed as a randomized 3 × 3 factorial design with 3 seasons (fall, spring, and summer) and 3 temperatures (5, 15 and 25 °C) as fixed main effects. The fine roots experiment was analyzed as a univariate repeated measures analysis with 2 seasons (growing and dormant) and a repeated temperature factor (5, 15 and 25 °C). Respiration data were log-transformed for the coarse and fine

roots, to correct for unequal variances. Relationship between respiration rate and *N* and *TNC* were tested with linear regression, and as covariates in analyses of covariance. Least Significant Difference (LSD) procedure was used for comparison of treatment means. SAS statistical package (SAS Institute Inc. 1996) was used for statistical analysis of the data. A significance level of $P \leq 0.05$ was chosen.

RESULTS

COARSE ROOTS

Examination of the coarse root sections showed that radial growth was either completed on the fall-collected roots, or not yet started on the spring- and summer-collected roots. Heartwood (central portion of xylem without live parenchyma cells) was not observed in any of the coarse roots, apart from occasional small areas of dead xylem, even in the largest roots. These dead areas were usually not located in the center portion of the xylem and made approximately less than 5% of the root volume. Average root diameter was 2.06 cm (range: 0.65 – 4.45 cm), and average root age was 29.87 years (range: 4 – 56 years). Levels of nitrogen (*N*) content did not vary among the three seasons ($P = 0.07$), averaging 0.44% on a dry weight basis (Fig. 4.1a). Average *TNC* concentration was 11.72% of the root dry weight for the fall, 15.37% for the spring and 17.11% for the summer-collected roots (Fig. 4.1b). Coarse roots collected in the fall had lower levels of total non-structural carbohydrates (*TNC*) than the roots from the spring

and summer ($P < 0.05$), while there was no difference in *TNC* between the roots from the spring and summer seasons ($P > 0.05$; Fig. 4.1b).

Coarse root respiration rate was significantly affected by the season of collection ($P = 0.002$; Table 4.1). Respiration rates were significantly higher for the fall-collected roots than for the roots collected in spring and summer ($P < 0.05$), while there was no difference between respiration rates of roots collected in spring and summer ($P > 0.05$; Table 4.2). As expected, respiration rates increased exponentially with measurement temperature ($P = 0.0001$; Table 4.1). The respiration response to changing temperature was the same for the three seasons, since the regression slopes between respiration rates and temperature were not significantly different ($P > 0.05$). Average Q_{10} over all three seasons was 2.15 between 5 and 25 °C, however the average Q_{10} for the 5-15 °C temperature increase was 1.72, and 2.57 between 15-25 °C.

Overall, respiration rate was negatively correlated with root diameter ($r^2 = -0.28$; $P < 0.0001$) and weakly positively correlated with nitrogen (*N*) content ($r^2 = 0.08$; $P < 0.0001$). Analysis of covariance showed that root diameter ($P = 0.0008$) and *N* ($P < 0.0001$) were significant covariates for coarse root respiration rates. However, much variability remained between the season of collection and measurement temperature that could not be explained by these covariates, since season of collection and measurement temperature were still significantly related to coarse root respiration after adjusting rates for root diameter and *N*. There were no significant relationships between *TNC* content and respiration rate across the different seasons and measurement temperature combinations ($P > 0.05$), and *TNC* content did not contribute significantly to the model as

a covariate (P = 0.76). Total non-structural carbohydrate (*TNC*) concentration was not related to root diameter (P = 0.85).

FINE ROOTS

The root systems of the seedlings were mostly comprised of roots less than 2 mm in diameter, but a small portion of the roots were larger, ranging up to 5 mm (~5% of total root mass). Nitrogen concentration of fine roots did not vary between the growing and dormant periods (P= 0.36), with an average of 1.58% dry weight (Fig. 4.2a). Fine roots had significantly higher *TNC* concentrations during the growing period (P = 0.03), with an average of 13.18% of the root dry weight, compared to 9.15% when dormant (Fig. 4.2b). This decrease in TNC suggests that carbohydrates were used for cell wall thickening during dormancy, because although root volumes were not different between the start and end of dormancy (P = 0.56), the roots were significantly heavier (P = 0.02; Table 4.3).

Respiration rates were on average 49% higher for growing seedlings, and were significantly higher from respiration rates measured on dormant seedlings. (P = 0.001; Tables 4.2 and 4.4, Fig. 4.2c). Average respiration rates at 15 °C were 1289.04 μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$ during the growing period, compared to 662.64 μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$ during the dormant period (Table 4.2). Respiration increased exponentially with increasing temperature, with an average Q_{10} of 3.06 over the 5-25 °C increase. However, the increase in respiration rates was significantly higher between 5-15 °C (Q_{10} = 3.90) than between 15-25 °C (Q_{10} = 2.19) (P = 0.001). The temperature response of respiration rate was the same between the dormant and growing seedlings (P = 0.31).

The analysis of covariance showed that *N* and *TNC* were not significant covariates for fine root respiration rate (*N*: $P = 0.06$; *TNC*: $P = 0.40$). However, when fine root respiration rates were analyzed separately for each measurement temperature, *TNC* was positively correlated with respiration rate at the 15°C measurement ($r^2 = 0.49$; $P = 0.03$) and at the 25 °C measurement ($r^2 = 61$; $P = 0.01$), while a correlation at 5 °C was not detectable ($r^2 = 0.27$; $P = 0.27$). However there was no significant relationship between *N* and respiration rate when respiration rates were examined separately for the three measurement temperature ($P > 0.05$).

DISCUSSION

As expected, the respiration of the fine roots, measured on growing seedlings, was nearly double that measured on dormant seedlings, which is usually assumed to represent maintenance respiration alone (Fig. 4.2c). However, although the seedlings did not grow new roots or increase in root diameter during dormancy, the roots increased in weight (Table 4.3), which could account for additional respiration expenditures not related to maintenance. Regardless of this possible overestimation, root respiration rates of the dormant seedlings of this study were 15-30% lower than other estimates for aspen: On a dry weight basis, we found 3.0 nmol·CO_2 g^{-1}·s^{-1} respiration at 15 °C on dormant seedlings compared to 4.4 nmol·CO_2 g^{-1}·s^{-1} measured at 15 °C from Lawrence and Oechel (1983), and 3.5–4.2 nmol·CO_2 g^{-1}·s^{-1} measured at 10 °C on field-excavated fine roots from Ryan *et al.* (1997). Lower respiration rates in our study may be attributed to the use of higher

CO_2 concentrations during measurement (3,000 compared to 500-1,400 ppm of CO_2 in Ryan *et al.* (1997). Low CO_2 levels artificially increase root respiration rates (Qi *et al.* 1994; Burton *et al.* 1997; Clinton and Vose 1999). Much higher estimates of maintenance respiration rates for fine roots of aspen were also reported in a study by Coleman *et al.* (1996; 15.3 nmol·CO_2 g^{-1}·s^{-1} at 20 °C), in which a concentration of only 350 ppm of CO_2 was used. These reported rates are almost twice the amount of total respiration measured on growing seedlings in this study (7.93 nmol·CO_2 g^{-1}·s^{-1}).

For the fall-collected coarse roots, it was expected that growth respiration would have stopped since the soil temperatures had dropped below 5 °C and the annual growth ring was fully developed on these roots. However, the fact that fall-collected roots had 31% higher respiration rates than roots from the spring and the summer (Fig. 4.1c), suggests that the respiration rates still comprised growth expenditures. Lavigne (1988) also noted high respiration rates in balsam fir (*Abies balsamea* [L.] Mill.) stems for over a month after radial growth had stopped. It is thus possible that the fall-collected roots retained high overall cell activity levels after a recent period of radial growth, possibly due to cell wall thickening, as suggested by the fine root data. High respiration rates could also be caused by increased cell activity related to the transformation of reserve starch into sugars with the onset of cold temperatures (Marvin *et al.* 1971).

Unexpectedly, the spring and early summer growth flush was not accompanied by higher coarse root respiration. During that time, the coarse roots had increased *TNC* levels compared to the fall (Fig. 4.1b). This seasonal pattern of *TNC* levels does not follow the generally acknowledged pattern for deciduous species which suggest high *TNC* levels in the fall, and low levels at and just after bud flush (Larcher 1995). The

low levels of *TNC* in the fall measured in this study suggest that root reserves could have been depleted by fall root growth, in conjunction with higher respiration rates, followed by a translocation of *TNC* to the coarse roots in the spring and summer in preparation for summer radial growth. This seasonal pattern of *TNC* has been observed in Sitka spruce (*Picea sitchensis* [Bong.] Carr.; Deans and Ford 1986) and sugar maple (*Acer saccharum* Marsh.) coarse roots (Wargo 1979), where substantial carbohydrate storage preceded radial root growth. Although shoots had started growing at the summer collection date, radial growth in the coarse roots had not started at that time. These results suggest that the role of coarse roots as carbohydrate storage organs for the flushing and early growth of mature trees might be limited. In mature aspen trees, above ground biomass represents approximately 60-80% of the tree biomass (Peterson and Peterson 1992), hence carbohydrates stored in the branches, twigs and stem may play a much more important role than coarse roots as *TNC* storage organs for bud flush and early growth. Sprugel (1990) also suggested this potential role of branches and twigs as major *TNC* storage for spring growth flush in pacific silver fir (*Abies amabilis* Doug.) trees.

The acid digestion method used here has been used in the past for determination of *TNC* levels in aspen roots (Shepperd and Smith 1993). However, in roots of grasses and legumes, it has been observed that this method is likely to over-estimate *TNC* concentrations when little starch is present and to under-estimate the *TNC* levels when large amounts of starch are present (Greub and Wedin 1969; Grotelueschen and Smith 1967). If the same holds true for aspen coarse roots, it could have affected the results since it is expected that starch levels be lower under cold temperatures than in summer (Kramer and Kozlowski 1979).

On a wet volume basis, fine root respiration rates at 15 °C were 2.5-3.5 times higher than coarse root respiration (Table 4.2). Higher respiration rates can be expected in fine roots, because they are physiologically more active and have higher proportions of meristematic and phloem tissues than coarse roots (Kramer and Kozlowski 1979). Although no 'heart wood' was observed in any of the coarse roots, sapwood xylem contains proportionally fewer living cells than cambium and phloem tissues (Ryan 1990). A recent study showed that *N* content of the root is a better indicator of root level activity and respiration than root size (Pregitzer *et al.* 1998). A large part of maintenance respiration is used for repair and replacement of protein (Amthor 1984), and since most of the N is associated with protein content (Lexander *et al.* 1970), N is usually a good indicator of root activity. Nevertheless, the relationship between maintenance respiration and *N* content was not clearly apparent in the data because of little variation in N within the samples of a treatment combination (Figs. 4.1a, 4.2a). Also, maintenance respiration may poorly match N in systems where N is in excess (Ryan 1995), which could explain why N was not a significant covariate for the fine roots respiration rates, since the seedlings were generously fertilized. However after pooling the data obtained from the coarse and fine roots to increase the range in N concentration as suggested by Pregitzer *et al.* (1998) for sugar maple (*Acer saccharum* Marsh), the relationship was evident and explained 65% of the variation in respiration rates ($P < 0.0001$; Fig. 4.3). Inferences from this figure must however be made carefully, because the coarse and fine roots come from two different populations of roots. The absence of a significant relationship between *N* and respiration rate of the coarse and fine roots, when separately analyzed, could simply

be due to the fact that maintenance respiration was never exactly isolated from growth respiration.

The increasing positive correlation between *TNC* and respiration rate with increasing temperature, observed for the fine roots, suggest that *TNC* became more limiting as temperature increased. This was not observed in the coarse roots, probably because they respire at much lower rates, even at the 25°C measurement temperature (Tab 4.2). This changing temperature dependency on *TNC* is probably due to the fact that affinity between enzymes and their substrate usually declines with temperature, and is modified by substrate concentration (Hunt and Loomis 1979). Limited access to *TNC* at high respiration rates could also explain the lower Q_{10} obtained between 15-25°C for the fine roots (Wassink 1972 *as cited by* Hunt and Loomis 1979). Lawrence and Oechel 1983 also found lower Q_{10} for the 15-25°C increase in temperature. These results show that Q_{10} is not independent of temperature (Thierron and Laudelout 1996), therefore it should be used carefully and in relation to the studied range of temperatures.

In summary, the respiration rates and *TNC* concentration suggest that the fall-collected roots still comprised growth expenditures, while the spring- and summer-collected roots were still dormant even though the above-ground portions of the trees had started to grow. The increased in dry weight of fine roots and low *TNC* levels during the period of dormancy also suggest growth expenditures. One must then be careful in assuming that respiration rates measured on dormant seedlings represent the maintenance component of respiration.

Table 4.1: Analysis of variance of log-transformed respiration rates of coarse aspen roots.

Source	d.f.	MS	*P*
Season	2	0.57	0.002
Temperature	2	9.55	0.0001
Season × Temperature	4	0.11	0.16
Error	245	0.15	

Table 4.2. Summary of aspen coarse and fine root respiration rates, measured at 5, 15 and 25 °C*.

	Respiration rate (μmol $CO_2 \cdot m^{-3} \cdot s^{-1}$)				
	Coarse roots			Fine roots	
Measurement Temperature (°C)	Fall	Spring	Summer	Dormant	Growing
5	189.67 (45.67) n = 23	120.77 (38.47) n = 31	138.04 (38.47) n = 31	154.80 (58.59) n = 9	414.05 (55.24) n = 9
15	372.83 (40.48) n = 28	228.45 (39.78) n = 29	181.18 (39.78) n = 29	662.64 (74.69) n = 9	1289.04 (70.42) n = 9
25	752.13 (43.73) n = 24	526.71 (39.11) n = 30	614.91 (39.11) n = 30	1631.56 (151.28) n = 9	2558.43 (142.63) n = 8

*Standard errors are given in parenthesis

Table 4.3: Average fine root volumes and dry weights*.

	Growing seedlings	Dormant seedlings
Volume (cm^3)	17.58 (4.93)	19.94 (10.89)
Dry weight (g)	2.60 (0.77)	4.51 (2.69)

* Standard deviations are given in parenthesis

Table 4.4. Univariate repeated measures analysis of fine roots respiration rates (log-transformed).

Source	d.f.	MS	*P*
Season	1	1.49	0.001
Error (among plants)	15	0.11	
Temperature	2	4.49	< 0.0001
Linear	1	8.68	< 0.0001
Quadratic	1	0.29	0.011
Temperature × Season	2	0.14	0.16
Error (within plants)	30	0.07	

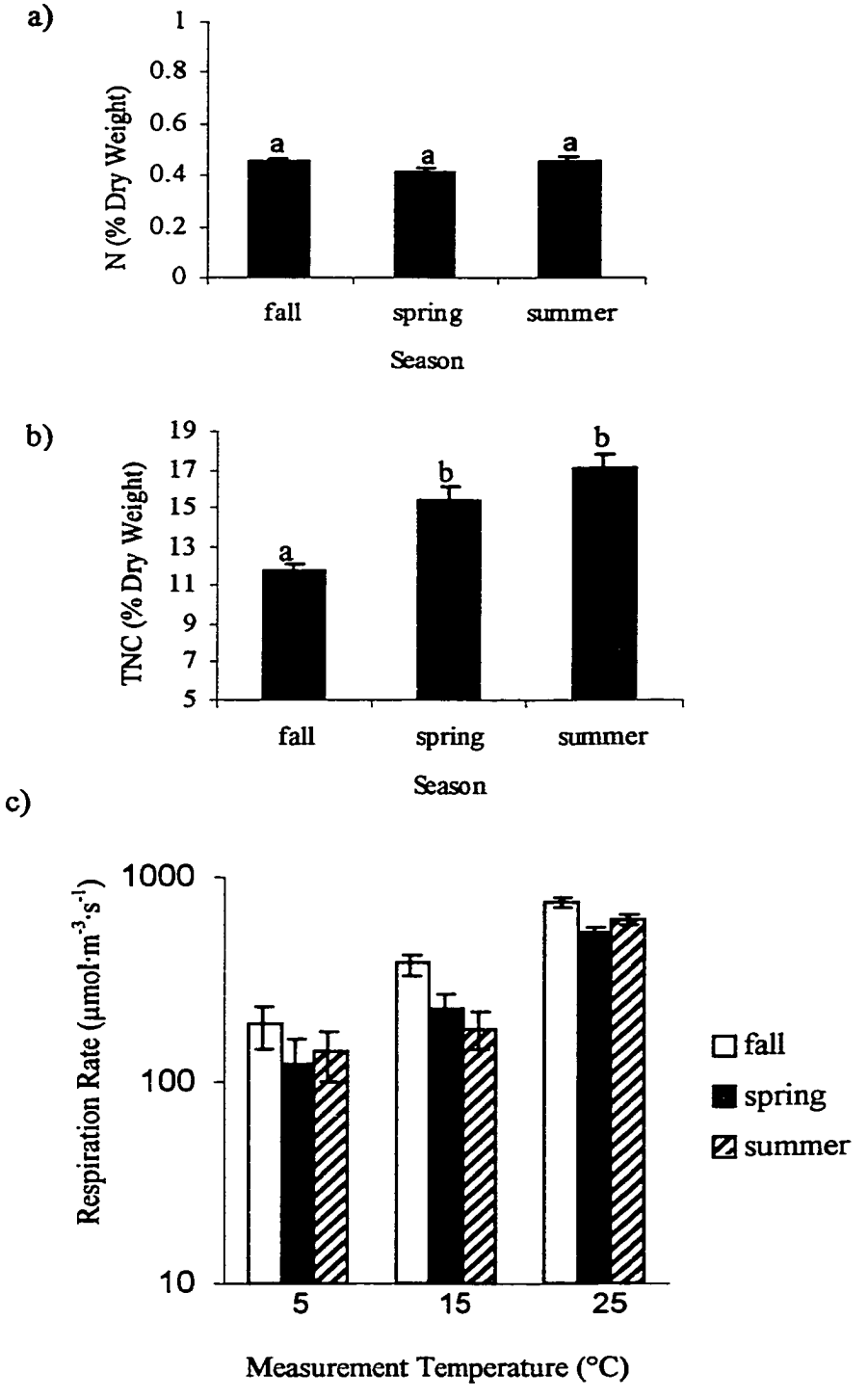

Figure 4.1. Coarse roots a) nitrogen concentration, b) total non-structural carbohydrates concentration and c) respiration rates measured at 5, 15 and 25 °C (log scale). Bars with different letters are significantly different ($p < 0.05$).

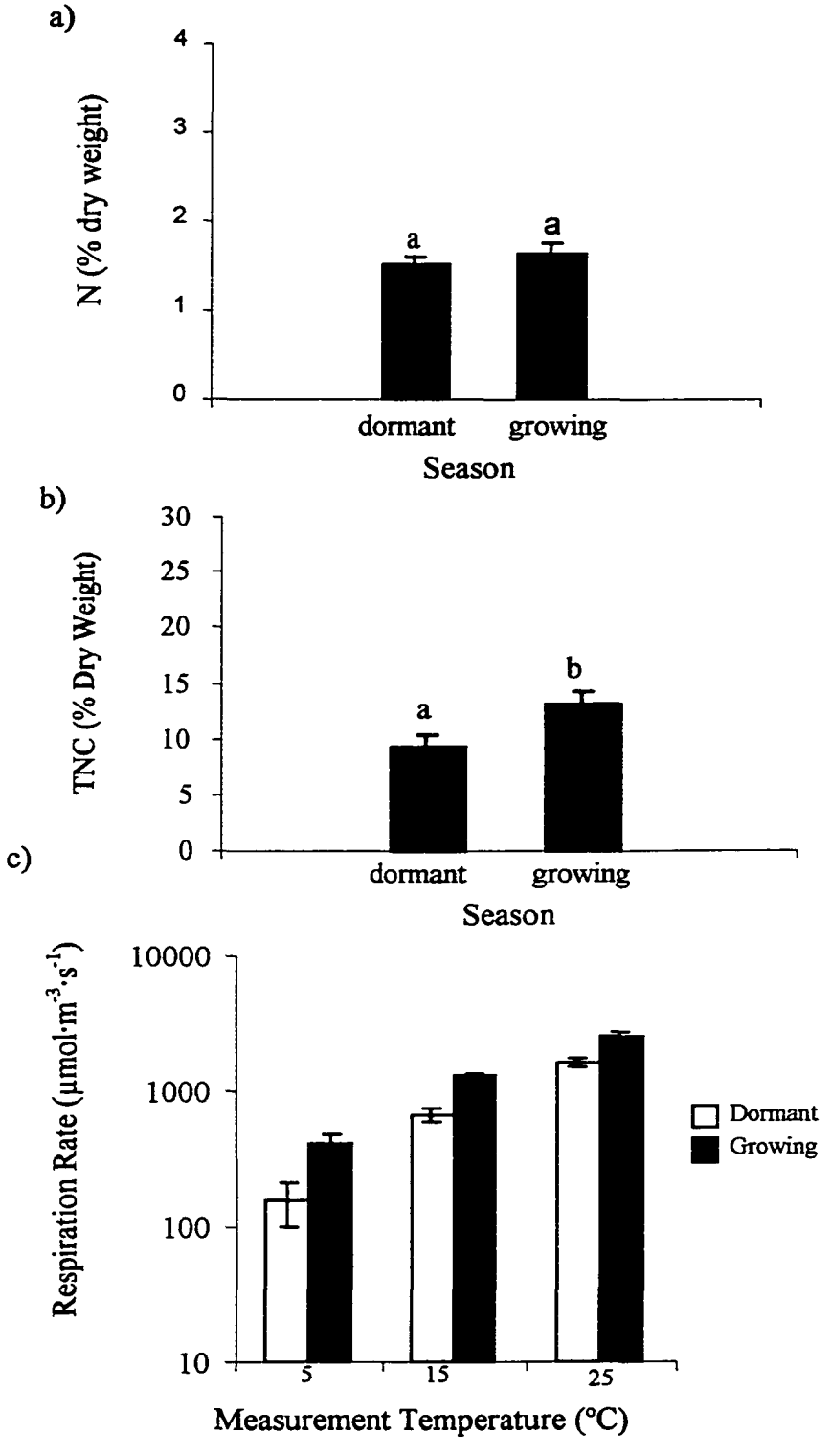

Figure 4.2. Fine roots a) nitrogen concentration, b) total non-structural carbohydrates concentration, and c) respiration rates (log scale) measured at 5, 15 and 25°C. Bars with different letters are significantly different ($p < 0.05$).

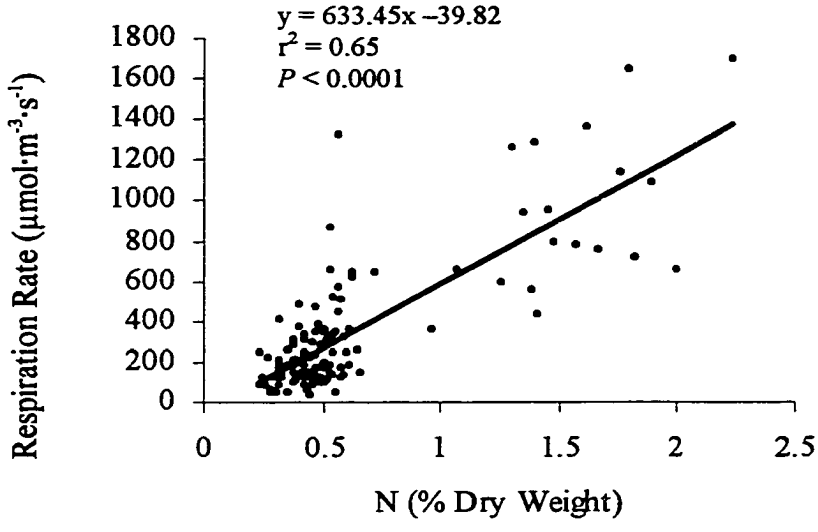

Figure 4.3: Relationship between respiration rate at 15°C and N, pooled data from coarse and fine roots.

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CHAPTER V

GENERAL DISCUSSION AND CONCLUSIONS

Traditionally, trees are looked upon as discrete entities, and competition is considered the most important driving force in stand dynamics. This research has demonstrated that aspen trees of sucker origin are not independent of each other. Parent roots are an integral part of a tree's root system, interconnecting trees of the same clone perhaps throughout their lifetime. Moreover, root excavations in declining stands showed that the trees were additionally joined by root grafts, increasing the level of interconnection between trees. These root connections allowed live trees to 'capture' the roots of trees after they had died, indicating that the root connections were physiologically functional. Injections of dyes or herbicides have further demonstrated that substances can travel through aspen root connections (Tew *et al.* 1969; Shepperd 1993). Auxins, for example, could be transferred from the shoots of live trees to the root systems of dead trees through root connections, inhibiting suckering in the canopy openings left by dead trees (Farmer 1962; Schier 1975). Translocation of physiological substances between trees could thus have significant implications in stand dynamics.

The use of a common network of roots has the potential to generate cooperative relationships between ramets, for example by delaying the death of suppressed trees through translocation of carbohydrates from dominant trees, slowing down the succession processes. However, despite their highly interconnected root systems, aspen stands are

reputed to undergo rapid self-thinning. Therefore, it could also be argued that root connections increase competition forces; larger members of the root complex may, at the expenses of the less vigorous trees, establish gradients that cause water and nutrients absorbed by the communal root system to move primarily to them (Bormann 1962). Larger trees, with their larger crowns, will transpire more than suppressed trees, creating a stronger sink for water and nutrients movement, perhaps hastening the death of connected smaller trees, quickening self-thinning and succession processes (Graham and Bormann 1966).

Canopy openings in stands where trees share a common root system are not really space available for invasion by other trees, since the roots systems of dead trees continue to occupy and use the soil, as extensions of the root systems of the remaining trees. It has been shown in this research, that roots of dead trees commonly remained alive if they were connected to a live tree, through a common parent root or root graft. Therefore, when trees die, the soil resources do not necessarily become available for new trees to establish and grow, but are rather redistributed within the clone.

Inheritance of roots from a dead tree can have a positive impact on the growth of residual trees, by increasing their absorptive area and access to soil resources and/or additional stored foods. However, since roots also respire, capturing the roots of a dead tree (or in the same way, inheriting roots from a previous generation of trees), will result in increased growth only if the respiration costs of the newly acquired root biomass can be compensated for by the use of these roots and by increased photosynthetic capacity. For grafted Douglas-fir (*Pseudotsuga menziesii*) trees, Eis (1972) superbly demonstrated that the amount of additional root biomass and residual photosynthetic capacity will determine

if the captured root biomass will have a positive or negative impact on growth of a residual tree; the addition of a large root system of a dominant tree became a burden for suppressed trees with insufficient leaf area to compensate for the increased respiration demand of the root system, while the contrary, the addition of a suppressed tree's root system to a dominant tree, was profitable for dominant trees. In the case of the sucker-regenerated aspen studied here, when suckering density was low, a higher proportion of the roots were found dead, probably reflecting the inadequate capacity of the suckers to support the inherited root biomass. The very high leaf area index observed in young stands of higher density, even higher than that of mature stands, is probably necessary to support the parent root biomass. Because a larger proportion of photosynthates is used to compensate for respiration as trees age, in mature aspen stands with interconnected root systems, death of a few trees can significantly increase the respiration demand, and this might rapidly trigger the decline of the stand.

ROOT RESPIRATION

Root respiration is a major component of the carbon balance of trees, and as discussed earlier, especially important for aspen stands with interconnected root systems. Following a suckering event, the suckers have to supply carbohydrates to a comparatively large underground biomass, which probably requires high numbers of suckers (high leaf area index). The 'cost' of maintaining a large root biomass can be evaluated by measuring root maintenance respiration rates.

Contrary to my findings about respiration rates of fine roots, respiration rates obtained for coarse roots were not as expected. The fall-collected roots reflected growth respiration expenditures, even though the trees were into dormancy and soil temperatures were below 5 °C. Low soil temperatures perhaps inhibit new root growth, but do not instantly lower overall root activity level and cell wall thickening. Also reflecting recent root growth, coarse root total non-structural carbohydrate (*TNC*) levels in the fall were low, at the opposite of the generally acknowledged *TNC* seasonal pattern (Larcher 1995). Furthermore, bud flush and shoot growth of the trees did not cause a decrease in *TNC* levels or an increase in respiration rates, suggesting that coarse root respiration rates and *TNC* levels are mainly affected by the root activity itself, and that coarse roots perhaps play a minor role in providing reserve *TNC* to shoots for spring bud flush and early growth. In young aspen stands, Tew (1970) observed that carbohydrate reserves of the root system were depleted for early-season growth flush, soluble sugars and starch were lower just after leaf flush in the spring. The different seasonal pattern of carbohydrate levels found here suggests that there might be fundamental differences between young and mature trees regarding the location of reserve carbohydrates. In mature trees, it seems logical that most of the carbohydrates used for spring growth flush come from twigs, branches and bole, because these tree parts are located much closer to the buds than roots. Moreover, above ground parts account for a larger part of total tree biomass than the roots (Peterson and Peterson 1992) and may thus contain larger quantities of reserve carbohydrates for spring growth flush.

IMPLICATIONS

The level of interconnection between trees demonstrated in this research certainly affects stand dynamics and should be accounted for in stand management. Root connections between trees may constitute high-speed networks for diseases to spread in a forest stand, and silvicultural techniques could be developed to isolate groups of affected trees to prevent further spread of diseases. These techniques could also be used to isolate groups of target trees if chemical treatments are to be used (fertilizers, herbicides, etc.). Isolation of infected trees from adjacent healthy or non-target trees can be achieved by means of trenches excavated to depths below the rooting plane.

In young stands, it was shown that suckers benefit from maintaining larger proportions of the parental root biomass, and that high leaf area index or sucker density were needed to maintain large amounts of parental root biomass. These results thus suggest that thinning young aspen stands might be detrimental to sucker height growth. Furthermore, if stands do not regenerate with good densities, action should be taken rapidly to avoid loosing the parental root biomass.

SUGGESTIONS FOR FURTHER RESEARCH

The use of a communal root system certainly affects inter-tree relationships and should be further investigated. The nature, quantities, or importance of the substances shared between interconnected trees still remain mostly unexplored. Examination of the processes involved in translocation of water, nutrients and assimilates between trees could

give good insight in the ways that interconnected root systems may affect stand dynamics. Processes involved in graft formation could be further investigated, especially factors promoting graft formation, but the timing of graft formation in stand development and with regard to death of trees.

The unexpected results of coarse root respiration should be further investigated by measuring respiration rates more often during the year, to provide a better estimate of maintenance and growth respiration, especially when radial growth is actually taking place. During the same time, total non-structural carbohydrate (*TNC*) levels should also be re-measured, to have a complete seasonal description of the *TNC* levels in relation to root growth and root respiration rates. The origin of the carbohydrates needed for leaf flush in the spring should be further investigated by analyzing carbohydrate levels in different tree compartments. If an excavation method that does not induce wound respiration could be developed, fine root respiration could be measured on mature trees in the field, to verify if they respire differently than fine roots from artificially-grown seedlings. The root respiration rates measured in this study should be used in conjunction with the root biomass estimates, to evaluate the amount of leaf area necessary to support a given root biomass. Respiration rates and *TNC* levels should also be utilized to estimate root longevity in the event of delayed suckering.

MAJOR CONTRIBUTIONS

In summary, this dissertation research demonstrated that aspen trees can remain interconnected throughout their lifetime, and that death of trees along the parent roots do

not necessarily favour the entry of rot into the root system and cause the breakage of root connections. Furthermore, the roots of dead trees can remain alive, if they are connected to a live tree through a common parent root or root graft. Dendrochronological analysis of the root system of mature trees showed that instead of being replaced by new roots, parent roots were incorporated in the root system of most trees. Occurrence of root grafting was also commonly observed, increasing the level of interconnection between trees.

A significant amount of data were collected from juvenile aspen stands of different sucker density: Live and dead parental root biomass (excluding fine roots), new root biomass, leaf area index and leaf biomass, root/shoot ratios, average parent root size and age at suckering. This research demonstrated that high-density regeneration and high leaf area were important for the maintenance of the parental root biomass. Greater biomass of parent roots/sucker seemed to favour height growth of the suckers. Contrarily as could be expected, differences in suckering density were not related to mean age or diameter of parent roots. Diameter of parent root, however, seemed to influence the time of new root production, which was not related to stand age or stand density, but was positively correlated to basal area of the suckers.

Aspen coarse and fine root respiration rates were estimated from dormant and active trees and seedlings, along with the temperature responses of respiration rates. The respiration rates suggested that dormant trees do not necessarily have dormant roots, and on the other hand, that active trees do not necessarily have actively growing coarse roots. The temperature response of coarse and fine root respiration was examined, and it was observed that the temperature response of aspen fine root respiration was not linear.

Nitrogen (*N*) content was a good predictor of root respiration only when data of coarse and fine roots were pooled, including a larger variation in *N* concentration. On the other hand, total non-structural carbohydrate (*TNC*) concentration was only related to root respiration at the higher respiration rates, reflecting a limited access to *TNC* at higher respiration rates. Finally, the role of coarse roots as storage organs for leaf flush was questioned, due to the high levels measured in the spring and early summer.

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