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Suckering Potential Of Declining Aspen And Mixedwood Stands In West-Central Saskatchewan

by

Pola Theresa Genoway

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

Master of Science

in

Land Reclamation and Remediation

Department of Renewable Resources
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ABSTRACT

As trembling aspen (*Populus tremuloides* Michx.) stands reach maturity they are already deteriorating. Research was conducted to assess suckering capacity and development and nonstructural carbohydrates of roots from declining aspen (no, low and heavy decline) and mixedwood stands in relation to time of year roots were collected. Vegetation characteristics of the sites were also assessed.

Heavy decline aspen stands had lower suckering capacity than no and low decline aspen in spring, summer and fall. All aspen and mixedwood stands had highest suckering capacity and nonstructural carbohydrates in fall and spring compared to summer. Mixedwood stands produced fewer suckers although carbohydrate content and live aspen root mass was higher throughout the season. The vegetation was typical of poplar and mixedwood stands. In aspen stands there were more forb and shrub species compared to mixedwood. Similar species dominated the pure aspen stands but there were different dominant species for the mixedwood sites.

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TABLE OF CONTENTS

CHAPTER III VEGETATION COMPOSITION OF DECLINING ASPEN AND MIXEDWOOD STANDS 64

LIST OF TABLES

LIST OF FIGURES

I. INTRODUCTION

1.0 BACKGROUND

1.1 Importance of Trembling Aspen

As early as 1918, Baker (1918) recognized the potential of trembling aspen (*Populus tremuloides* Michx.) as an important commercial forestry product due to its ease of propagation, rapid growth and simplicity of management. Aspen emerged from weed tree status to become important commercially within the past few decades (Alban et al. 1991). There have since been numerous studies on aspen propagation. Schier (1975) discussed the widespread aspen deterioration throughout the Intermountain Region. He explained that the ramets of most clones in the region originated in the 19th century before successful fire suppression. Many clones were thus reaching maturity and an increase in deteriorating forests was predicted for the next decade. Today, many forestry managers are faced with rejuvenation of decadent aspen stands (Mueggler 1989, Bartos et al. 1991).

Aspen forests are an important source of economic wealth and natural resources such as timber. They also provide intangible values, such as wilderness environment, recreation in a natural setting, rare or unusual natural features and aesthetics. Aspen contribute to scenic beauty of the landscape, especially in fall when leaves turn shades of yellow, orange, brown and red. Since aspen provide valuable watershed protection, big game habitat and summer range for livestock, its future is a major concern for the resource manager (Schier 1975). Aspen forests also contribute to plant biodiversity in areas that otherwise would lack diversity. Throughout its life aspen is associated with different species from neotropical migrant birds in their sapling and small pole stands to raptor perches and songbirds in the decadent declining stands (Alban et al. 1991).

1.2 Aspen Management Issues in the Study Area

The people of Saskatchewan expect forests to be managed to meet their diverse needs, while protecting and maintaining forest ecosystems to meet the needs of present and future generations (Strong et al. 1995). Accepted levels of timber use are based upon the ability of the environment to absorb the impacts of harvesting. The ability to establish and maintain these levels requires the involvement and cooperation of the people of Saskatchewan, the provincial government, research agencies and the forest industry.

Mistik Management Ltd. is the forest management company responsible for the planned harvest and renewal of forest stands within the Bronson Forest and the delivery of roundwood to the NorSask sawmill and Millar Western pulpmill. Mistik is wholly owned by NorSask and Millar Western (Mistik Management 1996).

The Bronson Forest lies southwest of Meadow Lake, Saskatchewan. The north-south boundaries are defined by the interface between forest and agricultural lands, while the east-west boundaries extend from the Alberta-Saskatchewan border to approximately 2 km east of Highway 26. The Bronson Forest is dominated by 45 to 60 year old aspen stands, possibly a consequence of fire history and softwood harvesting during the 1930s to satisfy railway tie demands. The Bronson Forest is not true Boreal Forest, but is classified as Boreal Transition, indicating the lack of, or decreased representation of, some boreal tree species. The two Boreal tree species with lower abundance in the Bronson Forest are black spruce (*Picea mariana*) and larch (*Larix laricina*) (Mistik Management 1996).

There are potentially thousands of hectares of decadent aspen stands of low vigor throughout the Bronson Forest. Aspen overstory mortality is estimated at 30 to 60%. The causes of low vigor and mortality have not been determined, but environmental stresses caused by years of drought, tent caterpillar epidemics and isolated soil site limitations has resulted in substantial mortality to this forest type.

Severe infestations by forest tent caterpillar (*Malacosoma disstria* Hbn.) occurred in some parts of Manitoba and Saskatchewan almost every year from 1922 to 1953. Most of the infestation declined in 1953 and 1954 and by 1954 the only stands showing measurable defoliation were near Meadow Lake, Saskatchewan. No traces of defoliation could be detected in either province in 1955 and 1956. In 1957 only light defoliation was observed (Hildahl and Reeks 1960). Extensive defoliation occurred in 1962 to 1964 (Hogg and Schwarz 1999). Major outbreaks of aspen defoliation then occurred in Saskatchewan in 1972. Maximum distribution was reached in 1979 to 1980 when moderate to severe defoliation ranged over a total area of 128,000 km^2 (Still 1981, Hogg and Schwarz 1999). Again, in 1981 and 1982, trembling aspen and frequently other associated deciduous tree species in the province of Saskatchewan, were moderately to severely defoliated. Extensive defoliation then occurred in 1985 to 1989 and very little defoliation occurred or was recorded between 1991 and 1995 in Saskatchewan (Cerezke and Gates 1992, Cerezke and Gates 1993, Hogg and Schwarz 1999).

Due to low wood volumes and scattered softwood distribution, the forest industry had not focused much attention on the Bronson Forest. However, with the increased demand for aspen fibre feedstock for the Millar Western BCTMP Mill, this area is now being viewed at as a potential area for fibre. In addition to using the Bronson Forest for wood supply, the land is presently used for cattle grazing, oil and gas exploration and development, cottage development and recreation. Although third party interests are in agreement with Mistik's operating plan, they are concerned with forest decline, increased forest fire risks and grazing impacts on recently cleared aspen stands (Mistik Management 1996).

The primary objective of Mistik Management is to minimize disturbances to the ecosystem associated with forestry activity. Identifying the causes and areal extent of aspen decline allow development of landscape and site-level management approaches to address the reductions in harvestable aspen volumes. Thus, strategic silvicultural methods to rejuvenate decadent aspen ecosystems may be implemented.

2.0 ASPEN ECOLOGY AND BIOLOGY

2.1 Aspen Ecology

Trembling aspen is the most widespread tree in North America and the second most widespread tree in the world (Barry 1966). Being one of the few transcontinental trees, it ranges from sea level to 3,048 m elevation. Aspen are short-lived, disturbance-dependent, fast-growing trees. Ecologically, the species occupies an important place in forest succession, readily colonizing burns, cut-over sites and old field areas (Einspahr and Winton 1977). If a disturbance, such as fire, windstorm or logging kills most of the aspen stand, aspen will dominate most sites, regenerating profusely from the vegetative propagation of aspen suckers. Thus, most aspen stands are even-aged, dense, uniform and often more-or-less pure stands of aspen clones. Without disturbance, aspen is usually replaced within a single generation by its associates (Moss 1932, Alban et al. 1991).

Aspen trees help prevent soil erosion and allow slower growing conifers to become established and eventually overtop and replace aspen (Moss 1932, Barry and Sachs 1968). With each subsequent disturbance, the clones will continue to expand until either the roots encounter unfavourable growing conditions or the ramets encounter strong competition from other clones or other vegetation. Intergrowth of two or more clones is possible and frequently occurs (Maini and Cayford 1968, Kemperman 1977).

Although sensitive to variations in site, climate and plant communities, aspen grow om a variety of soils from stony sands to heavy clay upland soils. Low moisture and restricted nutrient levels may cause reduced growth on the droughty soils. However, aspen live longest in cool climates, on calcareous parent material and on fertile sites (Einspahr and Winton 1977, Alban et al. 1991). Although a mineral surface may be favorable for emergence; physical and chemical heterogeneity of the surface and burial may be unfavorable. The inability of the seedling roots to penetrate shallow layers of soil may be attributed to weak turgor development and low nutrient reserves in the minute seeds (McDonough 1979).

The growth phase for aspen clones begins at age 25. In this phase, sucker numbers decrease to a fraction of their initial density. Stems grow larger and root volumes decrease as ramets develop new independent root systems. Assimilate storage per unit root volume increases, but total root assimilate storage per unit stand area remains stable (Sheppard and Smith 1993). After age 80, ramet density continues to decline at a very slow rate. Although root carbohydrate concentrations decrease, assimilate storage per unit area does not change. Root/shoot ratios in mature clones remain nearly stable, but gradually decline over time until overstory stems die and the cycle is reinitiated (Sheppard and Smith 1993).

Mueggler (1994) observed that the most obvious change as aspen stands age is the overall decrease in number of living trees as the trees become larger. Most mortality occurs in the first decade following stand regeneration. The first two growing seasons following fire or clearcutting suckers can exceed 12,140 ha^{-1}, but then usually decrease prematurely. This decline slows but continues as stands grow older and the tree size classes shift toward the larger diameters (Mueggler 1994). There is an inverse relationship between site quality for aspen growth and number of stems, at least in mid-age and older stands. Mueggler (1994) also found that although poorer sites produced more stems, the stems had smaller diameters than on the better sites.

Bella and De Franchesi (1980) estimated above-ground tree component dry weights for fully stocked aspen stands up to 40 years old on different sites in mixedwood forests of Alberta and Saskatchewan. They indicated that with increasing age, the proportion of leaf biomass declines while the proportion of stem wood biomass increases.

Mature stands (50 years of age) typically average 20 to 24 metres tall. Under the best conditions, a few aspen may eventually exceed 30 metres. In Eastern Canada, stands start to break up at 40 to 70 years. In the Rockies, stands sometimes persist to 200 years or more. Commercial rotations range from about 35 years in southern Michigan to about 120 years in the Rockies (Alban et al. 1991). The large size of aspen clones in Utah and Colorado indicates that seedlings were established many years ago and possibly that some clones may have been initiated during Pliocene or Miocene times, enlarging themselves asexually through many generations of ramets (Schier 1975).

2.2 Aspen Stand Decadence

Although large quantities of viable seed are produced each year by female aspen trees, successful seedlings rarely become established due to unfavourable environmental conditions and low seed viability over time (Brown 1935, Barnes 1969, Schier 1975). The reproductive success of trembling aspen can be attributed to vegetative reproduction by suckers that arise irregularly on lateral roots (Schier 1973b). These adventitious shoots develop after apical dominance is mediated by auxin (Schier 1982). Regeneration, however, is not complete with the development of new shoots; it also requires the formation of new roots. This is especially important in deteriorating stands where there has been considerable root dieback from death of overmature stems (Schier 1982). Thus, there is a growing concern in the forestry industry over the ability to regenerate stands that begin to break-up (Mueggler 1989, Bartos et al. 1991).

Breakup is usually coincident with extensive development of decay that weakens the tree and increases wind loss. Decay incidence and volume, the position and shape of rot columns and the interaction of these with site quality differs among clones, however genetics may not be as important as the micro-environment (Perala 1991). Aspen stand breakup is not yet well understood in the Boreal Region of the Prairie Provinces.

Stand breakup begins when growth slows to the point where canopy gaps caused by mortality cannot be refilled. Permanent openings in the canopy created by the death of individual stems is the first evidence of deterioration. In a relatively short time, a scattering of diseased stems is all that remains of a clone. Heightened stresses from evapotranspiration sap the vigor of the surviving trees. Pathogens of defoliating insects may also contribute to premature breakup. On many sites, deteriorating aspen clones are replaced by conifers. Dry sites often revert to rangeland dominated by shrubs, forbs and grasses. Sucker reproduction usually occurs beneath a deteriorating overstory, but often shoot numbers are insufficient to replace the mortality (Barnes 1969, Schier 1975).

In older stands, volume decline from decay is a major problem. Timing of decadence depends on inherent aspen stability and longevity and speed of the breakup process (Perala 1991). The amount and rate of decay leading to stand decline is influenced by age, site, genotype, presence of competing vegetation and browsing intensity by big game and livestock which may predispose stems and roots to attack by pathogens. Eventually, disease and reduced levels of carbohydrate reserves affect root suckering capacity. Damage to roots by livestock and wildlife, insect and disease attack and subtle environmental changes cause localized shifts in the hormone balance between root growth promoters and inhibitors that trigger sucker formation. If some roots are present and adventitious shoots are initiated and can grow into large stems, ramets will maintain a clone. Level of decay is difficult to predict and will vary since genotype may be the controlling factor in timing and rate of decline. Thus, deteriorating clones adjacent to a healthy one may occur because ramets of both probably were established at the same time

(Maini and Cayford 1968, Schier 1975, Shields and Bockheim 1981, Anderson and Evans 1996).

Sucker development may also be affected by correlative inhibition among developing suckers from auxin produced by established meristems which may inhibit development of new suckers (Eliasson 1971b, Schier 1973). In diseased overmature stems in deteriorating clones, the root system dies back because the photosynthate channeled to the roots is decreased by reduction in crown area. Sucker production continues to be generally inhibited because residual stems maintain auxin levels in the smaller root system (Farmer 1963, Schier 1975).

Aspen have periods of natural thinning which permit survival and growth. Drought encourages natural thinning but does not typically kill entire groups of trees. These waves of thinning are also attributed to the combined effects of insects and fungi (Bates et al. 1993). Pests may induce more mortality during dry periods than wet periods because the same amount of damage is more destructive when the tree is already stressed and pest invasions are often more successful when the tree is growing slowly in dry weather (Bates et al. 1993). This will be greatly altered if excessive browsing of aspen suckers prevent their growth and may even cause in-growth in the younger stands (Mueggler 1994).

Schier (1975) compared suckering capacity of deteriorating aspen clones with adjacent healthy clones. Low regeneration of deteriorating clones was unrelated to ability of roots to sucker or to root age although roots of deteriorating clones were younger than those from healthy clones. Necrotic areas in the bark of many roots of the deteriorating clones may have seriously impaired sucker formation. The number and size of necrotic areas on roots appeared to increase with root age and diameter and sucker numbers were inversely related to diameter (Schier 1975).

2.3 Aspen Reproduction

Populus is normally dioecious; however, abnormal floral organization in trembling aspen clones, comprising monoecious and polygamomonoecious stems has occurred. Aspen usually begin to produce seeds at about 10 to 15 years of age (Doucet 1989). Most flower buds are borne laterally on short shoots which terminate into foliar buds (Maini and

Cayford 1968). Root suckering is the most common mode of reproduction (Baker 1918, Maini and Cayford 1968, Kemperman 1977, Zufa 1971, Schier 1974, McDonough 1979). Sucker production increases with stocking of the parent stand and their numbers and vigor diminish with increasing density of the surviving overstory because aspen need nearly full light (Alban et al. 1991). The abundant production of suckers demonstrates that regeneration is usually no problem when an aspen stand is wiped out relatively fast. The rapid death of stems eliminates apical dominance while the original root system can still produce suckers (Schier 1975).

Baker (1918) and Maini and Horton (1966a) indicated that the rareness of seedling establishment was due to low or nonexistent germinability. However, McDonough (1979) found early production of seeds by a mature tree may yield 1.6 million seeds. Germinative capacity at seedfall usually exceeds 95% but the establishment of seedlings is rare because seedbed and microenvironment requirements for seedling establishment are narrow.

Low probability of successful seedling establishment has been attributed to several factors including a short period of seed viability and germination, as well as growth inhibitors in the seed hair (Barnes 1969, Maini and Cayford 1968, Kemperman 1977). Drought, frost, diseases, insects and competition from other vegetation also decrease their establishment. Unfavorable moisture conditions during seed dispersal on the upland sites that aspen usually inhabit and the susceptibility of seedlings to high temperatures that occur on soil surfaces blackened by fire also decrease their chances of surviving. Other factors include susceptibility of seedlings to fungal attack, adverse influence of diurnal temperature fluctuations on initial seedling growth and unfavorable chemical nature of some substrates on which seeds fall. Even good initial germination and first year survival does not ensure successful seedling establishment.

2.3.1 Germination requirements

Aspen produce abundant germinable seeds that have no dormancy, but a critical requirement for adequate soil water through germination and early seedling growth (McDonough 1979). Normal germination is substantially reduced at approximately -2.0 atm (-2 bars) and successively fewer seeds progress beyond the incipient germination stage with progressively lower soil water potentials. However, even when water supply is adequate through the first week or more, a continuing supply is required for the improved establishment that results from enlargement of the photosynthetic surface and increased capacity for water and nutrients. These limitations probably cause high mortality even under favorable field conditions.

Temperature also plays a critical role in seedling establishment (Barry 1966, Maini and Cayford 1968, McDonough 1979). Air temperature is the principal factor affecting time and duration of flowering. The wide range of temperature tolerance for germination and rapid germination rates favor large numbers of seedlings. Progressively higher temperatures become increasingly detrimental and lower temperatures near freezing are depressing, but not permanent if transferred to intermediate regimes for seedling establishment. Germination and slow growth near freezing suggest the possibility of seedling survival under an insulating snow cover. A daily mean maximum temperature exceeding 12 ^{0}C, over six days appears to be necessary for flowering of trembling aspen.

In central Alberta, natural longevity of trembling aspen and balsam poplar seeds is 2 to 4 weeks; however, the germinative capacity may be prolonged by storing seeds on calcium chloride at -5 ^{0}C. In laboratory tests, germination of freshly collected trembling aspen seed was over 95% (Maini 1966a) and laboratory tests on largetooth poplar (*Populus grandidentata*) and balsam poplar (*Populus balsamifera*) show similar germination.

2.3.2 Vegetative propagation

The processes controlling aspen reproduction by root suckering include three major factors: apical dominance, soil temperature and light available to emerging suckers (Navratil 1991). However, factors influencing sucker and root initiation of *Populus tremuloides* show there are several controls over suckering: time of year; age of the parent stand growth regulators, particularly auxins and cytokinins; root carbohydrate reserves; root size; the inherent ability of each individual clone to sucker; soil temperature; root depth; soil moisture levels; and vegetation competition. The amount of suckering also depends on the degree of stand disturbance. Stand age does not affect suckering ability, provided the stand is not breaking up because of decay. Some overmature stands may have reduced suckering ability because growth potential of aspen stands is dependent on an intact parent root system (Baker 1918, Barry 1966, Maini and Cayford 1968, Bates et al. 1993). However, Barring (1988) reported that aspen roots remain alive for a long period after disappearance of parent trees because aspen may form suckers continuously. Minimum, optimum and maximum temperature for sucker formation in a trembling aspen clone was 16, 24 and 35 ^{0}C, respectively. However, significant variation in suckering response to temperature can be found among different clones (Maini and Cayford 1968).

Vegetative propagation by rooting young suckers has several advantages. Suckers grow vigorously and behave similarly to seedlings. Stem cuttings from mature trees are affected by topophysis (a tendency of cuttings to retain characteristics of branches from which they were taken). Secondly, rooting suckers allow a fast initial propagation of a tree. Between and within species variation was observed in suckering and in rooting suckers (Zufa 1971).

2.3.3 The root system

The root system of aspen poplar is comprised of shallow, horizontally spreading lateral roots upon which are borne thinner fibrous feeder roots. Lateral roots may be within a few cm of the soil surface with the bulk of underground parts in the upper 0.6 to 1.2 m of soil (Brown 1935, Farmer 1963, Gifford 1966, Kempermann 1977, Bartos et al. 1991). Gifford (1966) found an individual aspen stem could have a widespread lateral root system, a very limited root system or no root system other than that of neighboring stems of the same clone. Although the majority of roots were concentrated in the top 1.2 m of soil; sinker roots extended to 3 m or more. Lateral spread reached as far as 8 m on single lateral roots; or the clone and interconnecting parent root lateral spread might exceed 34 m.

While the entire root system of aspen is capable of initiating suckers, vegetative shoots arise from adventitious buds on roots frequently less than 2 to 3 cm in diameter. These roots occur predominantly in the upper 60 cm of soil, and most suckering occurs where roots are 4 to 12 cm below the surface (Barry 1966, Kemperman 1977, Einspahr and Winton 1977, Bartos et al. 1991, Bates et al. 1993). One seedling can propagate itself vegetatively to form a clonal stand composed of genetically identical trees. Other types of natural suckering include occasional sprouting from stumps, roots and old groups of sprouts which have originally been root suckers (Baker 1918, Maini and Cayford 1968, Einspahr and Winton 1977). The shoots borne on the young distal portions of the root system are the most recently formed (Brown 1935). Supported by the pre-established root system, aspen suckers are capable of rapid initial growth. With time suckers will develop their own root systems but some suckers may remain interconnected for 90 years (Kemperman 1977).

The health of the intact aspen root system is vital to aspen stand development. DeByle (1964) found the aspen parent root system supplies food to suckers throughout their first summer, resulting in growth surpassing most competing vegetation. After initial development of the sucker stand, and after suckers have developed their own roots, the parent root system may still be important for the transfer of materials within each clone. Water and solutes can be translocated over long distances through the xylem of functional root connections between trembling aspen trees within a clone (Tew et al. 1969). Interconnected groups of stems may function as single units in competition with other trees and transport substances from stem to stem along diffusion and tension gradients.

Aspen suckers grow in abundance from superficial roots after fire or clearcutting kills the parent stand. Many suckers are connected through the parent root system and remain connected throughout their life. DeByle (1964) showed that these connections might remain functional for 50 years or more in bigtooth aspen clones growing on well-drained sandy soils. He also found a number of dead stumps with live root systems joined to living trees through parent roots. Tracers indicated that bigtooth aspen clones of sucker origin consist of a number of interconnected stem groups and the parent root connections among healthy trees do not decay. Tew et al. (1969) found as many as 43 stems connected on a common root system with the maximum lateral distance between a donor and a receptor tree being 16.9 m. The number of stems connected by roots was not related to site factors such as percent sand, gravel or clay in the soil, or to bulk density or to site elevation.

2.3.4 Vegetative reproduction

The sucker shoot is derived from a bud arising in the root phellogen. Vascular connection between bud and root may be made any time during the growing season (Brown 1935). Pre-existing shoot primordia also play an important role in development of adventitious shoots (suckers) from roots of trembling aspen after apical dominance mediated by auxin (Eliasson 1971a, Schier 1973) has been abolished or decreased by a disturbance. Eliasson (1971b) indicated that suckering in roots of intact aspen is prevented by auxin transported into roots from growing shoot parts. Roots of intact aspen in the field contain auxin throughout the growing season and auxin levels decrease rapidly in excised root segments (Schier 1973). Suckers developing in root cuttings may arise from newly initiated meristems developed after cuttings were made or from early primordia. Schier (1973) found gibberellins (GA_3) inhibited initiation of adventitious shoots and division of the first primordial cells; however, once primordia were developed, GA_3 stimulated shoot outgrowth.

Eliasson (1971a) found that with rooted cuttings of aspen, competition between growing shoots and roots for carbohydrates formed in photosynthesis is of importance for maintaining balance between root and shoot systems. Eliasson also found intense shoot growth might be the cause of poor root growth during shoot growth. The adverse effect of shoot growth occurs mostly with shortage of photosynthesis products. The inhibitory effect of growing shoots on root growth is due to the shoots competing with the roots for carbohydrates or other photosynthates. Therefore, a root system with surplus capacity will increase the ability of the shoot to compete for carbohydrates.

For proper establishment of an aspen sucker, development of a root system from the sucker is critical and disturbance of root growth impair sucker growth (Lyr and Hoffman 1967). Rooting of *Populus tremuloides* was influenced greatly by three factors: time of year, auxin and juvenility. Barry (1966) stated that adventitious stems in intermittent mist rooted 100% when taken from succulent, juvenile adventitious stems 2.5 to 8 cm long. Auxin treatments gave consistently higher rooting percentages than control treatments and extreme differences in rooting of hardwood cuttings is found between clones from two different latitudes (8^0 difference) possibly due to environmental and genetic factors. Rootability of aspen stem cuttings is extremely poor (Maini and Cayford 1968). Barry (1966) found time of year was the most important factor in rooting of stem cuttings. No rooting was obtained from hardwood cuttings taken in fall and winter.

In laboratory studies, good suckering establishment is dependent on optimum length of cuttings and greenhouse conditions. Optimum length of cuttings of aspen roots was 10 cm long with a diameter of 0.5 to 3.0 cm (Maini and Cayford 1968). All monthly collections of roots were satisfactory for propagation but samples from early spring were best. Baker (1918) also found that summer cutting as a rule resulted in an immediate production of sprouts and the maximum density of sprouting was greatest from spring cuttings. Relative location of the lateral root from the original ramet was not a factor in sucker production. A sand or sand-soil medium plus a nutrient solution, gave the best results. Timing of planting root cuttings was important. Lateral, freshly collected roots gave good growth of shoots and roots. However, 8 months of storage reduced viability, while 15 months of storage gave no growth. Temperature plays a significant role in sucker initiation. Aspen root cuttings 10 cm long and 1.2 to 2.5 cm thick grown in the dark in sand gave maximum incidence and growth of suckers at 23 ^{0}C, and declined below and above this temperature (Maini and Horton 1966a).

Tew (1970) found within geographic area, number and dry weight of suckers and total nonstructural carbohydrate percentage were related to date of collection and clone origin. Collection date had a significant effect on number and dry weight of suckers per cutting. Generally, seasonal trends in dry weight indicated sucker growth peaked in late summer or fall in response to carbohydrate reserve buildup (Zasada and Schier 1973). Although dry weight per cutting increased as number of suckers increased, dry weight per sucker decreased. Roots collected in midsummer had the least sucker production. Suckers on spring-collected root cuttings established independent root systems more often than those of fall cuttings (Tew 1970). Cuttings obtained in July produced fewer suckers than those gathered in spring or fall. Lack of vigor in June was attributed to low root carbohydrates, thus, spring root cuttings were depleted of root carbohydrates several days earlier than midsummer and fall cuttings. Number of suckers produced in root cuttings was more closely related to average stem diameter growth rate of the clone than to root carbohydrates. However, the time required for new suckers to deplete the reserves was related to carbohydrate levels.

2.4 Aspen Biology

2.4.1 Role of hormones

Apical dominance is expressed by the ratio of auxins to cytokinins in the roots. Auxins formed in aboveground parts of aspen suppress suckering. Cytokinins formed in roots promote suckering. Disturbance of the ratio of these hormones, for example, when the flow of auxins from aboveground parts to roots is interrupted, by cutting, burning, girdling, defoliating or wounding the roots, triggers sucker development (Navratil 1991). Schier (1975) hypothesized that in both healthy and deteriorating aspen clones, auxin produced in shoots is translocated downward into roots where it inhibits sucker formation. Deteriorating clones often fail to regenerate because auxin produced in declining crowns can still dominate the shrinking root system (Perala 1991). Interference with this auxin supply changes hormone balances in roots enabling other hormones and growth promoters such as cytokinins to initiate regeneration. Seasonal variation in number of suckers produced from root cuttings of trembling aspen clones is negatively related to the quantity of endogenous auxin in the roots when collected (Schier 1973).

Farmer (1963) found under greenhouse conditions, 94% of cuttings treated with 20 ppm indolebutyric acid (IBA) rooted, while as high as 87% of untreated aspen cuttings developed roots. Wolter (1968) found roots were initiated within 8 weeks by removing all cytokinins and substituting naphthaleneacetic acid (NAA) for 2,4-dichlorophenoxyacetic acid (2,4-D). Other auxins such as IBA, indole acetic acid (IAA) and 2,3,6-trichlorobenzoic acid (TCBA) also stimulated root formation, but were less satisfactory than NAA. Cytokinins such as kinetin or 6-benzylaminopurine (BAP) were inhibitory, and concentrations as low as 0.25 mg^{-1} prevented root formation at optimum concentrations of auxin (Wolter 1968). Hicks (1972) tested various concentrations of IAA, gibberellic acid (GA), kinetin and abscissic acid (ABA). IAA stimulated number of roots per cutting, whereas GA and kinetin inhibited root numbers. ABA had no effect on root number at the concentrations tested.

2.4.2 Clones

Aspen are among the few North American tree species that form naturally occurring multi-stemmed clones. Kempermann (1977) suggested clones in Minnesota date back to the late Pleistocene. In such cases, large clones may have had several hundred generations to expand to their current size. A clone consists of genetically identical stems which can number from a few to several thousand individual trees. The size to which individual clones expand varies within and between stands and geographic regions. To date, the largest known clones occur in the Central and Southern Rocky Mountains. The most important factors influencing clone size are number of seedlings established per unit area, site factors such as soils, competition for light and moisture, rate of spread and intergrowth of root systems, frequency of disturbance and the relative suckering and rooting ability of the clones and inherent longevity (Barnes 1969, Kemperman 1977).

The effect of clonal composition is important in nearly all biological studies of aspen stands since members of a clone are of the same genotype, and tend to perform uniformly and in a predictable manner. Clones, not individual trees, are the basic units in such stands (Zufa 1971, Barnes 1969, Kemperman 1977). The identification of aspen clones in the field is based primarily on phenological and morphological characteristics (Barnes 1969, Kemperman 1977). While occasionally only one or two characteristics are sufficient to distinguish a clone, the use of several characteristics is generally necessary to avoid bias in site quality assessments. On two sites of very different quality, the best clone on the poorer site can be nearly equal in height to the poorest clone on the better site.

Aging, and resistance to disease and insects may occur at a more rapid rate in some genotypes than others (Schier 1975) and may account for variation in clone condition. Possibly, clones with inherently poor suckering capacity are less able to reproduce during deterioration than those with high suckering capacity. There may even be genotypes in which apical control is weak or level of growth initiating factors is high so stands sucker vigorously at the least disturbance. Schier (1974) found large clonal differences in sucker production from root cuttings and in rooting of greenwood stem cuttings taken from nine Wyoming trembling aspen clones. However, there appeared to be no correlation between suckering and rooting capacity of a clone.

There is no evidence that declining clones produce seeds having lower germinability or seedlings with inferior growth (McDonough 1979). Any physiological basis for clone decline appears unrelated to factors that control vigor of seed germination and early growth. Declining clones may produce fewer seeds per unit of photosynthetic surface and a smaller total number of seeds but probably have about equal potential for contributing to seedling establishment as non-declining clones.

Clonal structure affects aspen mean annual shoot growth, shoot weight, mean size of parent roots that give rise to suckers, levels of root carbohydrate reserves and time of leaf flushing in a given clone (Barnes 1969, Einspahr and Winton 1977, Kemperman 1977, Schier 1982, Bates et al. 1993). Schier and Johnston (1971) found that differences in TNC among clones appeared genetic, with age and site additional factors causing differences among areas. Differences in root-carbohydrates among areas are probably due to site factors and age in addition to clonal variation. Immature clones had more abundant carbohydrate reserves than mature clones. Einspahr et al. (1963) found fiber length and strength, tree and crown volume, leaf size and shape and between-clone pulp yield to be under genetic influence.

Aspen trees are known to exhibit great phenotypic variability due to clonal growth habit. The interaction of genotype and environment causes differences in phenotypic expression (Barnes 1969). The influence of environmental factors may have a greater effect on the success and development of hybrid poplar clone trees than the initial size of planting stock. Competition normally exerts strong selection pressure between the genotypes of most forest tree species thus reducing the amount of variability of the species. In aspen, however, competition is often between suckers within a clone and not between clones (Barnes 1969, Kemperman 1977).

2.4.3 Total nonstructural carbohydrates

Amount of total non-structural carbohydrates (TNC) stored in roots are important in aspen regeneration (Schier and Zasada 1973). Carbohydrate reserves in the parent root fuel bud initiation and shoot growth untii the shoot emerges and can manufacture photosynthates. Inadequate carbohydrate reserves do not significantly limit number of suckers initiated, but do limit those that reach the soil surface (Perala 1991). Schier and Johnston (1971) found that although sugars are necessary for bud initiation, number of suckers were not a function of carbohydrate status but of hormone levels and ratios.

Alexander (1995) found that damage to aspen caused from drought, tent caterpillars and grazing affected the roots in that nonstructural carbohydrate reserves stored in the roots were too depleted to refoliate. More importantly, it would appear that the stresses that caused mortality to a large portion of the aspen canopy also resulted in substantial mortality of the shallow roots, which normally produce new aspen suckers.

Schier and Zasada (1973) found that TNC did not appear to affect number of suckers produced from root cuttings. However, TNC concentrations above or below a certain range may significantly affect sucker production. A substantial decrease in transport of photosynthate to roots (as after repeated defoliation) may reduce root carbohydrates to levels that significantly affect suckering. Limiting levels of reserves can also occur in roots of overmature trees as suggested by scarcity of vegetative reproduction in understocked, decadent aspen clones.

The decline in carbohydrates in aspen roots as a consequence of shoot production and the contribution of new shoots to root carbohydrate levels was investigated by FitzGerald (1983). Shoot growth in darkness was greater from roots with midseason clipping than clipping later in the season, suggesting some carbohydrate replenishment had taken place. Carbohydrate concentration in roots placed in three light regimes declined by approximately the same proportion over the 8 weeks of the experiment, but total weight of shoots was greater in light than in darkness, which suggests newly synthesized carbohydrates were retained in tops for growth. While shoots in normal and shade quality light were not phenologically different, shoots in normal light had greater leaf development than shoots in shade light and were heavier, possibly as a consequence of greater leaf development leading to greater net photosynthesis. Because sucker growth in darkness is affected by root carbohydrate concentration, number of suckers appearing would be positively correlated with levels of reserve carbohydrates. However, an increase in sucker number may cause an increase in competition among suckers for the limited TNC which might result in a decrease of dry weight per sucker (Schier and Zasada 1973).

Aspen bark produces sufficient photosynthate and starch to contribute to growth. Bark contains chlorophyll and is photosynthetically active. Chlorophyll pigments are more abundant in bark during the early growing season than in leaves, but become more abundant in leaves during the summer. The continuous trembling movement of the leaves which reflects light from leaf to leaf and into the branch structure could help contribute to corticular photosynthesis in stems (Barry 1966).

Season influences carbohydrate availability in aspen roots. Root carbohydrates are generally lowest in early summer immediately after leaf flush, then gradually increase through the growing season. Tew (1967) found sugars and starch were lowest after leaf flush in spring. Maximum aspen regeneration usually occurs following winter harvesting when root carbohydrate levels are highest (Schier and Zasada 1973). However, this seasonal relationship may not apply to northern boreal forests where soil temperature is more limiting (Bates et al. 1993). During spring and early summer, root carbohydrate reserves are relatively low, probably because a high proportion of photosynthate is being channeled to vigorous sinks in developing shoots and leaves. The increase in root TNC late in July can be attributed to tapering of shoot elongation and leaf expansion and to translocation of a larger quantity of assimilates to roots. Root TNC peaks in September, then decreases as photosynthesis declines in senescent leaves (Tew 1970, Schier and Zasada 1973). Root carbohydrates would be similar among stems within a clone, but differences could be expected between clones because of species genetic variability. Cycling of root carbohydrate reserves would be different because depletion of soluble sugar and starch during leaf flush would occur on different dates (Tew 1970). The change in total sugars was not as great during the season as for starch. Starch is more important as a reserve substance being approximately four times as abundant as sugar. The ratio of starch to sugar changes throughout the season, but differs for aspen clones. Tew (1970) found root carbohydrate reserves (soluble sugars plus starch) increased more than 5% of total dry mass from June to September in one growing season. Starch was approximately four times more abundant than soluble sugar. Both were lowest after leaf flush in spring.

3.0 ASPEN RESPONSE TO STRESS

3.1 Insects and Disease

Insects and disease have a significant effect on aspen stand productivity (Alban et al. 1991). For Canada these losses may equal the annual losses to forest fires. Although aspen are damaged by many diseases and insect pests throughout the rotation of a stand, only a few of them seriously injure or kill trees. Defoliated aspen can be predisposed to other damaging agents. There are a number of insects and diseases that affect juvenile aspen, but, the greatest damage and volume loss occurs in the older age classes.

Generally, when a clone is propagated vegetatively for a long time it becomes infected with viruses (Schier 1975). If vegetative parts of that plant are used for propagation the progeny will also be infected. This persistence of viruses means vegetatively propagated plants are continually affected by all the viruses they have ever contracted. Of all pathogens, viruses are the most likely to cause degeneration of clones with age, but systemic infection by fungi and bacteria might also be important.

Wood-boring insects can degrade wood, provide entry courts for fungi and bacteria, and weaken trees, subjecting them to wind breakage (Alban et al. 1991). The most damaging wood borer is the poplar borer (*Saperda calcarata*) which extensively tunnels in the cambium of infested trees. A number of wood-boring insects and insects that oviposit on aspen provide wounds that increase infection of aspen by Hypoxylon canker (*Hypoxylon mammatum*).

Leaf diseases caused by fungal pathogens such as *Marssonina*, *Septoria*, *Cibornia*, *Melampsora*, and *Venturia* species are widespread throughout the range of aspen (Alban et al. 1991). Except for shoot blight caused by *Venturia macularis* in young sucker stands, these diseases are of minor importance.

The greatest impact on aspen is a reduction in wood volume and quality caused by canker and decay fungi (Alban et al. 1991). *Phellinus tremulae*, the cause of white trunk rot, is the predominant decay organism that affects aspen in the Lake States. The most common canker disease resulting in stem breakage and tree death is caused by the fungus *Hypoxylon mammatum*. White trunk rot and Hypoxylon canker often limit the rotation age of aspen in the Lake States. Cankers caused by *Nectria galligena* or *Ceratocytis fimbriata* can also lower wood quality and weaken stems.

Massive defoliation over several years by forest tent caterpillars can drastically affect stem-wood production even when trees produce a second crop of foliage (Still 1981). The cumulative effect of years of defoliation can be serious. Other insect species, contributing significantly to aspen defoliation are aspen tortrix (*Choristoneura conflicta* Wlk.), early aspen leaf curler(*Pseudexentera oregonana* Wishm.), and spruce budworm, (*Operophtera bruceata* Hlst.).

Results of a study by Churchill et al. (1964) on the effects of aspen defoliation by the forest tent caterpillar in Minnesota indicated growth is significantly reduced one year beyond cessation of defoliation in stands where three successive heavy defoliations occurred. Growth increased significantly the third year after defoliation in aspen stands. Recovery of growth after cessation of defoliation appeared to take one growing season in the most severe cases. During the second growing season after cessation of defoliation there was no apparent effect of defoliation upon basal area growth.

Insects may sometimes aid in the reproduction of aspen. Schier (1975) found insect outbreaks may cause development of suckers in the understory of mature aspen. Defoliation of aspen by the large aspen tortrix in the Alaska interior from 1965 to 1968 resulted in suckering in some clones before the growth of new leaves.

3.2 Fire

Before development of a fire suppression program in the Intermountain region, wildfires played an important role in aspen ecology. Frequent fires perpetuated the species because aspen is especially adapted to reproducing after its aboveground parts have been killed (Barnes 1969, Schier 1975, Kay 1997). Aspen trees are extremely sensitive to fire because of their thin bark. Most stems are killed by fire, which stimulates suckering from the roots (Hungerford 1988). When fire and other major disturbances are excluded, the ramets of a clone become mature in 80 to 100 years, then show a rapid decline in vigor and increasing susceptibility to disease and insects with advancing age (Moss 1932, Schier 1975, Kay 1997). Horton and Hopkins (1966) found a moderate degree of burning that kills the tree canopy and undergrowth and eliminates litter and part of the duff will stimulate suckering. Lower intensities of burning will produce less dense and vigorous suckers. They also found insulation of half an inch of fine sand sufficient to protect roots against a few minutes of sustained high surface temperatures and protection would increase directly with increasing soil moisture. Intense burning results in less vigorous suckers than light burning and does not result in reduced suckering. However, moderate burning maximized suckering.

Fire also affects aspen suckering depending on time of year. Maini and Horton (1966b) found burning stimulated aspen suckering at midsummer and sucker density was generally lower when burned in the fall than in mid-summer. High suckering response at midsummer appeared to be related to relatively more intense disturbance occurring in the moderate burn treatments as well as in cut plots of the light and moderate scarification treatment.

The fire history of the stand is one of the most important factors affecting aspen stand quality (Stoeckeler 1948). Aspen quality declines are not obvious 10 to 20 years after burning due to rapid rotting leading to the disappearance of badly damaged trees and rapid healing and apparent recovery of trees less severely burned. Fire is a great aid to aspen establishment on lands formerly occupied by conifer or northern hardwoods. However, burning after aspen is established has serious consequences, reducing growth, causing fire scars that lead to decay, reducing stand densities and volume and causing vegetational retrogression and early stagnation and breakup of the stand. Fire consumes all or parts of litter layers, destroying many fine rootlets in the organic layer. Burning the organic layers reduces nitrogen available for plant growth and decreases infiltration and water holding capacity. Pritchett and Wells (unpublished) found increases in soil temperature and moisture after aspen canopy removal. In addition, the mixing of litter and debris with mineral soil increased biological activity and nutrient mobilization. Absence of a nutrient sink during initial stages of plantation establishment, may therefore result in nutrient losses and site degradation. Fires also open the stand to invasion by competing weeds and grasses.

Fire increases soil temperature, thus affecting formation and development of suckers. Cytokinn production by roots is increased with warmer temperatures and may cause degradation of auxin. Thus, temperatures may influence the cytokinin-to-auxin ratio (Wolter 1968). Bartos et al. (1991) found sites burned in spring produced more than twice as many suckers as those burned in fall. Although abundant aspen suckers often arise following burning or clearcutting of aspen stands, up to 120,000 ha^{-1} in some cases, sucker mortality and deformity from various causes in succeeding years in usually high.

Schier and Campbell (1978) studied rooted suckers after a burn in Wyoming and clearcutting in Utah to obtain depth and diameter of parent roots producing suckers, occurrence of new roots and effects of burn intensity on suckering. Compared to parent roots in Lake States aspen, those of western aspen were deeper and slightly larger. Clonal differences were found in the depth and diameter of parent roots and in the ability to initiate new roots around the base of suckers. Few suckers had well-developed independent root systems. A high burn intensity increased the depth from where suckers were initiated.

Hungerford (1988) found monthly average soil temperatures in a burned aspen stand ranged from 13 to 17 ^{0}C higher than in an unburned stand at depths to 30 cm for a site in southeastern Idaho. From June through August the first year after burning, soil temperatures were significantly different at all depths in burned and unburned stands (Hungerford 1988). Rapid regrowth of understory vegetation and emergence of aspen suckers shaded the burned treatment in years two and three, reducing temperatures to the level of the control. Following burning, soil temperatures at depths to 10 cm were favorable for sucker initiation.

Temperatures lethal to root tissue were attained only close to the surface in very dry soil under sustained high surface heating (Horton and Hopkins 1966). A moderate degree of burning that kills the tree canopy and undergrowth, eliminates litter and reduces duff, will most effectively stimulate suckering. Lesser intensities of burning will produce less dense and vigorous suckers.

3.3 Grazing

Grazing can alter plant community succession and therefore change potential development of ecosystems. These changes would be dictated by factors such as plant community composition and resiliency of individual species to grazing (Beck et al. 1996). Baker (1918) found sheep were responsible for severe damage to aspen reproduction regardless of variety and abundance of forage. Injury and mortality of sprouts was roughly proportional to grazing intensity. Three years of successive moderate grazing by sheep on clear-cut lands usually resulted in destruction of the entire stand of suckers. Cattle, however, consumed some leaves, young twigs and branches, but injury was never severe except where lands were overstocked (Baker 1918). Where cattle grazing was moderate and the stock properly distributed, reproduction was never browsed to the extent of endangering the establishment of a commercial stand. Beck et al. (1996) demonstrated that historical sheep grazing coupled with more recent increases in elk populations are probably the most dominant influences currently controlling aspen stand regeneration.

Weatherill and Keith (1969) studied an aspen forest near Rochester, Alberta to evaluate the effect of grazing by domestic livestock. Number of trees was significantly greater under grazing than no grazing and heavy grazing. There was no difference with individual herbivore species among grazing intensities and total trees were not correlated with grazing. Kay (1997) found aspen protected from ungulates such as elk (*Cervus elaphus*) in Kootenay and Yoho National Parks successfully regenerated without disturbance and developed multi-age structures. On grazed areas, forest succession differed with number of elk.

3.4 Chemicals

Manipulation of aspen ecosystems by spraying has been used to set back succession and to perpetuate the aspen community (Bartos and Harniss 1990). Usually these treatments are done under conditions of use by livestock and/or wild ungulates. Use of chemical methods in forestry has not been accepted by the public because of the large areas of forest that will be cut and the unknown long-term effects of chemical herbicides on native vegetation and wildlife. However, the use of chemicals for propagation of aspen may be beneficial. Harniss and Bartos (1985) found aspen stands sprayed with herbicides had a higher number of aspen suckers than adjacent unsprayed stands. Herbicides are most effective for stimulating aspen regeneration and conifer site preparation when applied soon after aspen reaches full leaf stage (Harniss and Bartos 1985).

Bartos and Harniss (1990) evaluated the effects of 2,4-D, wildlife and cattle on plant succession. Aspen overstory was killed as a result of spraying, with sufficient reproduction occurring to restock the stand. However, animal use drastically altered aspen reproduction and understory production. Total protection favored desirable understory species while the open area had fewer desirable species. Three years after spraying, the aspen overstory was uniformly killed across the treated area. Aspen subsequently reestablished itself where it was totally protected from animal use. Eventually the game and livestock exclosures had the same number of suckers after 19 years, but they were distributed differently. The differences within the two exclosures was attributed to clonal pattern and soil differences (Bartos and Harniss 1990) or a combination of the two.

3.5 Climatic Factors

In a study in the aspen parkland of Saskatchewan, Hogg and Hurdle (1995) indicated that in a dry climate (P – PET = - 13 cm), aspen had a strongly stunted growth form and a reduced biomass productivity. They found radial growth was reduced by up to 90% during severe drought periods.

Cold temperatures may also affect aspen. In 1958 considerable injury occurred to aspen growing in Manitoba as a result of unusual weather. A severe frost in late April, preceded by temperatures of above 27 ^{0}C, and lighter frosts that occurred periodically throughout May and June, caused extensive injury to buds and foliage of coniferous and deciduous trees (Cayford et al. 1959). Frost affected bud development to various extents. The amount of bud-killing depended on degree of bud development. Trees with light bud injury developed normal foliage. Where bud mortality was severe, initial aspen foliage consisted of widely scattered clusters of abnormally large leaves. Some trees completely foliated at a later date, while others produced no additional foliage (Cayford et al. 1959).

Maini and Horton (1966a) found temperature plays a significant role in sucker initiation. Maximum incidence and growth of suckers was at 23 °C, declining gradually below and above this temperature. They found suckers first appeared on the 8th day at 31 °C, the 14th day at 35 and 23 °C. Sucker emergence was progressively delayed with lower temperatures; appearing on the 16th day at 18 °C and the 26th day at 14 °C. Temperatures below 16 and near 35 °C may inhibit full use of potential energy from food material stored in roots. Growth of different suckers at extreme temperatures varied less than at intermediate temperatures possibly due to greater competition for limited nutrient reserves in the roots.

Zasada and Schier (1973) also found temperature had a significant effect on number and dry weight of suckers. Sucker development was poor at (maximum/minimum °C) 20/10 °C. At 25/15 °C and 30/20 °C only differences in dry weight were significant. Development as determined by dry weight and time elapsed before appearance of the first suckers improved at 30/20 °C. However, clones responded differently to temperature and the optimum temperature for sucker production of a single clone varied with time of collection. The greatest number and growth of suckers occurred at 24 °C. Apparently temperatures higher than 23 °C are inhibitory if held constant. Although metabolic processes are slower at lower temperatures (20/10 °C), suckers will develop.

Growth intensity of roots depends not only on temperature, but on soil moisture and shoot activity (carbohydrate supply), which are influenced by light, air temperature, humidity and root activity (Lyr and Hoffmann 1967). A long period of higher soil temperature can lead to a negative carbohydrate balance because of enhanced root respiration. The range of temperatures in which growth is possible lies between 2 and 35 °C. Physiological optimum values lie above 20 °C.

4.0 RESEARCH OBJECTIVES AND HYPOTHESES

4.1 Research Objectives

The majority of aspen stands in the West are aging (Mueggler 1989, Bartos et al. 1991). Resource managers frequently are concerned about regenerating these stands to maintain aspen as part of the wildland mosaic (Schier 1975, Bartos et al. 1991). Although the general pattern of aspen deterioration has been described, it remains unclear why the production of root suckers is often insufficient to replace overstory mortality in decadent aspen clones (Schier 1975). The importance of root carbohydrate reserves (soluble sugar plus starch) in the vegetative reproduction of aspen has been suggested, but little quantitative information is available (Tew 1970). There is still some concern whether carbohydrate levels are enough to sustain aspen rejuvenation, and there is still the question as to whether roots of declining aspen stands behave similar to those in non-declining and mixedwood stands.

The objectives of this research were to assess declining and non-declining aspen stands and mixedwood stands to determine total nonstructural carbohydrates, suckering capacity and sucker development of roots collected at different points in the growing season. A secondary objective was to characterize vegetation in the sampling areas of the Bronson Forest.

4.2 Research Hypotheses

Suckering capacity of roots is dependent on the degree of decline, time of year at which the roots were collected and the degree of total-nonstructural carbohydrates (CHO) in trembling aspen and mixedwood stands. It was expected that suckering capacity would be highest in no-decline and mixedwood stands because these would have the highest amounts of live roots and would also be the healthiest. The root system would be intact, thus photosynthates would be transported across the root system more efficiently. Carbohydrates should be lowest in heavy decline stands because less photosynthate would be channeled to the roots and more CHO would be required for tree maintenance.

Carbohydrates were expected to be highest in fall for all treatments because there should be CHO stored for the dormancy period. In early summer a seasonal low should be reached following spring leafing and leader growth which would require large amounts of photosynthate. During this period of low carbohydrate, few suckers would be expected. As carbohydrate reserves increase in the fall, more suckers would be expected. Suckers growing from different treatments would be expected to respond the same, i.e. length of shoot, number of leaves, and stage of growth. However, there would likely be fewer shoots per cutting for the heavy decline treatments. The time for sucker initiation was expected to be the same for all treatments, however, because there would be less CHO in the heavy decline sites, heavy decline shoots would be expected to die sooner since the carbohydrates would be depleted sooner.

The amount of understory vegetation was expected to be affectd by the degree of decline. The understory vegetation would be the highest for the heavy decline area because the percent of open canopy would be the highest. This would probably also mean the number of species would be highest for the heavy decline because there is more light reaching the forest floor and more plants would have the opportunity to compete for light.

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II SUCKERING CAPACITY, TOTAL NONSTRUCTURAL CARBOHYDRATES AND SUCKER DEVELOPMENT FROM DECLINING ASPEN AND MIXEDWOOD STANDS

1.0 INTRODUCTION

Trembling aspen (*Populus tremuloides* Michx.) is a fast growing, early successional dominant species of many forests throughout North America (Bates et al. 1993). Canada has an estimated volume of 4,000,000,000 m^3 of trembling aspen that has become a major forest resource in the prairie provinces over the last half of the century (Peterson and Peterson 1992). Although large quantities of viable seed are produced each year by female aspen, successful seedlings rarely become established due to unfavourable environmental conditions (Brown 1935, McDonough 1979, Kay 1997). The reproductive success of trembling aspen can be attributed to vegetative reproduction by suckers that arise irregularly on lateral roots (Schier 1973a). Regeneration requires the development of new shoots and the formation of new roots. This is especially important in deteriorating stands where there may be considerable root dieback as a result of death of overmature stems (Schier 1982). There is a growing concern in the forestry industry over the ability to regenerate stands that begin to break-up and decay (Mueggler 1989, Bartos et al. 1991).

Rate of decline in aspen stands depends on site, genotype, presence of competing vegetation and browsing intensity by big game and livestock (Schier and Campbell 1980, Kay 1997). Reduced clone vigor predisposes stems and roots to attack by pathogens. At some stage, disease and reduced levels of carbohydrate reserves affect suckering capacity of roots. Damage to roots causes localized shifts in the hormone balance between growth promoters and inhibitors in roots, which trigger sucker formation (Schier 1975).

The health of the intact aspen root system is essential to aspen stand development. DeByle (1964) found the aspen parent root system supplies energy to suckers throughout their first summer, resulting in growth surpassing that of most competing vegetation. After initial development of the sucker stand and after the suckers have developed their own roots, the parent root system may still be important for transfer of materials within each clone. Water and solutes can be translocated over long distances through the xylem of functional root connections between trees within a clone (Tew et al. 1969).

Roots are often at a disadvantage when a limited supply of photosynthate is being allocated. The rate of translocation and growth of part of the root system can be increased experimentally if the internal competition among roots is reduced (Eliasson 1971a, Wardlaw 1990). Schier and Zasada (1973) found total nonstructural carbohydrates (TNC) did not affect number of suckers produced from root cuttings. However, if repeated defoliation occurs, a substantial decrease in transport of photosynthate to roots may reduce root carbohydrates to levels that significantly affect shoot outgrowth. Limiting levels of reserves often occur in roots of overmature trees as indicated by scarcity of vegetative reproduction in understocked, decadent aspen clones.

Season influences carbohydrate availability in aspen roots. Root carbohydrates are generally lowest in early spring after leaf flush and increase through the growing season with carbohydrates reaching a peak in September (Tew 1967, Tew 1970, Schier and Zasada 1973). Schier and Zasada (1973) found early summer root carbohydrate reserves were relatively low because a high proportion of photosynthate was being channeled to vigorous sinks in developing shoots and leaves. This trend in TNC was also observed by Hogg and Lieffers (1991) in Marsh Reed Grass (*Calamagrostis canadensis*) rhizomes. TNC reached seasonal minimums between mid May and June. TNC levels increased substantially after June with the maximum reached in October. Adams et al. (1986) found starch concentrations in loblolly pine (*Pinus taeda* L.) showed seasonal fluctuations, with levels generally highest in early spring prior to budbreak and root starch concentrations lowest in autumn. Landhausser and Lieffers (1997) found in boreal shrub species such as Beaked Hazelnut (*Corylus cornuta*), Red Osier Dogwood (*Cornus stolonifera*), Prickly Rose (*Rosa acicularis*) and Low-bush Cranberry (*Viburnum edule*), sprouting was most vigorous when the TNC reserves were highest in August and September. TNC were lowest after bud flush but there was a rapid accumulation of TNC in rhizomes within the first month of the growing season. However, in mid-growing season the allocation of photosynthates to rhizomes was decreased because photosynthates were used for growth, wood accumulation or reproductive effort.

Generally sucker growth from root cuttings is lowest in midsummer and peaks in fall in response to carbohydrate reserve buildup (Tew 1970, Zasada and Schier 1973). As suckers from root cuttings grow, dry weight per sucker decreases as number of suckers per cutting increases. However, other factors may affect sucker production such as auxin in the root bark when collected (Schier 1973b), clone of origin, time of collection (Schier and Johnston 1971, Schier 1974) and establishing meristems (Schier 1975).

Causes of low root sucker production in decadent aspen clones are unclear. Whether carbohydrate levels can sustain aspen rejuvenation and whether roots of declining aspen stands behave similarly to those in non-declining and mixedwood stands is unknown. The objectives of this research were to assess declining and non-declining aspen stands and mixedwood stands to determine total nonstructural carbohydrates, suckering capacity and sucker development of roots collected at different points in the growing season.

2.0 MATERIALS AND METHODS

2.1 Study Site

The Bronson Forest, a distinct timber supply area, lies southwest of Meadow Lake and is within 1 km of Highway 26 between St. Walburg and Loon Lake, Saskatchewan (53^0 45 to 53^0 51'N and 109 08'W). The Forest Reserve is part of the Thickwood Hills Upland Section containing the Bronson Meadow Lake Hills Subsection, which forms the only physiographic division in the Forest Reserve (Rostad and Ellis 1972). The Upland is basically a wooded rolling morainal plain with gently to strongly rolling topography. Its elevation varies from 549 to 732 m. The topography in the east is mainly undulating to rolling while that in the west is hilly. The soils are mainly developed on glacial till and glacial-fluvial deposits.

2.1.1 Climate

The climate of the area is continental, characterized by moderately warm, short summers with wide variation in day and night temperatures, long cold winters and moderately low annual precipitation (Rostad and Ellis 1972). The climate of the Forest Reserve is classified as subhumid. Its northern boundary has an 80-day frost free period. Summers are cool with mean daily July temperatures between 16 and 19 ^{0}C and winters are cold with mean daily January temperatures between -15 and -20 ^{0}C. Mean annual precipitation ranges from 36 and 41 cm of which 25 to 30 cm fall between May and September.

2.1.2 Soils

The Loon River Soil Association consists chiefly of Luvisolic soils developed on medium to moderately fine, textured, weakly to moderately calcareous unsorted glacial till deposits (Rostad and Ellis 1972). Its texture ranges from heavy loam and sandy clay loam to clay loam.

2.1.3 Vegetation

The Forest Reserve is located within the Boreal Forest Region. The tree species are mainly a mixture of deciduous and coniferous types and include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white spruce (*Picea glauca* (Moench) Voss). The most common shrubs found in the sites were alder (*Alnus* sp. Mill.), rose (*Rosa* sp. L.), willow (*Salix* sp. L.), low-bush cranberry (*Viburnum edule* Raf.) and honeysuckle (*Lonicera* sp. L.). Low growing plants include grasses and forbs such as fireweed (*Epilobium angustifolium* L.), bunchberry (*Cornus canadensis* L.), marsh reed grass (*Calamagrostis canadensis* Beauv.), wild strawberry (*Fragaria virginiania* Duchesne) and wild sarsaparilla (*Aralia nudicaulis* L.).

2.2 Treatments

In summer 1995, based on crown dieback, three aspen decline and three mixedwood areas were identified by aerial survey, verified by ground reconnaissance and delineated within the Bronson Forest by Stan Navratil (Canadian Forest Service (CFS) presently with SIT.COR, Hinton AB), Roger Nesdoly (Mistik Management) and Rick Hurdle (Canadian Forest Service). Areas 1, 2 and 3 were located in pure trembling aspen stands. In each area, there were three clones selected by Stan Navratil based on visually assessed average percent crown dieback on an individual tree basis. Areas 4, 5 and 6 were located in mixedwood stands of non-declining aspen, balsam poplar, white spruce and other species. A circular plot with a radius of 10 m was established in each of the aspen decline classes and in each mixedwood area.

In each of the three trembling aspen decline areas, three treatment classes were based on health and vigor of the crown (crown dieback) (12 sampling sites).

1. No decline or minimal sign of decline; mean crown dieback of 0 to 15%.
2. Light to intermediate level of decline; mean crown dieback of 20 to 40%.
3. Heavy decline with high mortality; mean crown dieback of $\geq$ 45%.
4. Mixedwood

2.3 Field Sampling

All trees in the 12 sites were numbered with aluminum tags by Stan Navratil, Roger Nesdoly and Rick Hurdle. For each tree species, diameter at 1.3 m height and percentage crown dieback were recorded. In each site, four aspen trees were randomly selected. One 1 m^2 sample plot was randomly located 1 m from each of the four trees. Root sampling was restricted to lateral trembling aspen, balsam poplar and spruce roots located within 0.2 m of the soil surface. The sampled roots were bagged in plastic with a moisture supply from a water soaked cloth to eliminate drying. The roots were stored at 2 °C prior to initiation of the bioassay. The dates of sampling were October 23 to 26, 1995, May 22 to 24, July 2 and 3 and September 27 and 28, 1996. The experimental design was a randomized incomplete block with 6 blocks (Figure A.3).

2.4 Growth Chamber Bioassay

Roots were sorted into balsam poplar, trembling aspen and white spruce. Total tree root volume was determined for each 1 m^2 plot by measuring total length and diameter of all roots. Roots were further sorted into viable and non-viable categories. Non-viable roots were those with extensive lesions, extensive necrotic areas, rotting and mechanical damage from collection. Two cm cuttings were taken from each viable root cutting of diameter 0.5 to 2.0 cm planted and frozen at -20 ^{0}C for TNC analysis.

Only trembling aspen roots 0.5 to 2 cm in diameter were planted. These roots were cut into 10 cm segments and planted horizontally in 38 x 51 x 13 cm plastic containers of autoclaved sand and covered with styrofoam chips. Roots were planted in approximately 9 cm of sand with 4 cm of sand below and 5 cm of sand above the root. The experimental design was a randomized complete block with three blocks (Figure A.2).

The bioassay was conducted under controlled environmental conditions for approximately eight weeks. The temperature of the growth chamber was regulated at approximately 20 ^{0}C day and 15 ^{0}C at night, under no light conditions. Soil water was maintained at field capacity. To determine field capacity, sand was saturated and drained for 48 hours, then oven-dried. The wet and dry weights were used to determine field capacity. All containers were weighed weekly and water added to maintain field capacity.

The number of suckers emerging and dying were counted every second to third day until the increase in sucker number per block slowed to 2 to 3 suckers. Then counts were made once a week. Rate of development of individual suckers was assessed weekly by counting number of suckers and leaves per sucker and measuring sucker height. Sucker stage of development was also recorded as follows. Stage 1: sucker emerged and sucker apex had no development (white-tipped); Stage 2: sucker apex has begun to develop (sucker apex was yellow-tipped); Stage 3: sucker apex had turned green (first sign of leaf development); Stage 4: sucker apex had developed first leaves; Stage 5: leaves are on the sucker; Stage 6: sucker is dead. A smaller parallel trial was conducted as above in the light to assess growth response of suckers under light conditions (Appendix B).

Treatments were harvested in the order of planting and took approximately four days on average to complete. The number of suckers per root cutting were counted and their length and basal diameter measured. The length and diameter of the branches of the suckers, numbers of leaves per sucker and sucker health were determined. If roots were present on a sucker their diameter and length were measured. Leaf area indices of all leaves were measured with a leaf area metre machine (model 3100) on a cm^2 basis to see if roots with more TNC have larger leaf areas.

For each root cutting, diameter and length of new root development were measured. Callus development and health of the cuttings were assessed. Health of the root cuttings were assessed by noting rotting or rot spots and color. All suckers and cuttings were dried at 60 °C for 48 hours. Roots and suckers were weighed.

2.5 Carbohydrate Analyses

Total non-structural carbohydrates were determined using acid hydrolysis and anthrone as a color indicator according to Rose et al. (1991). Carbohydrate samples from all 4 sampling times were analyzed at the same time and randomized to avoid differences in sampling errors. Due to the variability and instability of anthrone, phenolsulphuric acid was used to determine sugar content.

2.5.1 Freezing and grinding

Roots were stored in a freezer at -20 to -30 ^{0}C. The roots were crushed under a machine press then ground in a coffee grinder. Subsamples of the ground aspen root sample were put in labeled vials. The roots were frozen at -70 ^{0}C for 24 hours, then ground in a 40 mesh screen in a Wiley Mill.

2.5.2 Extraction

Approximately 0.05 g of root sample from each vial was weighed into a Corex tube then transferred to a mortar with equal volumes of washed sand. The sample was ground into powder and transferred back into the Corex tube. The pestle and mortar were washed with 6 ml of ice-cold methanol, chloroform and water (MCW) (12:5:3) and decanted into a tube. The mortar was washed twice more with 2 ml each of ice-cold MCW and decanted into the tube. The samples were held in ice until all samples were done, then vortexed, left to stand for 10 minutes and vortexed again. The samples were centrifuged at 100% for 10 minutes. The supernatant was decanted into 80 mL test tubes. The pellet was resuspended in 5 ml ice-cold MCW and vortexed again. The samples were then put in ice for 10 minutes, vortexed and spinned as before. The extraction was repeated once more, combining supernatants (decant, resuspend, stand, spin, decant). The pellet was oven dried overnight at 55 ^{0}C. The supernatant was covered and refrigerated at 4 ^{0}C to store over night until the sugar analysis was performed.

2.5.3 Starch assay

The dried starch pellets from the extracted root samples were solubilized by adding 2 ml of 0.1N sodium hydroxide (NaOH) and vortexed. The test tubes were capped with a marble and incubated at 50 ^{0}C for 30 minutes with occasional swirling. The pellets were neutralized to pH 5.1 by adding 2.5 ml of 0.1N acetic acid (HOAc). The enzyme solution was prepared by adding 4.8 ul amyloglucosidase, 22 ul amylase and 973.2 ul sodium acetate (NaOAc) buffer for each 1 ml of enzyme solution needed. Half a ml of digest enzyme solution was added to each sample tube and vortexed. The test tube was capped with a marble and digested at 50 ^{0}C for 24 hours. After incubation, samples were vortexed and centrifuged at 100% for 10 minutes. A 200 ul aliquot was removed from each test tube to a fresh tube for the assay. A 200 ul buffer blank and 10 mg dl^{-1} glucose standards were prepared. 2.0 ml PGO enzyme-dianisidine solution was added to each test tube. Samples were then developed at 22 °C for 45 minutes and the absorbance read at 450 nm.

2.5.4 Sugar assay

To the crude sugar solution, 7.5 ml deionized water was added and vortexed thoroughly. The sample was centrifuged at 100% for 10 minutes. The upper aqueous phase was aspirated off, put into a clean test tube and stored covered in a refrigerator at 4 ^{0}C. The organic phase was dumped into a waste jar in the fume hood. The methanol was evaporated off in a rotary evaporator (40 ^{0}C). The solution was made up to 25 ml in a graduated cylinder with deionized water and mixed well.

2.5.5 Anthrone assay

Two ml of anthrone reagent were added to each test tube and chilled in an ice bath. In a third set of test tubes, 2 ml of sample was placed and 1 ml $Ba(OH)_2$ was added and vortexed. 1 ml $ZnSO_4$ was added to the tubes and vortexed thoroughly. To settle the precipitate, test tubes were centrifuged at 30% for 10 minutes. To each anthrone tube, 0.1 ml of deproteinized supernatant was added. The tubes were vortexed and developed at 90 ^{0}C for no longer than 15 minutes so the colour would not degrade. The samples were chilled before decanting into cuvettes, which were read at an absorbance of 625 nm.

2.5.6 Phenolsulfuric acid assay

To 100 ul crude sugar solution, 0.5 ml of 4% phenol was added. Tubes were vortexed briefly and 2.5 ml concentrated H_2SO_4 added, then vortexed again and left to sit for 30 to 60 minutes. The absorbance was read at 490 nm using water as a blank.

2.6 Statistical Analyses

2.6.1 Roots, suckers and carbohydrates

Root, sucker and total nonstructural carbohydrate data were tested for normality of distribution using the Univariate Procedure (Pr<W) (Sas Institute Inc. 1996). Variables tested for roots were total length of dead roots, total length and volume of live roots, live roots with 0.5 to 2 cm diameters and suckering capacity of roots. Total length of dead roots, live roots, live roots between 0.5 and 2 cm diameters and live root volume were not normally distributed and were transformed with square root transformations (y1=squrt (variable)).

Sucker variables tested for normality were average sucker number, average sucker weight, average number of leaves and leaf area index per leaf and per sucker. All variables were non-normal and therefore, six different transformations were done and compared. Square root transformation (y=squrt(variable)), square root transformation plus 0.5 (y=squrt(variable+0.5)), log transformation (y1=log10(variable)), log transformation (y1=log10(variable=0.5), inverse transformation (y=1/variable) and variable times 2 transformation (y=variable**2) were used. None of the transformations improved the normality of the data, thus data were not transformed. For total starch, sugar and total nonstructural carbohydrates, the same transformations were tested as the data were not normal. All transformations were unsuitable, thus data were again not transformed for the analysis.

Root, sucker and carbohydrate variables were analyzed with a general linear model (Table A.1) (SPSS 1996). These variables were first tested for main effects of treatment and random variation of area within time and then the interaction of time and area (random effects). To test for significance of the main treatment effect, the Scheffe test was used ($p<0.05$). Significant results at $p<0.10$ were also noted because sampling sizes were small and the Scheffe test is conservative. Over time, a general linear model tested for the main effect of time, treatment and the random variation of area and time*treatment*area interaction (random effects). To test for significance for main effects, the Scheffe test was used ($p<0.05$) (SPSS 1996).

2.6.2 Development

Polynomial regression analysis was used to establish quantitative equations for the number of suckers, length of suckers, stage of suckers and number of leaves per sucker from the May July and September 1996 data. October 1995 data were not used because only the number of suckers was collected. Calculations were made to test the significance between slopes, coefficients and intercepts of the equations established. The equations used are in Table A.2. A sample calculation is in Table A.3.

3.0 RESULTS

3.1 Roots

3.1.1 Root length within sampling times

Within a given sampling time, dead root length was similar among treatments except in October 1995 when the heavy decline had significantly higher total length of dead roots (Table 2.1). Overall, the heavy decline had the most dead roots (34%) and the no decline had the least (14%).

Live root length was significantly lower in the heavy decline treatment for nearly all sampling times (Table 2.1). In September 1996, the low decline treatments were significantly lower than the mixedwood treatments only. For the four sampling periods, the heavy decline had the lowest total live roots (1055 cm). The mixedwood site had the most live roots (2558 cm). The no and low decline treatments were similar with 1879 cm and 1815 cm, respectively.

For live roots with diameters of 0.5 to 2.0 cm, the trend was similar to total live roots (Table 2.1). In September 1996 the mixedwood site had the most live roots (905 cm). Overall, the mixedwood site had the most live roots (1022 cm) and the heavy decline had the least live roots (336 cm). The no and low decline treatments were similar with 649 and 624 cm of roots, respectively. Generally, mass of roots (g m^{-2}) was highest in mixedwood for each sampling time. Overall, mixedwood was significantly higher (387 g m^{-2}) and heavy decline was significantly lower (88 g/m^2). The no and low decline were intermediate (250 and 213 g/m^2, respectively).

3.1.2 Root length over time

Total length of dead roots was similar in no decline and mixedwood treatments for each sampling period (Table 2.1). Total length of dead roots was lowest for low decline and heavy decline treatments in September 1996.

Total live root length was lowest in July for no decline and mixedwood treatments (Table 2.1). For low decline and heavy decline treatments, there was no significant change in total live root length over time. Total live roots, with diameters of 0.5 to 2.0 cm, did not change over time for any decline treatment. However, at $p<0.10$, the no decline had a significantly lower amount of live roots in July 1996. The mixedwood sites had significantly less live roots with diameters of 0.5 to 2.0 cm in July 1996.

Over time, root mass was similar for all treatments. Although not significant, mass of roots were higher in the heavy decline in October 1995 and May 1996. At $p<0.10$, the no decline had significantly less root mass in September 1996.

3.2 Suckers

3.2.1 Treatment effects within sampling times

The heavy decline treatment had the lowest suckering capacity (Table 2.2). No decline had the highest suckering capacity in October 1995, May 1996 and September 1996, while low decline had the highest suckering capacity in July 1996. Overall, the no decline and low decline treatments were significantly higher than the heavy decline and mixedwood (Table 2.2).

The mixedwood treatment had significantly lower suckers per 0.1 m^2 cm of cutting for all four sampling times (Table 2.2). The low decline was significantly higher in October 1995 and July 1996. Overall, the no and low decline treatments were significantly higher (6.7 and 6.9 suckers 0.1 m^{-2}, respectively) and the mixedwood treatment (2.4 suckers 0.1 m^{-2}) was significantly lowest with only half the number of suckers relative to the pure stands. Among the pure aspen stands, the heavy decline had the fewest suckers (4.6 suckers 0.1 m^{-2}).

The mixedwood treatment had significantly lower average sucker weight for both fall sampling times. In July 1996, the heavy decline had lowest mean sucker weight. Averaged over time, the mixedwood was significantly lower than the aspen treatments.

For mean sucker weight, number of leaves and leaf area, only suckers that grew were assessed. Mean leaf area per leaf was not done for the October 1995 leaves because number of leaves measured for leaf area were not counted. The heavy decline treatment had the lowest average number of leaves per cutting among treatments for October 1995, May 1996 and July 1996, however, for September 1996, the mixedwood treatment had the lowest average number of leaves (Table 2.3). Overall, the average number of leaves was similar among the treatments.

Treatments were similar in leaf area per leaf at each sampling time and overall (Table 2.3). For leaf area per cutting (cm^2 $sucker^{-1}$), the low decline treatment was lower than the other treatments in July 1996 and the mixedwood was significantly higher. Overall, treatments were similar (Table 2.3).

3.2.2 Treatment effects over time

Suckering capacity over time for the no and low decline treatments was highest in October 1995 and lowest in July 1996 (Table 2.2). Although not significant, heavy decline had lowest suckering capacity in July 1996 as well. For mixedwood, there was no significant change over time. However, at $p<0.10$, the suckering capacity was significantly higher in October 1995. Overall, suckering capacity was lowest in July 1996 and highest in October 1995.

Sucker number was significantly higher for all treatments in October 1995, except for heavy decline which was highest in September 1996 (Table 2.2). The no decline and heavy decline had significantly lower suckers in July 1996. Overall, sucker number was lowest in July 1996 and highest in October 1995. Mean sucker weight for all treatments was significantly lower for the no, low and heavy decline sites in July and significantly higher in May 1996 for all treatments. The mixedwood had lowest sucker weight in September 1996. Sucker weight was significantly higher in the two fall sampling times and significantly lower in the July 1996 sampling time.

For leaf area per leaf no decline and low decline treatments were highest in September 1996 and lowest in July 1996 and the heavy decline treatment was similar at each sampling time (Table 2.3). The mixedwood had highest area per leaf in July 1996. Generally, all treatments had the highest mean number of leaves per cutting in October 1995 and lowest in the July 1996 sampling time except for heavy decline which was similar at each sampling time. Overall, number of leaves was and leaf area per root was significantly lower in July 1996 and generally higher in the fall sampling times.

3.3 Carbohydrates

Within a given time period starch was significantly higher in the mixedwood treatment in October 1995 and July 1996 (Table 2.4), although overall, no significant differences were detected. There was no significant treatment difference for sugars within individual sampling times, but, overall, the mixedwood had more sugars. Glucose was significantly lower in the heavy decline treatment for all sampling times. Overall, glucose was lower in the heavy decline and higher in the mixedwood treatment. Generally, in a 1 m^2 area, the mixedwood had the highest amount of glucose (overall mean of 72 g m^2) and the heavy decline had the least (15 g m^2).

When assessed over time, starch and glucose were significantly higher in September 1996 for each treatment (Table 2.4). Sugar was significantly lower in July 1996 for the no and low decline treatments. When all treatments were averaged for each time, glucose was lowest in July 1996 and highest in September 1996. Glucose per 1 m^2 was similar over time for each treatment. However, when treatments were averaged per time, highest glucose was found in October 1995 and lowest in July 1996.

3.4 Development of Suckers

For the variables sucker stage, length of sucker and number of leaves per sucker, only roots that grew suckers were used in the analysis.

3.4.1 Number of suckers

For each growth chamber period, number of suckers that grew per cutting in the no and low decline treatments were higher over time than for heavy decline and mixedwood treatments (Figure 2.1). Generally, mixedwood treatments had the lowest number of suckers over time, except in July. In October 1995, the heavy decline treatment started suckering 23 days after planting and the other treatments started 28 days after planting. Suckers appeared 20 to 23 days in the May 1996 sampling period. In September 1996, all treatments started suckering at 18 days after planting. In July 1996, the specific date suckers started growing was not recorded.

According to the polynomial regression equations (Table A.4), each treatment had a different intercept and coefficient for each time of the year, indicating they were significantly different.

3.4.2 Stage of development

Generally, the suckers quickly reached stage 3 in development at the beginning of their growth, and between 25 to 35 days after planting, the suckers already began to develop leaves (stage 4) (Figure 2.2). According to the polynomial equations, in May and September 1996, the treatments had significantly different intercepts. However, in July 1996, one curve represents the growth pattern of all treatments (Table A.5).

3.4.3 Average length of suckers

Generally, the length of the suckers was higher over time for the mixedwood treatment (Figure 2.3). By the end of the growing period, the average length of suckers the treatments was between 11 and 16 cm for the May and July cuttings. However, in September, average sucker length was between 8 and 11 cm. The polynomial regression equations gave statistically different intercepts for each of the treatments. In the September 1996 growth period, the equation also gave statistically different coefficients for each of the treatments (Table A.6).

3.4.4 Average number of leaves per sucker

Although leaves per sucker increased over time for May and September, the reverse occurred in July (Figure 2.4). This is probably because the exact date at which suckers started to grow was missed. As number of suckers increased, although more leaves may have been produced, new suckers with fewer leaves would be included in the average. In the beginning of the growth period, there may have been fewer suckers, however those with leaves, would have produced more leaves on average per sucker. The polynomial equations (Table A.7) indicate statistically different intercepts for each of the treatments.

4.0 DISCUSSION

4.1 Roots and Suckers

As expected, the heavy decline had the greatest length of dead roots (Table 2.1). Schier (1975) hypothesized that in diseased overmature stems in deteriorating clones, the root system dies back because photosynthate channeled to the roots is decreased by reduction in crown area. In the Bronson forest, the dieback in the crown of the heavy decline averaged 51% whereas in the no and low decline, it was 18 and 37%, respectively (Chapter 3, Table 3.1). The length of live roots in the heavy decline was significantly lower than the other sites (Table 2.1). This may indicate photosynthates were being diverted to other areas and functions of the tree or that theamount of photosynthates were too low to enable more root growth. This would agree with Schier and Zasada (1973) who found a substantial decrease in photosynthate transport to roots in decadent aspen clones.

The higher amounts of dead root length in the heavy decline treatment could have resulted from caterpillar defoliation and drought. The aspen stands may have had to rely heavily in the past on root carbohydrates for maintenance rather than carbohydrates from photosynthesizing leaves causing severe dieback and root deterioration. Schier and Zasada (1973) found after repeated defoliation, there was a reduction in root carbohydrates to levels that significantly affect sucker outgrowth. Hogg (1998) examined growth responses of trembling aspen to the combined effects of climate and insect defoliation in the Bronson Forest. He concluded repeated defoliation with relatively dry conditions were the most important factors causing the recent crown dieback of the Bronson Forest. Milthorpe and Davidson (1965) observed root deterioration in grasses when there was not enough photosynthetic area for maintenance of the grass plant after repeated defoliation over time. They found cessation or reduction in root growth, a decrease in nutrient uptake and decreased root respiration, often accompanied by decomposition of roots following defoliation. Recovery in root activity did not occur until the new leaf surface attained a considerable size.

Other stresses on the aspen stands may have also increased the occurrence of root dieback. Defoliation and crown dieback may have allowed opportunity for defoliation by other organisms such as the large aspen tortrix (*Choristoneura conflicta* (Wlk.)) or entry for fungi, bacteria and wood-boring insects. In some of the aspen sites, grazing by cattle occurred and grazing may have impacted the roots through compaction and impeded sucker development. On the other hand, Schier (1975) found a close relationship between deterioration and clone characteristics suggesting that genotype may be the controlling factor in the timing and rate of decline. Therefore, aspen clones in this study may be responding to the genetic control of decline. Decline treatments may merely be a reflection of clone susceptibility to crown dieback.

Suckering capacity was generally higher in the no decline treatment, indicating that more carbohydrates were able to initiate sucker production (Table 2.2). Heavy decline had lower sucker production than the no or low decline treatments at each sampling time which may be due to low carbohydrates as well as necrotic areas on heavy decline cuttings which may prevent adventitious suckers from growing from the root cambium (Schier 1975). Many of the heavy decline root segments had calluses which formed in the growth chamber. Schier (1973c) found that abscisic acid (ABA) inhibited sucker development and promoted callus formation from cambium exposed at cut ends of excised roots.

Sucker development may also be affected by levels of reserve carbohydrates in this study. Generally the pattern of suckering response in aspen stands was consistent with the carbohydrate reserve fluctuations; high suckering in spring leaf flush and in fall and lowest in July. These results are consistent with other studies (Tew 1970, Schier and Zasada 1973). Other factors may have also influenced sucker production such as residual auxin from the parent root system and correlative inhibition among developing suckers (Eliasson 1971a, Schier 1973b), however, these factors were not measured.

The suckering response in mixedwood was unexpected. Mixedwood treatments had the lowest sucker number(Table 2.2). Since carbohydrates and number of live roots between 0.5 and 2.0 cm diameter were generally higher in mixedwood treatments other factors must have affected the roots. Schier (1974) indicated physiological and anatomical condition of aspen roots at the time of collection, to which site and other nongenetic influences may be important contributors, appears to have a strong effect on subsequent sucker development. Auxin levels in the mixedwood root system may have been higher at the time of root extraction; so sucker production continued to be inhibited after being transplanted in growth chambers. Inhibition of suckers may have been induced by conditions at the mixedwood sites due to the presence of white spruce such as allelopathy. Changes in soil pH affect nutrient availability, thus aspen roots may have been deficient in nutrients critical for sucker production. Changes in soil pH may also affect important mycorrhizal associations between aspen roots and soil nutrients. Although TNC components such as starches, fructans and sugars are thought to be the primary sources of carbon for sucker regrowth, carbon may also be supplied by other substances including proteins and amino acids. Nitrogenous substances may also be used to satisfy the respiratory demands of belowground organs following defoliation (Hogg and Lieffers 1991). Belowground stores of N influence bud dormancy and the mobilization of stored carbon for sucker regrowth.

It is interesting that mean sucker weight of the mixedwood treatment was lower at the two fall sampling periods than the aspen treatments despite the mixedwood sites producing fewer suckers (Table 2.2). This contrasts a study by Schier and Zasada (1973) who found as there was an increase in sucker number per root cutting, dry weight per cutting decreased possibly due to inter-sucker competition for carbohydrate reserves. This further suggests full sucker development may have been inhibited by factors such as lower nutrient status or different hormone levels of auxins. Paulsen and Smith (1968) found trends in available carbohydrates in Smooth Bromegrass (*Bromus inermis* Leyss.) indicated N favored utilization of photosynthate for the production of new topgrowth rather than for root and rhizome growth or for the accumulation of carbohydrate reserves.

Number of leaves per sucker was significantly lower for the heavy decline area at each sampling time, however, leaf area per leaf was not significantly different for each treatment (Table 2.3). This suggests that less carbohydrates are channeled for leaf production in the heavy decline treatment. Leaf area per leaf and per cutting was significantly higher at fall sampling times and lowest in July. This coincides with the pattern of carbohydrates which are highest in fall and lowest in July.

4.2 Carbohydrates

Although carbohydrates have been successfully determined with anthrone in soil organic matter, the anthrone sugar assay gave inconsistent results within and between sampling times for carbohydrates in aspen roots. Piccolo et al. (1996) determined that the anthrone-sulfuric acid method for total soil carbohydrates is not accurate. This method gave consistently poorer results than the phenol-sulfuric acid method. Due to unreliability, the Phenolsulfuric Acid Assay was used. Dr. Ollie Hindsgaul, carbohydrate researcher at the University of Alberta, recommended this procedure.

Carbohydrate patterns for all treatments were typical of other studies; lowest carbohydrates in summer (July) and highest in fall (Table 2.4). The October 1995 carbohydrates, however were similar to the May 1996 carbohydrates. The October 1995 results may have been affected because the roots were in storage longer before being ground and dried for sugar analysis. Thus roots would have respired longer than the September 1996 roots before carbohydrate analysis. Higher precipitation in 1996 than 1995, thus, may have also differentially affected carbohydrate content of roots in 1995. Other studies also indicate fall is the time of maximum carbohydrate content in roots (Sheppard and Smith 1993). Tew (1967) found the total change in starch from June to September averaged slightly more than 4% and that sugar increased by only 1%, making the total change in available carbohydrates approximately 5%. In this study, there was a large increase of 40% in starch content between the June and fall sampling times. Adams et al. (1986) found starch concentrations in loblolly pine (*Pinus taeda* L.) were highest in early spring prior to budbreak and root starch concentrations lowest in autumn. Landhausser and Lieffers (1997) found in species such Beaked Hazelnut (*Corylus cornuta*), Red Osier Dogwood (*Cornus stolonifera*), Prickly Rose (*Rosa acicularis*) and Low-bush Cranberry (*Viburnum edule*), TNC reserves were highest in August and September and lowest immediately after bud flush. Schier and Zasada (1973) also found early summer root carbohydrate reserves were low due to photosynthates allocation to developing suckers and leaves. In a study with Marsh Reed Grass (*Calamagrostis canadensis*) rhizomes October (Hogg and Lieffers 1991), TNC reached seasonal minimum values of 8 to 10% between mid May and June. After June, TNC levels increased substantially with maximum of 18.5% being reached in October.

The lower levels of carbohydrates in the heavy decline treatments could be explained partially by a greater clonal susceptibility to repeated defoliation by forest tent caterpillars as well as the drought in the Bronson Forest (Table 2.4). Alexander (1995) found that damage to aspen from drought, tent caterpillar attacks and grazing affected content of nonstructural carbohydrate reserves in aspen roots. Milthorpe and Davidson

(1965) reported that retardation of photosynthesis relative to growth, as by darkness or low light and optimal temperature and defoliation, will reduce the soluble carbohydrate content. On the other hand, any factor that delays growth relative to photosynthesis, e.g. high light, low temperatures, low availability of mineral nutrients and increased age, will lead to an increase in soluble carbohydrates. The amount and type of leaf surface remaining after defoliation also greatly influences subsequent growth.

Low carbohydrate reserves do not explain the poor regrowth in the mixedwood treatment because carbohydrate levels were higher than in the pure aspen stands. The poor regrowth suggest that site factors affect root cuttings even after removal from the site. Aspen are shade intolerant, thus environmental factors in the mixedwood may have affected suckering. In addition, soil temperatures or nutrients may have affected the hormonal status of roots in mixedwood sites. Hormones such as auxins affect not only apical dominance and suckers produced, but the allocation of carbohydrates to the suckers being produced (Wardlaw 1990). Schier and Johnston (1971) found that differences in root-carbohydrate percentages among the areas are likely due to site factors and age in addition to clonal variation. Starch concentrations are also sensitive to changes in available soil nutrients and water (Adams et al. 1986).

In the treatments in this study, glucose per area was lowest for the heavy decline and highest for the mixedwood within a given sampling time. However, over time, this did not affect the amount of glucose in the roots in an area for each treatment. In a study by Shepperd and Smith (1993), the resulting total volumes per hectare of nonstructural root carbohydrate did not vary appreciably between age class, because higher TNC concentrations in 20 to 80 year old clones were offset by lower root volumes in that age group. They also found that if pre-existing roots are an initial source of carbon for rapid sucker growth in these successfully regenerated stands, young suckers are apparently quickly able to replenish carbon and maintain roots to provide access to water and nutrients needed to support rapid carbon fixation.

4.3 Sucker Development

As expected, the number of suckers that grew over time was lower for the heavy decline treatment (Figure 2.1). In May, the sucker numbers in the heavy decline began to decrease at about 45 days after planting whereas in the no decline and low decline treatments, the number of suckers slowed but did not decrease during the 8 weeks. It was unexpected that mixedwood suckers followed the same trend as heavy decline suckers with lower numbers produced and numbers declining sooner. It was hypothesized that suckers in the heavy decline stands had depleted their carbohydrates, since total carbohydrates were lower for heavy decline roots.

Another interesting observation is the number and average sucker length over time in the fall. Although fall is usually the time when cuttings will sucker the most, it appears there was a big difference in sucker number and vigour between 1995 and 1996. Aspen roots may require a vernalization time to break dormancy; which may be temperature controlled. This difference in growth may have been caused by the difference in the length of time the roots were in cold storage. The May roots were in storage for about 30 days whereas the September 1996 cuttings were in storage for approximately 2 to 3 days.

Cuttings collected in July had lower number of leaves produced over time than the May and September 1996 growing periods(Figure 2.4). This may be a reflection in carbon allocation to growing suckers, although stages of development were similar in May, July and September sucker growth (Figure 2.2).

5.0 CONCLUSIONS

Sucker production, amount of dead and live roots and total nonstructural carbohydrates were used to evaluate suckering. Sucker production was related to root carbohydrates for pure aspen stands but not mixedwood stands. Heavy decline aspen stands had lower suckering capacity, lower live root mass, more dead roots and lower nonstructural carbohydrates than low or no decline aspen stands. Lowest root mass and total nonstructural carbohydrates were found in heavy decline aspen stands in spring, summer and fall. However, for all aspen stands, highest suckering capacity and highest total nonstructural carbohydrate reserves were found in fall. In mixedwood stands the tendency to produce abundant suckers was lower than in pure aspen stands, although total nonstructural carbohydrates were generally higher and live root mass was higher throughout the season than in the pure aspen stands, thus other factors must be involved that determine sucker density. Number of suckers produced was affected by the amount of live and dead roots in the treatment.

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Table 2.1 Root length and mass of aspen in the no decline (ND), low decline (LD), heavy decline (HD) and mixedwood (MW) from October 1995 to September 1996.

	October 1995		May 1996		July 1996		September 1996		Overall	
Root Class	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Dead Roots (cm)										
ND	149 bx	205	235 ax	161	233 ax	116	133 ax	110	187 c	155
LD	228 bxy	291	403 ax	314	300 axy	180	144 ay	132	269 bc	253
HD	720 ax	506	477 axy	281	306 ay	188	231 ay	159	434 a	358
MW	290 bxXY	212	481 axX	315	382 axXY	205	239 axY	150	348 ab	240
Live Roots (cm)										
ND	1919 aBxy	905	2312 aABx	1023	1531 ay	870	1755 abBxy	676	1879 b	897
LD	1905 aBx	878	2256 aABx	905	1564 ax	721	1534 bBCx	814	1815 b	859
HD	861 bCx	515	1438 bBx	780	859 bx	618	1062 bCx	748	1055 c	694
MW	2769 aAx	746	3003 aAx	1362	1786 ay	684	2673 aAx	886	2558 a	1037
Live Roots 0.5 to 2.0 cm Diameter (cm)										
ND	861 abxX	444	719 abxXY	435	497 abAxY	204	519 bBxXY	249	649 b	371
LD	740 bx	353	698 abx	349	562 aAx	274	496 bBCx	225	624 b	312
HD	338 cx	217	422 bx	310	283 bBx	222	299 bCx	249	336 c	250
MW	1337 axX	443	1067 axyXY	432	779 aAyY	361	905 aAxyY	437	1022 a	458
Root Mass Per Area (gm m^{-2})										
ND	353 axX	200	310 abxXY	257	187 abxXY	96	150 bxY	157	250 b	200
LD	267 abx	158	223 bx	157	231 abx	136	129 bx	120	213 b	148
HD	97 bx	126	130 bx	137	63 bx	74	63 bx	54	88 c	104
MW	389 ax	197	516 ax	286	278 ax	248	365 ax	265	387 a	258

Means within a column followed by the same lower case letters a, b and c are not significantly different at $p<0.05$. Means within a column followed by the same uppercase letters A, B and C are not significantly different at $p<0.10$. Means within a row followed by the same lower case letters x, y and z are not significantly different at $p<0.05$. Means within a row followed by the same uppercase letters X, Y and Z are not significantly different at $p<0.10$. SD - standard deviation.

Table 2.2 Aspen suckering capacity, number of suckers and average sucker weight in the no decline (ND), low decline (LD), heavy decline (HD) and mixedwood (MW) treatments from October 1995 to September 1996.

	October 1995		May 1996		July 1996		September 1996		Overall	
Root Class	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Suckering Capacity (suckers m^{-2})										
ND	762 aAx	625	534 aAxy	731	184 aby	137	340 aAxy	182	455 a	526
LD	674 aABx	356	382 aABxy	214	317 ay	174	257 abABy	106	408 a	276
HD	192 bCx	242	147 aBx	130	82 bx	77	181 bBx	215	150 b	177
MW	351 abBCxX	228	208 aABxXY	175	179 abxY	128	171 abBxY	129	227 b	180
Overall	501 x	451	318 xy	413	190 y	154	237 y	173		
Number of suckers 0.1 m^{-2} Root										
ND	8.6 bx	7.2	6.9 axy	12.9	3.8 bz	5.6	6.6 ay	6.9	6.7 a	8.9
LD	10.2 ax	9.3	5.7 ay	6.8	5.7 ay	6.9	5.5 ay	8.2	6.9 a	8.1
HD	5.4 cxy	7.0	3.8 byz	5.9	3.3 bcz	5.8	5.9 ax	7.5	4.6 b	6.6
MW	3.0 dx	4.4	2.0 cy	3.7	2.4 cxy	3.9	2.0 by	3.3	2.4 c	3.9
Overall	6.5 x	7.5	4.3 yz	8.2	3.7 z	5.6	4.5 y	6.6		
Sucker Weight (gm)										
ND	0.082 axy	0.091	0.093 abx	0.108	0.064 ay	0.087	0.080 axy	0.095	0.081 a	0.096
LD	0.078 axy	0.079	0.080 bx	0.108	0.052 aby	0.073	0.098 ax	0.133	0.077 a	0.099
HD	0.080 axy	0.102	0.149 ax	0.481	0.038 by	0.043	0.072 axy	0.082	0.092 a	0.277
MW	0.048 bx	0.088	0.061 bx	0.089	0.046 abxy	0.059	0.028 by	0.047	0.046 b	0.076
Overall	0.080 x	0.089	0.099 x	0.236	0.055y	0.076	0.084 x	0.107		

Means within a column followed by the same lower case letters a, b and c are not significantly different at $p<0.05$. Means within a column followed by the same uppercase letters A, B and C are not significantly different at $p<0.10$. Means within a row followed by the same lower case letters x, y and z are not significantly different at $p<0.05$. Means within a row followed by the same uppercase letters X, Y and Z are not significantly different at $p<0.10$.
SD – standard deviation.

Table 2.3 Number of leaves and leaf area of aspen suckers in the no decline (ND), low decline (LD), heavy decline (HD) and mixedwood (MW) treatments from October 1995 to September 1996.

	October 1995		May 1996		July 1996		September 1996		Overall	
Root Class	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mean Number of Leaves 0.1 m^{-2} Root										
ND	5.3 axy	6.9	4.9 axy	7.1	3.6 aby	5.9	5.6 abx	8.7	5.0 a	7.2
LD	4.8 aby	6.7	3.6 abyz	5.4	2.7 abz	4.2	7.1 ax	10.0	4.4 ab	6.8
HD	3.1 by	4.9	3.2 by	5.0	2.4 by	4.7	7.0 ax	10.1	3.9 b	6.7
MW	4.3 abx	7.7	4.1 abx	6.4	4.4 ax	6.4	3.3 bx	7.4	4.0 ab	7.1
Overall	4.7 xy	6.6	4.1 yz	6.2	3.5 z	5.1	5.4 x	9.5		
Leaf Area (cm^2 leaf^{-1})										
ND	.	.	0.29axy	0.56	0.22ay	0.32	0.42ax	0.37	0.32a	0.45
LD	.	.	0.23axy	0.21	0.13ay	0.10	0.40ax	0.34	0.26a	0.27
HD	.	.	0.28ax	0.24	0.14ax	0.15	0.46ax	0.85	0.32a	0.57
MW	.	.	0.48axX	0.81	0.28axY	0.38	0.40axXY	0.31	0.38a	0.58
Overall	.	.	0.33 x	0.58	0.21 y	0.31	0.42 x	0.44		
Leaf Area (cm^2 0.1 m^{-2} Root)										
ND	4.2 ax	4.0	2.4 ayz	3.3	1.3 abz	1.9	3.6 axy	4.9	3.1 a	4.0
LD	3.6 ax	3.8	2.0 ayz	2.5	0.7 bz	0.7	3.2 axy	2.9	2.5 a	3.0
HD	2.5 ax	2.8	2.2 ax	2.7	1.0 abx	1.2	3.0 ax	3.8	2.3 a	3.0
MW	4.4 ax	3.9	3.3 axy	4.1	2.1 ay	2.0	3.9 ax	4.5	3.3 a	3.8
Overall	4.0 x	3.9	2.6 y	3.4	1.5 z	1.8	3.5 x	4.2		

Means within a column followed by the same lower case letters a, b and c are not significantly different at $p<0.05$. Means within a column followed by the same uppercase letters A, B and C are not significantly different at $p<0.10$. Means within a row followed by the same lower case letters x, y and z are not significantly different at $p<0.05$. Means within a row followed by the same uppercase letters X, Y and Z are not significantly different at $p<0.10$.
SD – standard deviation.

Table 2.4 Total starch, sugar and glucose from aspen root cuttings in the no decline (ND), low decline (LD), heavy decline (HD) and mixedwood (MW) treatments from October 1995 to September 1996.

	October 1995		May 1996		July 1996		September 1996		Overall	
Root Class	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Starch (gm gm^{-1})										
ND	0.057 aby	0.020	0.054 by	0.015	0.041 by	0.017	0.130 ax	0.035	0.071 a	0.042
LD	0.054 aby	0.027	0.059 aby	0.026	0.049 by	0.023	0.138 ax	0.047	0.075 a	0.048
HD	0.035 by	0.022	0.050 by	0.020	0.046 by	0.016	0.133 ax	0.058	0.066 a	0.051
MW	0.079 ay	0.037	0.082 ay	0.037	0.072 ay	0.021	0.122 ax	0.036	0.089 a	0.038
Overall	0.056 y	0.031	0.061 y	0.027	0.052 y	0.023	0.130 x	0.044		
Sugar (gm gm^{-1})										
ND	0.107 axyX	0.020	0.111 axX	0.015	0.087 aByY	0.008	0.106 aABxyX	0.020	0.103 b	0.019
LD	0.118 axy	0.025	0.121 ax	0.019	0.094 aABz	0.015	0.100 aByz	0.017	0.108 ab	0.022
HD	0.104 ax	0.025	0.113 ax	0.018	0.104 aAx	0.019	0.102 aABx	0.020	0.105 ab	0.020
MW	0.121 ax	0.026	0.119 ax	0.009	0.102 aABx	0.018	0.116 aAx	0.013	0.114 a	0.019
Overall	0.112 x	0.025	0.116 x	0.016	0.096 y	0.016	0.106 xy	0.018		
Glucose (gm gm^{-1})										
ND	0.164 aby	0.034	0.165 by	0.025	0.127 bz	0.016	0.236 ax	0.038	0.173 b	0.049
LD	0.171 abyYZ	0.044	0.180 abyY	0.030	0.143 byZ	0.026	0.238 axX	0.055	0.183 ab	0.053
HD	0.139 by	0.037	0.163 by	0.033	0.149 aby	0.026	0.234 ax	0.055	0.171 b	0.054
MW	0.200 axy	0.053	0.201 axy	0.036	0.174 ay	0.030	0.237 ax	0.037	0.203 a	0.045
Overall	0.168 yz	0.047	0.177 y	0.034	0.148 z	0.030	0.237 x	0.045		
Glucose (gm 1m^{-2})										
ND	57 aABx	34	49 abx	51	24 abx	13	33 bx	34	41 b	37
LD	46 abBx	28	42 abx	34	32 abx	19	31 bx	31	38 b	28
HD	14 bcx	21	21 bx	24	9b bx	11	14 bx	12	15 c	18
MW	78 aAx	41	75 ax	55	48 ax	42	88 ax	68	72 a	53
Overall	49 xX	38	47 xXY	46	28 xY	28	42 xXY	49		

Means within a column followed by the same lower case letters a, b and c are not significantly different at $p<0.05$. Means within a column followed by the same uppercase letters A, B and C are not significantly different at $p<0.10$. Means within a row followed by the same lower case letters x, y and z are not significantly different at $p<0.05$. Means within a row followed by the same uppercase letters X, Y and Z are not significantly different at $p<0.10$. SD - standard deviation.

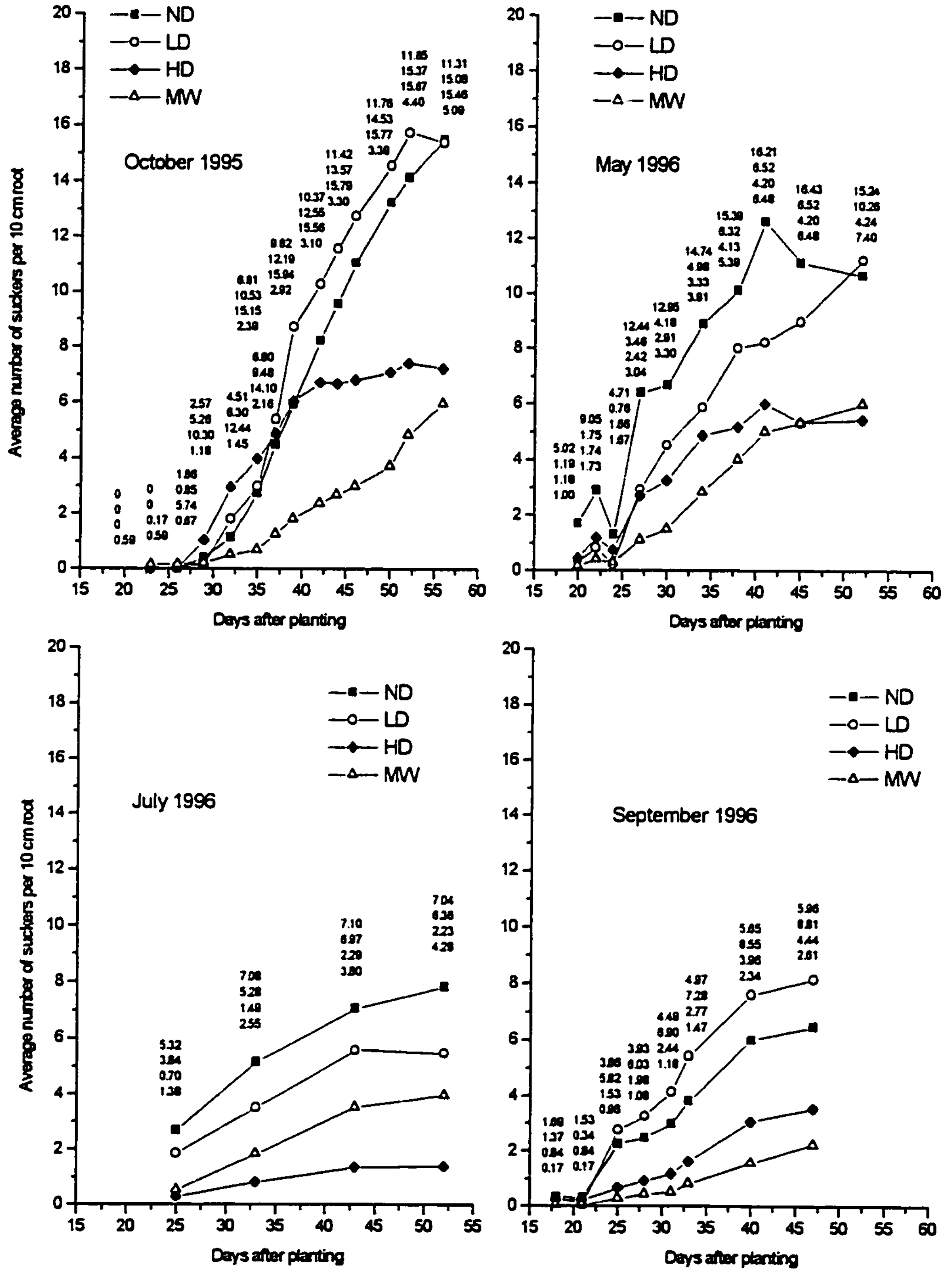

Figure 2.1 Average number of suckers per treatment from aspen roots collected in October 1995 and May, July and September 1996. Numbers at each point are standard deviations in the order of treatments on the legend.

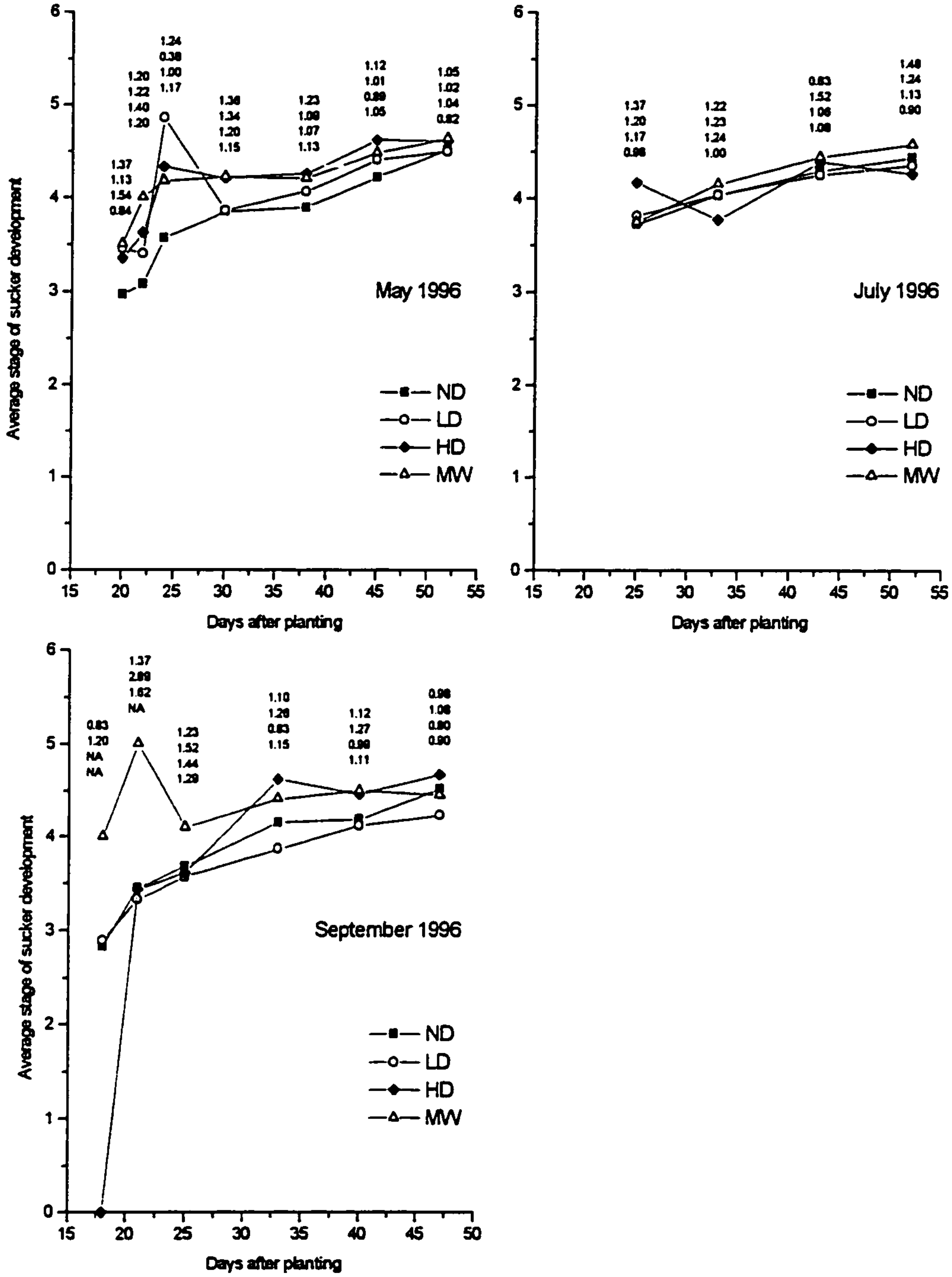

Figure 2.2 Average stage of suckers per treatment from aspen roots collected in May, July and September 1996. Numbers at each point are standard deviations in the order of treatments on the legend.

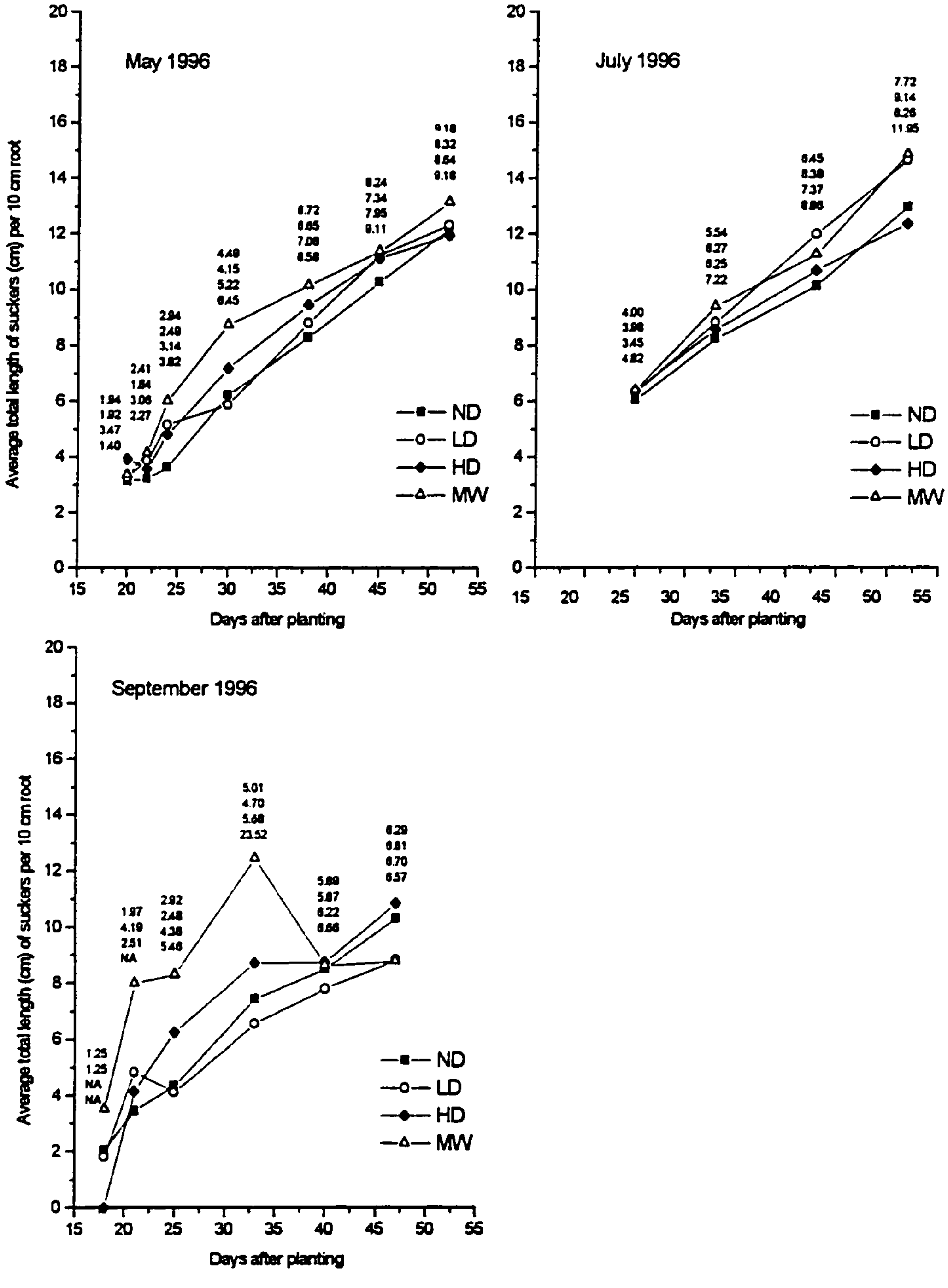

Figure 2.3 Average length (cm) of suckers per treatment from aspen roots collected in May, July and September 1996. Numbers at each point are standard deviations in the order of treatment on the legend.

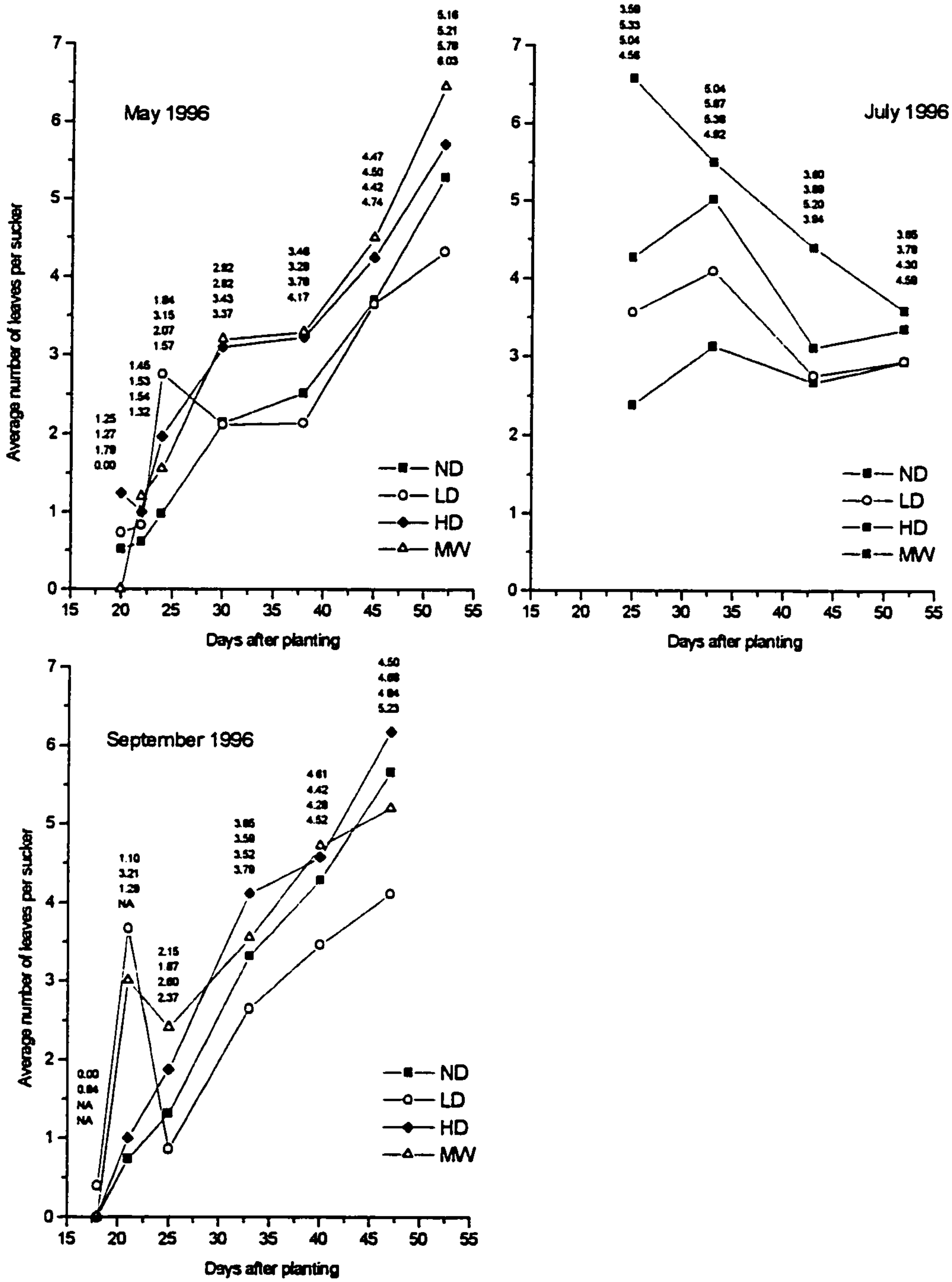

Figure 2.4 Average number of leaves per treatment from aspen roots collected in May, July and September 1996. Numbers at each point are standard deviations in the order of treatment on the legend.

III. VEGETATION COMPOSITION OF DECLINING ASPEN AND MIXEDWOOD STANDS

1.0 INTRODUCTION

Edaphic and disturbance factors account for much of the mosaic patterning of forest communities in a given microclimate in many regions of the world (Strong and La Roi 1985). Trembling aspen (*Populus tremuloides* Michx.) is a substantial component of forests in most of Canada (Peterson and Peterson 1992a) with fire and climate changes altering species distribution (Moss 1932, Spurr and Barnes 1973). Kay (1997) found most aspen stands that had not been burned in 60 years or more due to modern fire suppression and elimination of aboriginal burning were heavily invaded by conifers. In the absence of fire or other disturbance, most aspen clones in the southern Canadian Rockies will eventually be replaced by more shade-tolerant species. Rowe (1956) found that soil moisture is the most important determinant of growth and variations in moisture regime are reflected in vegetation composition variations.

White spruce (*Picea glauca*) rather than *Populus* spp. may be the main constituent of climax vegetation for most of the region now dominated by poplar spp. (Moss 1932, 1953, Bergeron and Dubuc 1989, Kay 1997). Fire suppression and under-utilization have prevented renewal of decadent stands (Moss 1932, Rowe 1955, Doucet 1989, James et al. 1989). Climatic factors and fire suppression may predispose trees to insects and disease attacks by intensifying an epidemic once it is initiated. Drought conditions on sites with shallow soils and severe moisture-stress may lead to root deterioration, rootlet mortality, crown decline, reduced growth and ultimately death of trees (Spurr and Barnes 1973).

Moss (1932) found aspen and white spruce stands thrived in similar situations with the rare occurrence of spruce in aspen stands a consequence of frequent burnings. Bergeron and Dubuc (1989) stated all species in succession are present in the first 50 years following fire with successional processes explained by species longevity and shade tolerance. Rowe (1956) described two types of successional trends; either toward a white spruce or white spruce and fir type. Succession from a hardwood to a mixedwood is sometimes prevented because seed sources have been destroyed by fire; the hardwood type is then relatively permanent. Spruce invade poplar stands upon maturation when they reach seed-bearing size, near age 60; then, progression toward a mixedwood type is initiated. For example, in a mixedwood stand with 100 to 120 year old trees, the spruce was uneven-aged and represented in all size classes and poplar (mostly aspen) was limited in age and size distribution (Rowe 1955). The recruitment period of white spruce is probably related to the amount of light reaching the forest floor. The overstory canopy of aspen stands transmits sufficient light to support white spruce growth (Lieffers et al. 1996) while spruce-dominated stands have low light.

As old poplars die, numerous young aspen and balsam appear, but, not quickly enough or in sufficient numbers to maintain the dominance of poplar in the community (Smith 1982). Instead, other woody plants increase, becoming dominant locally and producing a patchy community. Vegetation communities are formed by replacement of species by others more adapted to the prevailing environmental conditions (West et al. 1982), which in turn are modified by the species themselves. Trees respond to establishment and growth according to their tolerance to shading until the most tolerant individuals within the region have established a climax forest (Smith 1982, West et al. 1982).

Herbaceous species such as marsh reed grass (*Calamagrostis canadensis*) and fireweed (*Epilobium angustifolium*) become abundant (Moss 1932, Lieffers and Stadt 1994) in the initial stages of aspen stand disturbance. Lieffers and Stadt (1994) found the greater the hardwood basal area in mixedwood stands, the more light was transmitted by the canopy, thus increasing understory vegetation. Cannell and Grace (1993) found that dry matter production by each component in plant communities was roughly proportional to the amount of light it intercepted.

Each successional stage can be explained by the disappearance of early successional species that are unable to reproduce under a closed canopy (Bergeron and Dubuc 1989). As succession proceeds, shade tolerant species become progressively more abundant. Despite this, early succession species such as paper birch (*Betula papyrifera*) and *Populus tremuloides* may be abundant in the canopy for more than 200 years. Rowe (1956) found there are major understory differences between spruce-dominated stands and aspen-dominated stands. The most conspicuous difference is the relatively poor development of herb and shrub cover and substantial development of moss cover, under spruce canopies. In contrast, no distinct moss layer occurs in aspen-dominated stands, but herb and shrub understories are exceptionally well-developed (Rowe 1956).

Aspen ecosystems typically have a substantial herb and shrub understory compared to coniferous stands on similar sites in the same region (Peterson and Peterson 1992b). Understory vegetation plays an important role in the cycling of nutrients in aspen ecosystems because it contributes higher total aboveground nutrient input in *Populus* ecosystems due to higher litter biomass. Plants rarely compete for light without simultaneously competing for nutrients and water. Root systems exploit soil volumes proportional to their sizes, although large plants have greatest access to both aboveground and belowground resources. From a successional perspective, the location of roots close to the source of recyclable nutrients is important for nutrient interception (Strong and La Roi 1985). In the boreal forest, succession from deciduous to coniferous trees may cause a reduction in soil nutrient availability such as nitrogen due to the loss of herbs to facilitate nutrient turnover. This early stage progressively changes to a mixed forest and then to a conifer-dominated stage (Bergeron and Dubuc 1989, Pare and Bergeron 1996). A higher forest floor pH was found under aspen, while a greater accumulation of organic matter and nutrients was found on the forest floor of spruce due to a slower litter decomposition rate (Pare and Bergeron 1996).

Understory species diversity, canopy cover and current year production appear to be strongly influenced by overstory structure in forested stands (Zamora 1981). A large percentage of species have life cycle strategies that take advantage of conditions created by recurring disturbance (Zamora 1981) and can maintain viable populations under less than optimum environmental conditions present under forest canopies of mature stands. In a study by Henderson (1981) in western Washington trends in understory composition parallel those of the overstory (tree) layer, although many of the changes that take place are compressed into early successional stages. Fireweed can dominate early stages but does not persist past about 20 years.

Mixedwood forests are generally younger than many other forest regions in North America because fire occurs frequently (Peterson and Peterson 1992b). This is typified by dominant species such as fireweed (*Epilobium angustifolium*), willow (*Salix* sp.), alder (*Alnus* sp.), marsh reed grass (*Calamagrostis canadensis*) and other aggressive pioneer species that provide substantial interspecific competition. These early seral are characterized by very high growth rates, high production, and dynamic changes is species composition when contrasted with the late seral.

The objectives of this study were to determine the cover and height of the herb and shrub layers and characteristics of the tree layer in heavy, low and no decline aspen stands and mixedwood stands.

2.0 MATERIALS AND METHODS

2.1 Study Site

The Bronson Forest, a distinct timber supply area, lies southwest of Meadow Lake and is within 1 km of Highway 26 between St. Walburg and Loon Lake, Saskatchewan (53^0 45 to $53^{\ 0}$ 51'N and 109 08'W). The Forest Reserve is part of the Thickwood Hills Upland Section containing the Bronson Meadow Lake Hills Subsection, which forms the only physiographic division in the Forest Reserve (Rostad and Ellis 1972). The Upland is basically a wooded rolling morainal plain with gently to strongly rolling topography. Its elevation varies from 549 to 732 m. The topography in the east is mainly undulating to rolling while that in the west is hilly. The soils are mainly developed on glacial till and glacial-fluvial deposits.

2.1.1 Climate

The climate of the area is continental, characterized by moderately warm, short summers with wide variation in day and night temperatures, long cold winters and moderately low annual precipitation (Rostad and Ellis 1972). The climate of the Forest

Reserve is classified as subhumid. Its northern boundary has an 80-day frost free period. Summers are cool with mean daily July temperatures between 16 and 19 °C and winters are cold with mean daily January temperatures between -15 and -20 °C. Mean annual precipitation ranges from 36 and 41 cm of which 25 to 30 cm fall between May and September.

2.1.2 Soils

The Loon River Soil Association consists chiefly of Luvisolic soils developed on medium to moderately fine, textured, weakly to moderately calcareous unsorted glacial till deposits (Rostad and Ellis 1972). Its texture ranges from heavy loam and sandy clay loam to clay loam.

2.1.3 Vegetation

The Forest Reserve is located within the Boreal Forest Region. The tree species are mainly a mixture of deciduous and coniferous types and include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white spruce (*Picea glauca* (Moench) Voss). The most common shrubs found in the sites were alder (*Alnus* sp. Mill.), rose (*Rosa* sp. L.), willow (*Salix* sp. L.), low-bush cranberry (*Viburnum edule* Raf.) and honeysuckle (*Lonicera* sp. L.). Low growing plants include grasses and forbs such as fireweed (*Epilobium angustifolium* L.), bunchberry (*Cornus canadensis* L.), marsh reed grass *(Calamagrostis canadensis* Beauv.), wild strawberry (*Fragaria virginiania* Duchesne) and wild sarsaparilla (*Aralia nudicaulis* L.).

2.2 Treatments

In summer 1995, based on crown dieback, three aspen decline and three mixedwood areas were identified by aerial survey, verified by ground reconnaissance and delineated within the Bronson Forest by Stan Navratil (Canadian Forest Service (CFS) presently with SILCOR, Hinton AB), Roger Nesdoly (Mistik Management) and Rick Hurdle (Canadian Forest Service). Areas 1, 2 and 3 were located in pure trembling aspen stands. In each area, there were three clones selected by Stan Navratil based on visually assessed average percent crown dieback on an individual tree basis. Areas 4, 5 and 6 were located in mixedwood stands of non-declining aspen, balsam poplar, white spruce and other species. A circular plot with a radius of 10 m was established in each of the aspen

In each of the three trembling aspen decline areas, three treatment classes were identified based on the health and vigor of the crown (crown dieback) (12 sampling sites). Treatments were no decline or minimal sign of decline; mean crown dieback of 0 to 15%, light to intermediate level of decline; mean crown dieback of 20 to 40%, heavy decline with high decline; mean crown dieback of ≥ 45% and mixedwood.

All trees in the 12 sites were numbered with aluminum tags by Stan Navratil, Roger Nesdoly and Rick Hurdle. For each tree species, diameter at 1.3 m height and percentage crown dieback were recorded. Age of aspen trees was also recorded. Stand characteristics are provided in Tables 3.1, 3.2 and 3.3.

Vegetation inventories were conducted on the tree, shrub and herbaceous layers (Tables C.4 and C.5). Sampling size for each layer reflected differences in structure and diversity. For the tree layer, total stems per circular plot of 10 m radius of *Populus tremuloides*, *Populus balsamifera* and *Picea glauca* were counted. Shrub plots, 5 x 5 m in size, were centered in the tree plots and included all woody shrub species. Height range of the shrub and herbaceous species (measured to the nearest 1 m interval) and percent within the plot were taken. Three herbaceous vegetation plots were nested within shrub plots. Ground cover of all herbaceous and shrub species less than 1.0 m in height was recorded. Plant species within the circular plot but not found within shrub and herbaceous plots were recorded. Vegetation composition and ground cover for shrub and herbaceous layers were done by ocular assessment.

2.3 Statistical Analyses

The variables of percent vegetation cover, litter, bareground and moss data were tested for normality of distribution using the Univariate Procedure (Pr<W) (Sas Institute Inc. 1996). All data were normal. The average number of forbs and shrubs as well as average number of heights for grasses, forbs and shrubs were also tested for normality and found to be distributed normally. All the above variables were analyzed with a general

linear model (SPSS 1996). These variables were tested for the main effect of treatment and random variation of area. A post-hoc mean comparison was done on all treatments using a Scheffe test ($p<0.05$).

3.0 RESULTS

3.1 Species Composition

Forb and shrub composition were generally similar among pure aspen stands (Table 3.4). Although the mixedwood area had some similar species as the aspen stands, dominant species varied. For example, the dominant forbs in the aspen areas were generally *Epilobium angustifolium*, *Cornus canadensis* and *Calamagrostis canadensis*. For the mixedwood sites, dominant species were *Fragaria virginiana*, *Aralia nudicaulis* and *Cornus canadensis*. The dominant shrubs in the shrub layer for the aspen sites were *Alnus*, *Rosa* and *Salix* species (Table 3.5). For the mixedwood, dominant shrubs were *Rosa woodsii*, *Viburnum edule* and *Lonicera* species.

The ten most abundant forbs comprised 75% of the species composition in the no decline, 74% in low decline, 71% in heavy decline and 83% in mixedwood (Table 3.4). For shrubs, the three most abundant species were 65% in the no decline, 77% in the low decline, 78% in the heavy decline and 75% in the mixedwood. Species richness in the aspen forb understory varied from 26 to 33 species and in the shrub layer, species number varied from 13 to 26. In the mixedwood, forb species averaged 28 and the shrub layer averaged 14 species.

For the decline areas, the average number of forb species found in a quadrat was generally about twelve, whereas the mixedwood was lower with nine species. For the shrub species, the mixedwood was significantly lower with approximately four and the heavy decline was significantly higher with 5.6 species of shrubs (Table 3.6).

3.2 Ground Cover

Live vegetation cover was significantly lower for mixedwood sites than the low decline and heavy decline (Table 3.7). Litter in the treatments was similar for the no decline and mixedwood at approximately 90%, which was significantly higher than the low decline and heavy decline at approximately 84% (Table 3.7). The moss cover varied among the treatments; with the mixedwood significantly higher with 4.2% and the no decline significantly lower with 0.3% (Table 3.7).

3.3 Average Height of Forbs, Grasses and Shrubs

The average height of forbs was generally similar for the pure aspen stands (0.55 to 0.59 m) but the mixedwood site was significantly lower (0.33 m) (Table 3.7). Grass height was variable between the aspen and mixedwood stands although not statistically different. Grass height was between 0.56 and 0.73 m for the aspen stands whereas in the mixedwood, heights were 0.48 m. Average height of shrubs for aspen stands was 0.73 to 0.89 m and for mixedwood was significantly lower at 0.56 m. Average height of tall shrubs (shrubs >1.0 m) was between 2.05 and 2.17 m for the aspen stands and 1.83 m for mixedwood, although this was not statistically significant.

4.0 DISCUSSION

As expected, the understory of the mixedwood was different from the aspen stands. Although little variation in species occurred among the pure aspen stands species, the type of species dominating a site varied. The pure aspen had a more vigorous forest understory vegetation than the mixedwood stands as forb and shrub species covered more ground and were generally taller. Rowe (1956) also found that a poplar canopy allowed more light to penetrate to the forest floor than does a spruce canopy, consequently tall shrubs are able to flourish under aspen forests and the height of the forest undergrowth species bears an inverse relationship to tolerance. Although, the principal factor controlling the structure of the undergrowth is light, other factors such as temperature, root competition, litter accumulation, and other soil characteristics influence composition (Rowe 1956).

At the study sites, moss varied from 0.3 to 2.0% in pure aspen stands and for the mixedwood site (Table 3.7). The percentage of moss on the forest floor was 4.2%. This is consistent with Rowe (1955) who found the percent cover contributed by tall shrubs decreased steadily from poplar through mixedwoods to spruce stands, while the percentage of cover contributed by mosses rises (Rowe 1956). Dix and Swan (1971) also found a number of stands dominated by the pioneer species jack pine and aspen that had no organic mat.

In the mixedwood site 4, shrub height ranged from 5 to 50 cm tall resulting in sparse cover of plants (Table 3.7). Where more light was available, there were more plants as was expected. The low decline treatment in site 1 was dominated by *Alnus* species. Most were trees greater than 2 metres. The heavy decline area was also dominated by *Alnus* species. in site 1. There was also a lot of slash from fallen dead aspen trees that may have affected composition of the site, as this could change available light and soil temperature. Doucet (1989) found that slash will also affect suckering, through its effect on soil temperature and may physically hinder sucker growth.

Our results showed that the understory vegetation of the aspen stands had greater species numbers and greater spp. richness as compared to mixedwood stands. This is in agreement with Constabel and Lieffers (1996) who compared light transmission in pure young aspen, pure old aspen and mixed old aspen – white spruce stands. They found in the old aspen stands, there was generally more light transmission through the overstory in spring and autumn, which led to increased light interception at that level and an increased understory cover. Cannell and Grace (1993) found that dry matter production by each component in plant communities was roughly proportional to the amount of light it intercepts. The increase in light to the forest floor of the aspen sites led to an increase in the composition of competitive understory vegetation such as *Calamagrostis canadensis* (Michx.) Beauv. and *Epilobium angustifolium* L. Lieffers and Stadt (1994) studied the potential for using of a partial canopy for controlling growth of *Calamagrostis canadensis* (Michx.) Beauv., *and Epilobium angustifolium* L. among regenerating *Picea glauca* (Meonch) in the lower boreal cordilleran ecoregion of Alberta. Their studies found that the average cover of *Calamagrostis canadensis* and *Epilobium angustifolium* was correlated with the amount of transmitted light and are almost virtually eliminated in stands with decreased light transmission as in the mixedwood stands. They found it may be possible to use height or cover of *Calamagrostis canadensis* or *Epilobium angustifolium* in the understory as quick indicators of light status. This observation could be verified by the higher heights of understory species found at the aspen verses mixedwood sites. At our sites, *Calamagrostis canadensis* varied in the aspen stands from 6.8 to 14.0% composition in heavy and 2.3% in the mixedwood (Table 3.4). *Epilobium angustifolium* varied from 20.4 to 24.4% in the aspen stands and only 2.3% in the mixedwood. Heights of forbs and grasses were generally between 0.55 to 0.7 m in the aspen stands and only 0.33 to 0.48 m in the mixedwood (Table 3.7). This may indicate there is more incident light, thus possibly increasing soil temperatures in the aspen stand as portrayed by the increase composition and height of forb/grass species such as *Calamagrostis canadensis* and *Epilobium angustifolium*. The drop in percentage of *Calamagrostis. canadensis* and *Epilobium angustifolium* in the mixedwood stand is an agreement with the findings of Lieffers and Stadt (1994).

It appears that *Calamagrostis canadensis* is strongly associated with hardwoods. Rowe (1956) stated that the common line of succession from poplar to spruce is marked by a diminution of light on the forest floor. In more open poplar and poplar-spruce stands, a distinctive tall herb stratum is formed by *Calamagrostis canadensis* along with other species such as canada anemone (*Anemone canadensis* L.), aster (*Aster umbellatus* var. *pubens* Mill.) and drooping wood reed (*Cinna latifolia* (Trev.) Griseb.).

Rowe (1956) found as poplar forest grades into spruce, shrubs decrease slowly and only a few such as *Viburnum edule* and *Ribes* species are persistent where light intensities are low. In the aspen stands of the Bronson forest, *Viburmun edule* ranked approximately 6 and 7 most abundant of all species, whereas for the mixedwood, this species was second highest (Table 3.5). *Ribes* species were ranked at 13 to 18 in the aspen stands. In the mixedwood sites *Ribes* ranked 7.

The average ages of the aspen found at our sites were between 57 and 63. A study in Saskatchewan by Cayford (1957) of three age groups (55 to 60, 70 to 75 and 95 to 100) of mixedwood stands in Saskatchewan found that free-growing white spruce overtopped aspen in the stands between the ages of 40 and 65 years. Height growth of suppressed spruce approached that of aspen at ages above 50 or 60 years. Kagis (1952) and Lees (1967) also found that mixedwood stands at ages of 50 to 75 years in Saskatchewan had spruce that were able to grow through the overstory as the aspen became decadent.

Succession to a spruce stand may occur as the aspen sites with higher nutrient cycling prepare the area for the succession to spruce stands (Moss 1932, 1953). Rapidly decaying aspen leaves rapidly return nutrients to the soil (Corns 1989). Moss (1953) found the white spruce (*Picea glauca*) association is regarded as the climax for the region. In the absence of burning, the spruce gradually replace the shorter-lived poplar, while most shrubs and herbs are replaced by mosses. Gale and Grigal (1987) found early successional species are also able to adapt to sites limiting in water and nutrients because of their ability to exploit larger volumes of soil. Late successional or shallow-rooted species are better adapted to sites where resources are concentrated near the soil surface as the result of biocycling and soil development. Pare and Van Cleve (1993) suggested that the development of a trembling aspen clump after clear-cutting contributes to the acceleration of overall nutrient cycling and the development of herbaceous communities.

Alnus ranked as number one in the no decline and low decline treatments and number one in the heavy decline (Table 3.5). In the mixedwood site, it ranked number five. Bormann and Sidle (1990) found the nitrogen-fixing shrub Sitka alder (*Alnus sinuata*) dominated recently deglaciated sites along Glacier Bay but was replaced by Sitka spruce (*Picea sitchensis*) after about 80 years (Bormann and Sidle 1990). While *Alnus* dominated, soil organic matter and nitrogen (N) increased very rapidly. Above-ground biomass accumulated much more rapidly as *Picea* gained dominance over *Alnus*. The increase in biomass was accompanied by a decline in soil N. N2-fixing plants such as *Dryas drummondii* and *Alnus sinuata* are thought to improve the site and then succumb to competition from later successional species. The stands at our sites are about 60 years old. The *Alnus* has a percentage of about 26% in the no decline, 43% in the low decline and 31% in the heavy decline, whereas in the mixedwood it is only 3.3%. Possibly *Alnus* may eventually gain dominance and increase the nitrogen in the area. This may aid growth of aspen suckers considering they are not being outcompeted by other more shade tolerant species in the area, under the growing vegetation in the area. If *Picea* invade however, this will contribute to a drop in the N in the area. Since *Populus* need N, they will further decline in composition, unless a disturbance like a fire helps to regenerate the stands and remove the *Picea* encroachment. Although there were no seedlings of spruce in the decline areas, the sites were surrounded by mixedwood areas, thus, seeds from the *Picea* trees may have the oppurtunity to blow in and establish in the area.

5.0 CONCLUSIONS

Declining aspen stands in the Bronson Forest were characteristic of a poplar stands. The open canopy of the pure aspen stands resulted in an increase of forb understory such as *Calamagrostis canadensis* and *Epilobium angustifolium*. There was also an increase in height and number of the forbs and shrubs in aspen stands. The mixedwood understory species tended to be shorter and not as dense. Percent moss on the mixedwood forest floor was higher than on the pure aspen stands. Although there tended to be differences in species that dominated a declining aspen stand, generally, the same species were present in all stands. However, there was a change in dominant species for the mixedwood sites. Ecologically important species such as *Alnus* an N-fixer, were dominant in the understory shrub layer of the pure aspen sites only. The composition of species found in the aspen stands, along with the decadent aspen trees, and surrounding mixedwood areas indicate the possibility of movement towards a spruce-poplar or mixedwood stand.

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Table 3.1 Characteristics of trembling aspen in the aspen decline and mixedwood stands.

Class	Site	Total Trees	DBH[1]		Crown Mortality		Age in 1995 (years at DBH)	
		Live and Dead	Mean	Range	Mean	Range	Mean	Range
Heavy Decline	1	32	13.3	9.2-18.8	57.8	0-100	56	53-57
Low Decline	1	21	16.5	8.1-23.8	33.3	0-100	55	51-57
No Decline	1	24	17.3	5.4-21.4	16.9	0-100	49	46-51
Heavy Decline	2	24	17.1	12.3-28.1	39.8	5-100	62	52-66
Low Decline	2	35	15.3	9.7-21.3	39.0	0-100	62	51-65
No Decline	2	52	15.8	10.8-25.5	21.2	0-100	64	62-65
Heavy Decline	3	27	16.8	9.9-21.0	53.0	0-100	63	61-64
Low Decline	3	26	19.2	12.9-24.7	36.7	5-100	60	49-65
No Decline	3	44	15.2	5.7-31.2	14.7	0-100	58	46-65
Mixedwood	4	32	18.4	10.4-32.9	12.2	0-100	70	67-72
Mixedwood	5	23	15.0	8.4-21.4	9.1	0-100	55	49-57
Mixedwood	6	24	16.3	6.4-36.9	51.5	0-100	64	61-66
Heavy Decline	1-3	77	15.6	9.2-28.1	51.0	0-100	60	52-66
Low Decline	1-3	111	16.8	8.1-24.7	36.8	0-100	59	49-65
No Decline	1-3	97	15.9	5.4-31.2	17.9	0-100	57	46-65
Mixedwood	4-6	79	16.9	6.4-36.9	23.2	0-100	63	49-72
All classes	1	32	15.4	5.4-23.8	38.4	0-100	49	46-51
All classes	2	33	15.9	9.7-28.1	30.8	0-100	64	62-65
All classes	3	37	16.7	5.7-31.2	31.2	0-100	58	46-65
All stands	1-3	102	16.2	5.4-36.9	30.0	0-100	59	46-66

Some information obtained from Hogg and Schwarz 1999 in press.

[1] DBH - Diameter at breast height (cm).

Table 3.2 Characteristics of balsam poplar in the aspen decline and mixedwood stands.

Class	Site[1]	Total Trees	DBH[2]		Crown Mortality	
			Mean	Range	Mean	Range
Heavy Decline	1	1	13.6	NA[3]	90.0	NA
Low Decline	1	4	13.4	13.0-13.8	0.0	0-0
No Decline	1	8	7.5	4.5-12.1	5.9	0-40
Heavy Decline	2	1	16.0	NA	100.0	NA
Low Decline	2	-	-	-	-	-
No Decline	2	-	-	-	-	-
Mixedwood	4	2	14.6	11.0-18.1	100.0	100-100
Mixedwood	5	6	12.6	9.3-15.7	69.2	0-100
Mixedwood	6	5	19.1	9.7-30.5	61.0	0-100
Heavy Decline	1-3	2	14.8	13.6-16.0	95.0	90-100
Low Decline	1-3	4	13.4	13.0-13.8	0.0	0-0
No Decline	1-3	8	7.5	4.5-12.1	5.0	0-40
Mixedwood	4-6	13	15.4	9.3-30.5	68.3	0-100

Some information obtained from Hogg and Schwarz 1999 in press.
[1] Note: No balsam poplar found in site 3 (aspen stand).
[2] DBH - Diameter at breast height (cm).
[3] NA – not applicable because no measurements were done.

Table 3.3 Characteristics of white spruce in the aspen decline and mixedwood stands.

Class	Site[1]	Total Trees	DBH[2]		Crown Mortality	
			Mean	Range	Mean	Range
Mixedwood	4	30	1.3	5.5-28.0	NA[3]	NA
Mixedwood	5	16	11.0	4.4-51.3	NA	NA
Mixedwood	6	18	11.5	6.8-17.5	NA	NA
Mixedwood	4-6	64	12.2	4.4-51.3	NA	NA

Some information obtained from Hogg and Schwarz 1999 in press.
[1] Note: No white spruce found in sites 1-3 (aspen stands).
[2] DBH - Diameter at breast height (cm).
[3] NA – not applicable because no measurements were done.

Table 3.4 Relative species composition of grasses and forbs based on canopy cover for aspen and mixedwood stands in 0.5 m^2 plots.

Decline Class	No Decline			Low Decline			Heavy Decline			Mixedwood		
Species	Mean	SD	Rank	Mean	SD	Rank	Mean	SD	Rank	Mean	SD	Rank
Achillea millefolium	0.1	0.3	27	0.4	1.3	24	0.3	1.0	28	0.0	0.0	29
Agropyron sp.	3.0	6.6	11	4.7	4.3	7	3.3	4.9	9	1.9	4.0	11
Aralia nudicaulis	3.0	3.9	12	5.8	5.4	3	1.9	3.3	17	15.8	19.7	2
Artemisia campestris	0.0	0.0	34	0.0	0.0	34	0.6	1.7	25	0.0	0.0	36
Aster conspicuus	4.6	7.8	7	0.0	0.0	27	0.0	0.0	34	1.2	3.7	18
Aster laevis	0.4	1.3	21	0.4	1.3	25	0.0	0.0	35	0.0	0.0	30
Aster sp.	1.4	2.5	19	2.9	2.5	14	2.9	4.4	10	1.6	3.0	14
Bromus inermis	3.6	2.7	8	1.3	2.2	17	2.6	5.4	13	0.1	0.3	25
Calamagrostis canadensis	6.8	3.8	5	9.4	9.7	2	14.0	14.4	2	2.3	5.0	8
Campanula rotundifolia	0.4	0.9	22	0.2	0.7	26	0.1	0.3	33	1.0	3.0	20
Carex sp.	1.6	2.8	18	1.0	1.8	21	2.6	7.7	14	0.0	0.0	31
Cornus canadensis	10.3	7.6	2	5.7	5.1	4	6.0	6.1	4	13.8	16.4	3
Disporum trachycarpum	0.8	1.3	20	2.7	4.5	15	4.4	5.1	5	1.9	2.3	12
Elymus innovatus	0.0	0.0	30	0.0	0.0	28	0.3	1.0	29	0.0	0.0	32
Epilobium angustifolium	20.4	17.4	1	24.4	24.0	1	20.8	17.6	1	2.3	3.8	9
Equisetum arvense	0.0	0.0	31	0.0	0.0	29	1.7	4.3	18	0.1	0.3	26
Fragaria virginiana	7.6	6.5	4	4.1	3.7	10	8.1	6.4	3	18.1	22.8	1
Galium boreale	2.7	3.3	14	3.3	2.4	13	2.3	1.8	15	0.0	0.0	33
Galium sp	0.1	0.3	28	0.0	0.0	30	0.3	1.0	30	0.0	0.0	34
Galium triflorum	0.0	0.0	32	0.0	0.0	31	0.6	1.7	24	0.0	0.0	35
Geranium sp.	0.0	0.0	33	0.0	0.0	32	0.0	0.0	36	0.4	1.3	22
Gramineae sp.	3.3	3.5	9	0.0	0.0	33	0.0	0.0	37	1.3	2.6	16
Lactuca sp.	0.0	0.0	35	1.4	4.3	16	0.0	0.0	38	0.0	0.0	37
Lathyrus ochroleucus	2.9	2.8	13	4.2	3.6	9	4.2	3.4	6	0.0	0.0	38
Lathyrus venosus	0.0	0.0	36	0.0	0.0	35	0.7	1.4	23	0.0	0.0	39
Ledum groenlandicum	0.0	0.0	37	0.0	0.0	36	0.0	0.0	39	0.0	0.0	40
Linnaea borealis	2.3	5.4	16	4.6	5.9	8	2.8	3.6	12	5.9	13.4	5
Maianthemum canadense	2.6	4.5	15	3.9	4.0	11	0.4	1.0	26	5.0	6.5	7
Mitella nuda	0.2	0.7	26	0.0	0.0	42	0.0	0.0	43	0.0	0.0	44
Mushroom sp.	0.1	0.3	29	0.0	0.0	37	0.0	0.0	40	0.1	0.3	27
Oryzopsis sp.	0.0	0.0	42	0.0	0.0	43	0.0	0.0	44	1.4	3.4	15

Table 3.4 Relative species composition of grasses and forbs based on canopy cover for aspen and mixedwood stands in 0.5 m^2 plots (continued).

Decline Class	No Decline			Low Decline			Heavy Decline			Mixedwood		
Species	Mean	SD	Rank	Mean	SD	Rank	Mean	SD	Rank	Mean	SD	Rank
Petasites sagittatus	3.3	2.7	10	5.1	4.8	6	3.4	5.1	8	2.2	3.1	10
Plantago major	0.0	0.0	38	0.6	1.7	23	0.4	1.1	27	0.0	0.0	41
Poa compressa	0.3	1.0	25	0.0	0.0	38	1.3	3.3	22	0.0	0.0	42
Pyrola sp.	0.0	0.0	39	0.0	0.0	39	0.2	0.7	31	0.0	0.0	43
Rubus pubescens	10.0	8.8	3	3.7	5.6	12	2.9	7.6	11	12.1	13.6	4
Smilacina stellata	0.0	0.0	40	0.0	0.0	40	0.0	0.0	41	1.3	3.0	17
Sphagnum sp.	0.0	0.0	41	0.0	0.0	41	0.0	0.0	42	5.3	9.7	6
Taraxacum officinale	0.4	1.0	23	1.1	2.0	19	2.1	3.3	16	0.1	0.3	28
Thalictrum sp.	2.0	5.0	17	1.3	2.7	18	1.6	2.5	19	1.0	2.0	21
Trifolium hybridum	0.0	0.0	43	0.0	0.0	44	1.6	4.7	20	0.0	0.0	45
Trifolium repens	0.0	0.0	44	1.1	3.3	20	0.0	0.0	45	0.0	0.0	46
Vicia americana	0.4	1.3	24	1.0	1.2	22	1.4	2.1	21	0.4	0.7	23
Viola adunca	0.0	0.0	45	0.0	0.0	45	0.0	0.0	46	0.2	0.7	24
Viola renifolia	0.0	0.0	46	0.0	0.0	46	0.2	0.4	32	1.1	1.7	19
Viola sp.	5.2	6.4	6	5.6	4.2	5	3.9	4.3	7	1.8	4.1	13

Table 3.5 Relative species composition of shrubs and trees for aspen and mixedwood stands in 5 x 5 m plots.

	No Decline			Low Decline			Heavy Decline			Mixedwood		
Species	Mean	SD	Rank	Mean	SD	Rank	Mean	SD	Rank	Mean	SD	Rank
Alnus sp.	25.9	32.5	1	31.3	32.3	1	30.6	33.9	2	3.3	10.0	5
Amelanchier alnifolia	9.4	15.3	5	6.7	13.8	4	5.4	10.3	5	0.0	0.0	15
Arctostaphylos uva-ursi	0.2	0.4	11	0.0	0.0	14	0.3	0.5	11	3.0	6.2	6
Betula papyrifera	0.0	0.0	12	0.0	0.0	15	0.0	0.0	14	0.3	1.0	12
Corylus cornuta	0.0	0.0	13	0.0	0.0	16	0.0	0.0	15	0.1	0.3	13
Ledum groenlandicum	0.0	0.0	14	0.3	1.0	10	0.1	0.3	13	1.3	4.0	10
Linnaea borealis	0.0	0.0	15	0.2	0.7	12	0.0	0.0	16	0.0	0.0	16
Lonicera dioica	0.0	0.0	16	0.0	0.0	17	0.3	0.7	12	0.0	0.0	17
Lonicera involucrata	0.0	0.0	17	0.0	0.0	18	0.4	1.3	10	17.4	32.6	3
Populus balsamifera	1.4	4.3	8	5.7	17.0	5	0.0	0.0	17	0.0	0.0	18
Populus tremuloides	11.2	12.1	4	2.4	5.0	7	15.0	26.5	3	0.0	0.0	19
Ribes triste	0.0	0.0	18	0.2	0.7	13	0.0	0.0	18	2.2	5.3	7
Rosa woodsii	23.7	22.0	2	22.9	28.1	2	9.1	6.9	4	34.9	27.1	1
Rubus idaeus	0.3	1.0	10	2.4	2.7	8	4.4	3.5	6	1.0	3.0	11
Salix sp.	15.2	14.9	3	22.7	26.6	3	32.3	25.7	1	2.1	6.0	8
Shepherdia canadensis	0.9	2.7	9	0.0	0.0	19	0.0	0.0	19	2.1	6.3	9
Symphoricarpos albus	0.0	0.0	19	0.3	0.7	11	0.6	0.9	8	0.1	0.3	14
Symphoricarpos occidentalis	9.0	12.3	6	0.9	1.4	9	0.6	1.1	9	8.9	12.4	4
Viburnum edule	2.7	3.4	7	4.1	7.0	6	0.8	1.2	7	23.1	24.4	2

Table 3.6 Average number of species per quadrat in each treatment.

	No Decline		Low Decline		High Decline		Mixedwood	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Forbs/Grasses	12.4 a	2.55	12.4 a	2.7	11.8 a	4.0	9.1 a	3.4
Shrubs	4.7 ab	1.1	5.0 ab	1.4	5.6 a	1.1	3.9 b	1.5

Means within a column followed by the same lower case letters a, b and c are not significantly different at $p<0.05$.

Table 3.7 Percentage ground cover and average height of the aspen decline and mixedwood stands.

	No Decline		Low Decline		High Decline		Mixedwood	
Vegetative Characteristic	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Ground Cover								
Vegetation	9.0 b	3.1	13.4 a	3.1	14.9 a	4.0	5.3 c	2.9
Litter	90.7 a	3.1	84.6 b	3.8	83.9 b	4.3	90.4 a	8.3
Moss	0.3 b	1.0	2.0 ab	2.7	1.2 b	2.0	4.2 a	6.3
Bare ground	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Average Heights								
Forbs (m)	0.59 a	0.19	0.55 a	0.15	0.55 a	0.17	0.33 b	0.21
Grass (m)	0.73 a	0.16	0.56 a	0.29	0.72 a	0.55	0.48 a	0.23
Shrubs (m)	0.73 ab	0.19	0.89 a	0.28	0.75 ab	0.11	0.56 b	0.27
Tall Shrubs (m)	2.05 a	0.51	2.03 a	0.31	2.17 a	0.36	1.83 a	0.00

Means within a column followed by the same lower case letters a, b and c are not significantly different at $p<0.05$.

IV. SYNTHESIS

1.0 SUMMARY OF RESEARCH

Clones of aspen are reaching maturity and an increase in deteriorating aspen forests has been noted within the Aspen Parkland and Boreal Forests. This trend was observed in the Bronson Forest near Meadowlake, Saskatchewan. With the increased demand for aspen fibre feedstock, areas of aspen with low wood volumes and scattered softwood distribution within the Bronson Forest are being viewed as potential sources of fibre. Thus, forests with severe dieback need to be assessed for their rejuvenation potential.

In this study, sucker production, amount of dead and live roots and total nonstructural carbohydrates were used to evaluate suckering capacity of declining (low and heavy) and nondeclining aspen and mixedwood stand roots collected at different times in the growing season. A secondary objective was to characterize vegetation in the sampling areas of the Bronson Forest. Other research indicated suckering capacity of roots was dependent on degree of decline, time of year roots were collected and amount of total-nonstructural carbohydrates in trembling aspen stands.

The ability of aspen roots to produce suckers was related to root carbohydrates for the aspen treatments, but was unrelated for the mixedwood stands. Number of suckers produced in aspen treatments was affected by the amount of live and dead roots. Live root length was lower in the heavy decline treatment for all sampling times. Overall, the heavy decline had higher total dead root length and lower total live root length than the other treatments. This was also the trend for root mass. Overall, the mixedwood treatment had the highest live root length and mass.

The aspen heavy decline treatment had the lowest suckering capacity and the no and low decline had the highest. The mixedwood treatment had significantly fewer suckers per cm of cutting for all sampling times and overall. Lower suckering potential of the mixedwood may have been a result of condition of roots at the time of suckering. Factors such as nutrient status of the sampling area and roots or different levels of hormones in the roots may have been causal agents of the lower suckering capacity because levels of carbohydrates and live root mass and length were generally higher in the mixedwood sites. Over time, all treatments had their highest suckering capacity in the fall and lowest in July.

Generally, the mixedwood treatment had the lowest mean sucker weight in all sampling times and overall. Sucker weight was generally highest for all treatments in May and lowest for the July 1996 sampling time, except for the mixedwood treatment which was lowest in September 1996. Mean number of leaves and leaf area were highest for the September 1996 sampling time. Lowest leaf area was in July 1996. Generally, the heavy decline treatment had the lowest mean number of leaves within a sampling time. Although leaf area per leaf was similar at each sampling time for each treatment, the heavy decline was generally lower in leaf area per root cutting.

Root starch level was generally highest for the mixedwood treatment and similar within the aspen treatments; sugar was not significantly different within a sampling time. Glucose was generally lowest for the heavy decline and highest for the mixedwood overall and within sampling time, except in September 1996 when all aspen treatments were similar. Glucose per m^2 was significantly lower for the heavy decline at each sampling time and overall and the mixedwood was significantly highest. Lower suckering potential of the heavy decline cuttings may have been affected by necrotic areas on the cutting and the formation of calluses at the end of the root cuttings.

Generally, carbohydrate patterns for all treatments were typical of other studies; lowest carbohydrates in summer and highest in fall. Over time, starch, sugar and glucose were significantly higher for the September 1996 sampling time and there was no significant difference over time for glucose per m^2 for all treatments. Lower glucose levels were generally found for the July 1996 sampling time. For glucose per m^2, there was no significant difference over time for treatments, however, with all treatments averaged together, October 1995 had significantly higher glucose per m^2 and July 1996 was significantly lower.

Although sucker production for all treatments commenced at similar points in time for all treatments at each sampling time, the number of suckers in heavy decline and mixedwood treatments generally stopped increasing sooner than the no and low decline treatments. For each growth chamber period, the no and low decline treatments produced more suckers. Approximately 35 days after planting, the no and low decline treatments generally continued to increase in sucker numbers produced whereas the heavy and mixedwood treatments began to taper off although some new suckers continued to be produced. Generally, suckers began to grow approximately 20 days after planting for all sampling times. The development of suckers was similar among treatments although there was some variation in average length and number of leaves produced within each sampling time.

Previous studies indicate that understory species diversity and cover appear to be strongly influenced by overstory structure in forest stands. In this study, forb and shrub composition was generally similar within the pure aspen stands. Mixedwood had similar species as the aspen stands, however, the identity of the dominant species varied. Percent live vegetation cover was lower in the mixedwood stands and percent moss was higher. Average heights of forbs, grasses and shrubs were lower for the mixedwood stands than for the aspen stands. Differences in understory composition may be attributed to canopy cover as previous studies indicate high percentages of marsh reed grass (*Calamagrostis canadensis*) and fireweed (*Epilobium angustifolium*) could be used to indicate amount of light transmission. These two species were ranked the highest within the aspen sites. Species such as alder (*Alnus*), which was one of the most abundant species found in the aspen sites, are often recognized as species that improve a site as they are nitrogen-fixing plants before they succumb to competition by species such as spruce (*Picea*).

2.0 MANAGEMENT IMPLICATIONS

Although the aspen stands are showing signs of decline and there is evidence of root dieback within the Bronson Forest, this study does indicate that these aspen stands have regeneration potential. There was, however, variation within a site in amount of root dieback and suckering potential between decline and non-decline areas. Although carbohydrate status in mixedwood stands is generally better than in the pure aspen sites, for suckering potential to reach full capacity on these sites, silvicultural techniques that improve suckering capacity of the roots at these sites may be needed. However, further research into reasons why the aspen in mixedwood sites have lower sucker potential is needed.

Measures to remove competing vegetation such as *Calamogrostis canadensis*, which may inhibit sucker development in the aspen stands may have to be considered, especially in the heavy decline areas where carbohydrate concentrations in the roots are low. It would be important for suckers to have full photosynthetic capacity to compensate for the lack of carbohydrates in the roots. The suckers would need to develop their own rooting system, as they cannot depend on the root system of the clone to aid in delivering photosynthates needed to compete with aggressive herbaceous species. This is particularly important because areas of the roots in the heavy decline site have begun to deteriorate. However, the aspen roots that have not died back, do have suckering potential. It may also be important to delineate certain areas for aspen harvest only because the presence of species such as white spruce (*Picea glauca*) may potentially reduce aspen regeneration even if aspen roots have high carbohydrate content. In other words, measures would have to be made to keep these sites from moving into the next successional stage including invasion by *Picea glauca*.

3.0 FUTURE RESEARCH

Some possibilities for future research include the analysis of carbohydrates at different times of the year over a period of years on healthy, declining and mixedwood stands to determine if carbohydrates in the decline sites eventually reach similar levels as the no decline and mixedwood sites. It would also be useful to examine the immediate and longer-term impact of defoliation on root carbohydrate levels, dieback and suckering capacity. Limitations to this type of study, however, would be that large areas of aspen clones would be needed because root analysis requires excavation of roots which over time may influence carbohydrate levels within aspen clones. Also, a high degree of replication may be needed to address variability in carbohydrate levels among clones.

A complete analysis of nutrient status of roots and soil site conditions from declining, nondeclining and mixedwood sites at the time of root extraction may be also needed to determine how factors such as nitrogen levels may affect root suckering capacity. Amount of hormones present in roots of declining, nondeclining and mixedwood stands at the time of root extraction may also be important to understand suckering potential of these stands and studies that measure these levels over time and between treatments would be important.

Research that assesses suckering capacity of aspen and mixedwood stands in the field following harvesting would be necessary to determine if assumptions made under growth chamber conditions can be extrapolated into the field. Aspen cuttings from decline and mixedwood sites grew suckers under controlled environmental conditions, however, this response may not be the case in a field situation as the effects of understory vegetation such as *Calamagrostis canadensis*, litter and vegetation may affect growth of the suckers. A study that would remove aggressive plant species at different heights and densities would also indicate whether there is a specific biomass of plants sufficient to allow maximum suckering capacity of roots in declining stands.

Assessing aspen stands in similar decline conditions and mixedwood sites in other areas such as Alberta, Manitoba and areas of the United States where this trend in aspen decline is observed could be done. This would give information as to whether or not other aspen sites have similar patterns of carbohydrate reserves in pure aspen and mixedwood sites.

APPENDIX A

DEVELOPMENT EQUATIONS AND STATISTICAL MODELS FOR CHAPTER 2

Table A.1 General Anova table for the field and growth chamber data.

Source of Variation	Degrees of Freedom (df)	Sum of Squares (SS)	Variance (ms)	F ratio
Blocks	(6-1) = 5	SS for blocks	SS blocks/df blocks	Variance of blocks
Treatment	(4-1) = 3	SS treatment	SS treatment/df treatment	Variance of error
Error	23-(6+4) = 13	SS error	Ss error/df error	
Total	24-1 = 23	SS total		

Table A.2 Polynomial regression formulas derived for average number of suckers, average length and stage of suckers and average number of leaves per sucker.

Shoot Number
October 1995 $= \alpha_I + \beta_i(\mathrm{DAP}) + \delta(\mathrm{DAP})^3$
May 1996 $= \alpha_i + \beta_i(\mathrm{DAP}) + \gamma(\mathrm{DAP})^2$
July 1996 $= \alpha_i + \beta(\mathrm{DAP})$
September 1996 $= \alpha_i + \beta_i(\mathrm{DAP})$

Stage of Shoots
May 1996 $= \alpha_i + \beta_i(\mathrm{DAP}) + \gamma(\mathrm{DAP})^2 + \delta(\mathrm{DAP})^3 + \lambda(\mathrm{DAP})^4$
July 1996 $= \alpha + \beta(\mathrm{DAP})$
September 1996 $= \alpha_i + \beta(\mathrm{DAP}) + \gamma(\mathrm{DAP})^2$

Length of Shoots
May 1996 $= \alpha_i + \beta(\mathrm{DAP})$
July 1996 $= \alpha_i + \beta(\mathrm{DAP})$
September 1996 $= \alpha_i + \beta_i(\mathrm{DAP})$

Number of Leaves
May 1996 $= \alpha_i + \beta(\mathrm{DAP}) + \gamma(\mathrm{DAP})^2 + \delta(\mathrm{DAP})^3 + \lambda(\mathrm{DAP})^4$
July 1996 $= \alpha_i + \beta_i(\mathrm{DAP}) + \delta(\mathrm{DAP})^3$
September 1996 $= \alpha_i + \beta(\mathrm{DAP})$

Where:
α = intercept.
β = regression coefficient associated with (DAP).
γ = regression coefficient associated with $(\mathrm{DAP})^2$.
δ = regression coefficient associated with $(\mathrm{DAP})^3$.
λ = regression coefficient associated with $(\mathrm{DAP})^4$.
(DAP) = days after planting.

Table A.3 Sample calculation for obtaining significant differences between intercepts and coefficients for the Polynomial Regression Equations obtained.

Models fitted for length of shoots

Model 1 = $\alpha_i + \beta_i(DAP) + \gamma_i(DAP)^2 + \delta_i(DAP)^3 + \lambda_i(DAP)^4$
Model 2 = $\alpha_i + \beta_i(DAP) + \gamma_i(DAP)^2 + \delta_i(DAP)^3 + \lambda(DAP)^4$
Model 3 = $\alpha_i + \beta_i(DAP) + \gamma_i(DAP)^2 + \delta_i(DAP)^3$
Model 4 = $\alpha_i + \beta_i(DAP) + \gamma_i(DAP)^2 + \delta(DAP)^3$
Model 5 = $\alpha_i + \beta_i(DAP) + \gamma_i(DAP)^2$
Model 6 = $\alpha_i + \beta_i(DAP) + \gamma(DAP)^2$
Model 7 = $\alpha_i + \beta_i(DAP)$
Model 8 = $\alpha_i + \beta(DAP)$
Model 9 = $\alpha + \beta(DAP)$ – this equation tests if β is equal to zero.

Example: Determining length of shoots between treatments in May 1996.

1) Models being fitted:

a. Model 1 verses model 2
Null hypothesis: $\lambda_{ND}=\lambda_{LD}=\lambda_{HD}=\lambda_{CON}=\lambda$
Variance ratio $= \dfrac{(158963 - 158939)/3}{158939/1839}$
$= 0.093$
F critical = 2.60
Non-significant

b. Model 2 verses model 3
Null hypothesis: $\lambda=0$
Variance ratio: $= \dfrac{(159003 - 158963)/1}{158963/1842}$
$= 0.46$
F critical = 3.84
Non significant

c. Model 3 verses model 4
Null hypothesis: $\delta_{ND}=\delta_{LD}=\delta_{HD}=\delta_{CON}=\delta$
Variance ratio: $= \dfrac{(159411 - 159003)/3}{159003/1843}$
$= 1.58$
F critical = 2.60
Non-significant

d. Model 4 verses model 5

Null hypothesis: $\delta=0$

Variance ratio: $$= \frac{(160080 - 159411)/1}{159411/1846}$$

$= 7.74$

F critical = 3.84

Significant

e. Model 5 verses model 6

Null hypothesis: $\gamma_{ND}=\gamma_{LD}=\gamma_{HD}=\gamma_{CON}=\gamma$

Variance ratio: $$= \frac{(160622 - 160080)/3}{160080/1847}$$

$= 2.08$

F critical = 2.60

Non-significant

f. Model 6 verses model 7

Null hypothesis: $\gamma=0$

Variance ratio: $$= \frac{(160627 - 160622)/1}{160622/1850}$$

$= 0.06$

F critical = 3.84

Non significant

g. Model 7 verses model 8

Null hypothesis: $\beta_{ND}=\beta_{LD}=\beta_{HD}=\beta_{CON}=\beta$

Variance ratio: $$= \frac{(166328 - 160627)/3}{160627/1851}$$

$= 21.9$

F critical = 2.60

Significant

h. Model 8 verses model 9

Null hypothesis: $\alpha_{ND}=\alpha_{LD}=\alpha_{HD}=\alpha_{CON}=\alpha$

Variance ratio: $$= \frac{(174736 - 166329)/3}{166329/1854}$$

$= 31.2$

F critical = 2.60

Significant

Therefore, the model would be equal to: $= \alpha_i + \beta_i(DAP) + \delta_i(DAP)^3$

Table A.4 Polynomial regression equations for average number of suckers per treatment from aspen roots collected in October 1995 and May, July and September 1996.

Time	Estimated Equation	R^2	Significance
<u>October 1995</u>			
No Decline	$= -14.7295 + 0.54238295(DAP) + 0.0000007(DAP)^3$	0.21	0.0001
Low Decline	$= -15.4280 + 0.58581213(DAP) + 0.0000007(DAP)^3$		
Heavy Decline	$= -5.3351 + 0.25325264(DAP) + 0.0000007(DAP)^3$		
Mixedwood	$= -4.8106 + 0.17441935(DAP) + 0.0000007(DAP)^3$		
<u>May 1996</u>			
No Decline	$= -12.5453 + 0.8523(DAP) - 0.0072(DAP)^2$	0.18	0.0001
Low Decline	$= -15.2694 + 0.8728(DAP) - 0.0072(DAP)^2$		
Heavy Decline	$= -10.6893 + 0.6868(DAP) - 0.0072(DAP)^2$		
Mixedwood	$= -12.4571 + 0.7153(DAP) - 0.0072(DAP)^2$		
<u>July 1996</u>			
No Decline	$= 3.199 + 0.1265(DAP)$	0.17	0.0001
Low Decline	$= 1.6406 + 0.1265(DAP)$		
Heavy Decline	$= -1.5208 + 0.1265(DAP)$		
Mixedwood	$= 0 + 0.1265(DAP)$		
<u>September 1996</u>			
No Decline	$= -4.0115 + 0.23327(DAP)$	0.23	0.0001
Low Decline	$= -5.2878 + 0.30466(DAP)$		
Heavy Decline	$= -2.4430 + 0.12724(DAP)$		
Mixedwood	$= -1.6605 + 0.07881(DAP)$		

Table A.5 Polynomial regression equations for average stage of suckers per treatment from aspen roots collected in October 1995 and May, July and September 1996.

Time	Estimated Equation	R^2	Significance
May 1996			
No Decline	$= -21.5560 + 2.8159(DAP) - 0.1162(DAP)^2 + 0.0021(DAP)^3 - 0.0000128(DAP)^4$	0.097	0.0001
Low Decline	$= -21.1298 + 2.8085(DAP) - 0.1162(DAP)^2 + 0.0021(DAP)^3 - 0.0000128(DAP)^4$		
Heavy Decline	$= -20.7272 + 2.8034(DAP) - 0.1162(DAP)^2 + 0.0021(DAP)^3 - 0.0000128(DAP)^4$		
Mixedwood	$= -20.6546 + 2.8011(DAP) - 0.1162(DAP)^2 + 0.0021(DAP)^3 - 0.0000128(DAP)^4$		
July 1996			
No Decline	$= 3.270284314 + 0.022993208(DAP)$	0.033	0.0001
Low Decline	$= 3.270284314 + 0.022993208(DAP)$		
Heavy Decline	$= 3.270284314 + 0.022993208(DAP)$		
Mixedwood	$= 3.270284314 + 0.022993208(DAP)$		
September 1996			
No Decline	$= 1.4241 + 0.12102157(DAP) - 0.001217429\ (DAP)^2$	0.070	0.0001
Low Decline	$= 1.2303 + 0.12102157(DAP) - 0.001217429\ (DAP)^2$		
Heavy Decline	$= 1.6598 + 0.12102157(DAP) - 0.001217429\ (DAP)^2$		
Mixedwood	$= 1.5797 + 0.12102157(DAP) - 0.001217429\ (DAP)^2$		

Table A.6 Polynomial regression equations for average length of suckers per treatment from aspen roots collected in October 1995 and May, July and September 1996.

Time	Estimated Equation	R^2	Significance
<u>May 1996</u>			
No Decline	$= -2.2152 + 0.275473582(\mathrm{DAP})$	0.117	0.0001
Low Decline	$= -1.7580 + 0.275473582(\mathrm{DAP})$		
Heavy Decline	$= -1.5642 + 0.275473582(\mathrm{DAP})$		
Mixedwood	$= -0.8258 + 0.275473582(\mathrm{DAP})$		
<u>July 1996</u>			
No Decline	$= -1.2165 + 0.273739653(\mathrm{DAP})$	0.102	0.0001
Low Decline	$= 0.0994 + 0.273739653(\mathrm{DAP})$		
Heavy Decline	$= -1.1908 + 0.273739653(\mathrm{DAP})$		
Mixedwood	$= 0.1159 + 0.273739653(\mathrm{DAP})$		
<u>September 1996</u>			
No Decline	$= -1.6871 + 0.2570639(\mathrm{DAP})$	0.077	0.0001
Low Decline	$= -0.5056 + 0.2032439(\mathrm{DAP})$		
Heavy Decline	$= 1.2820 + 0.19993736(\mathrm{DAP})$		
Mixedwood	$= 12.3379 - 0.0754641(\mathrm{DAP})$		

Table A.7 Polynomial regression equations for average number of leaves per treatment from aspen roots collected in October 1995 and May, July and September 1996.

Time	Estimated Equation	R^2	Significance
May 1996			
No Decline	$= -54.1773 + 6.1833(DAP) - 0.2510(DAP)^2 + 0.00443(DAP)^3 - 0.00002828(DAP)^4$	0.101	0.0001
Low Decline	$= -54.5423 + 6.1833(DAP) - 0.2510(DAP)^2 + 0.00443(DAP)^3 - 0.00002828(DAP)^4$		
Heavy Decline	$= -53.5491 + 6.1833(DAP) - 0.2510(DAP)^2 + 0.00443(DAP)^3 - 0.00002828(DAP)^4$		
Mixedwood	$= -53.2240 + 6.1833(DAP) - 0.2510(DAP)^2 + 0.00443(DAP)^3 - 0.00002828(DAP)^4$		
July 1996			
No Decline	$= 3.2465 - 0.02134472(DAP) + 0.000005637(DAP)^3$	0.020	0.0001
Low Decline	$= 5.6265 - 0.06904440(DAP) + 0.000005637(DAP)^3$		
Heavy Decline	$= 9.7662 - 0.13461399(DAP) + 0.000005637(DAP)^3$		
Mixedwood	$= 7.0325 - 0.08979352(DAP) + 0.000005637(DAP)^3$		
September 1996			
No Decline	$= -2.0223 + 0.15831817(DAP)$	0.097	0.0001
Low Decline	$= -2.9716 + 0.15831817(DAP)$		
Heavy Decline	$= -1.4797 + 0.15831817(DAP)$		
Mixedwood	$= -1.9020 + 0.15831817(DAP)$		

Figure A.1 Experimental design in the field for no decline (N), low decline (L), heavy decline (H) and mixedwood treatments.

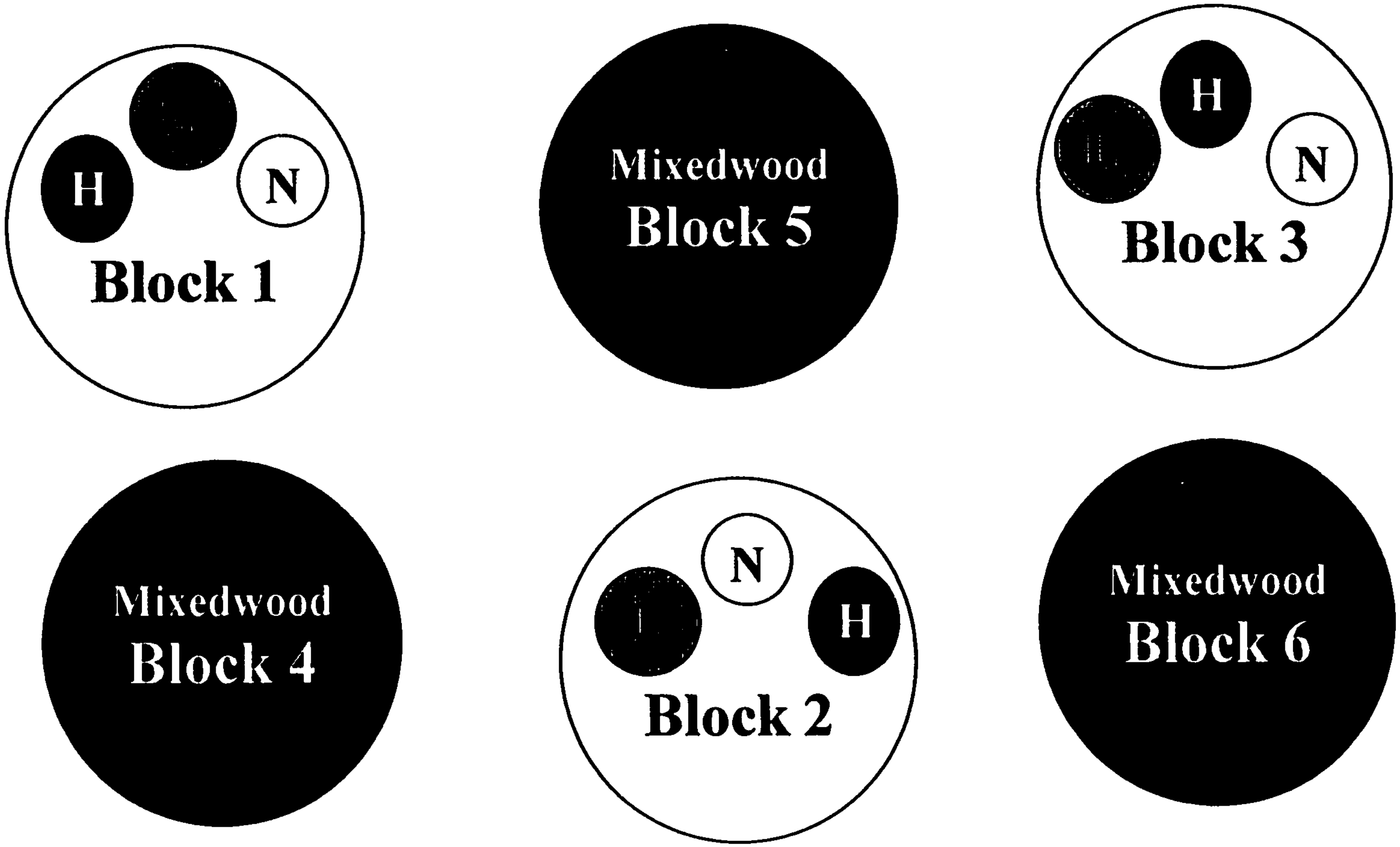
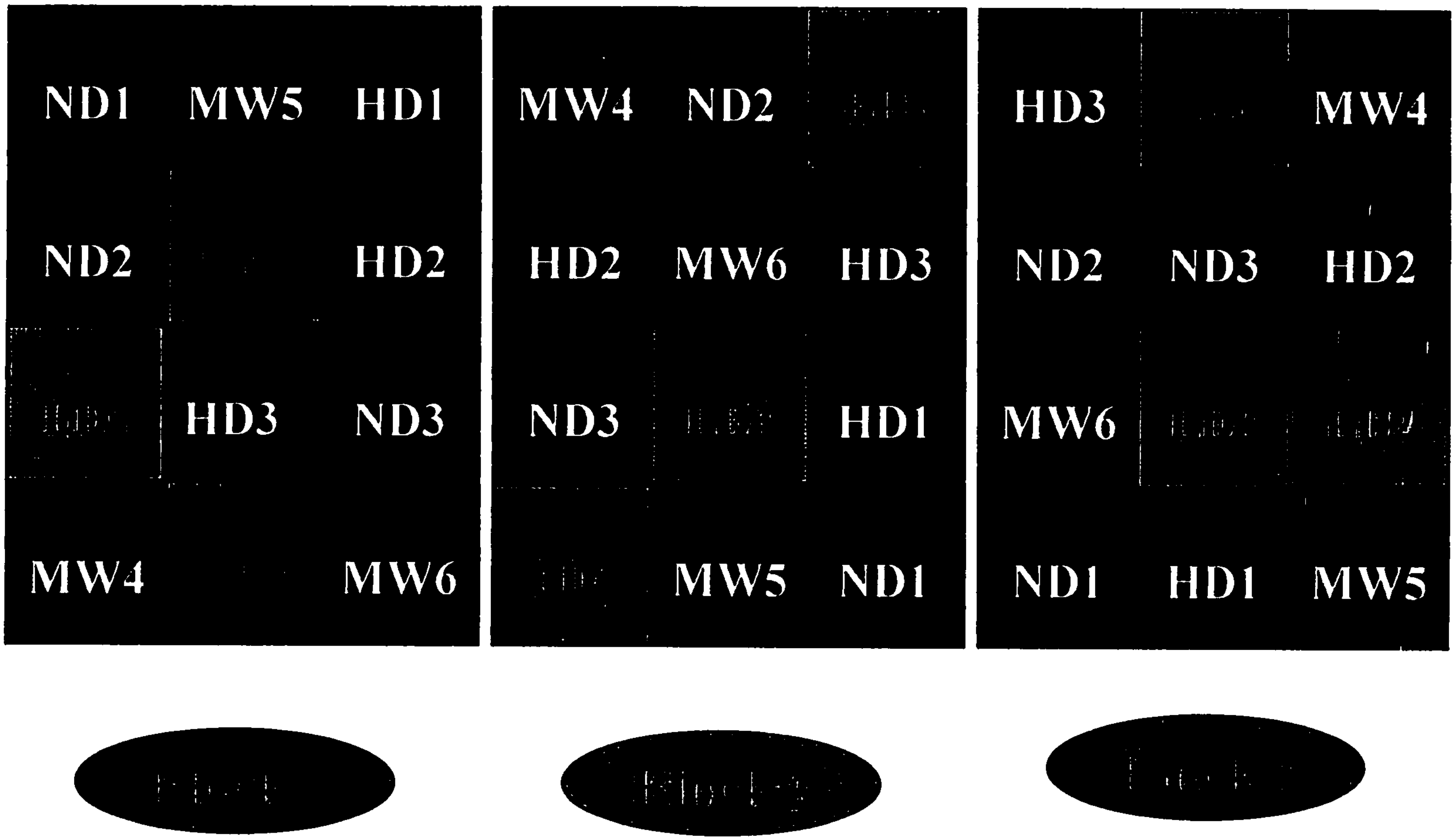


Figure A.2 Experimental design in the growth chamber for no decline (ND), low decline (LD), heavy decline (HD) and mixedwood (MW) treatments.



APPENDIX B

LIGHT EXPERIMENT

SUCKERING CAPACITY AND CARBOHYDRATES FROM DECLINING ASPEN AND MIXEDWOOD STANDS GROWN IN THE LIGHT

1.0 INTRODUCTION

The objectives of this experiment were to assess suckering capacity, total nonstructural carbohydrates and sucker development of roots from declining and non-declining trembling aspen stands and from mixedwood stands in relation to the time of year the roots were collected when grown in the light and compare suckering capacity and sucker characteristics to those grown under no light conditions. It was hypothesized that there would be higher suckering from the roots grown in light conditions. Development of the suckers grown in the light would also be faster than those in the dark.

Carbohydrate content of the roots after growth in the light would be expected to have decreased or be the same depending on time of year collected. It was expected that initially carbohydrates are used only for growth of sucker. In the spring and summer, carbohydrates are generally used for growth of leaves and suckers. In the fall, some carbohydrates are expected to be stored for the winter. However, because these are newly developed suckers, this may not be the case as photosynthates produced by the leaves are primarily used for development of the sucker.

2.0 METHODS

Treatments and methods for this experiment were similar to those in Chapter II, except only 1 site was used for the excavation of roots from each of the aspen and mixedwood treatments. The aspen site chosen was site 2 and the mixedwood was site 4 which were located adjacent to each other. These sites were chosen because there was enough room available for excavation of the roots, after excavation of roots for the main study.

The experiment was conducted in the greenhouse under natural light for a period of 16 hours, supplemented with high intensity discharge (HID) light with a maximum of 450 $u.E.m^2.s^{-1}$. The temperature in the greenhouse ranged from about 18 ^{0}C at night to 22 ^{0}C during the day.

3.0 RESULTS

Although interesting observations were noticed, further investigation with increased sampling size with various clones is needed. Many of the trends may be a reflection of inter clone differences rather than treatment differences.

3.1 Roots

The heavy decline had the highest total length of dead roots in the July and September (Table B1). In May 1996, the mixedwood had the highest total length of dead roots. Overall, the heavy decline and mixedwood treatments had the highest total length of dead roots. The mixedwood had the highest total live root length and the heavy decline had the lowest within each time and overall (Table B.1). When comparing pure aspen stands, the low decline had the highest amount of live roots at each time and overall. This trend was also observed for live roots between 0.5 and 2.0 cm diameter.

3.2 Suckers

3.2.1 Treatment effects within sampling times

Heavy decline generally had the lowest suckering capacity within each time and overall except for in September 1996 and did not sucker at all in July (Table B.2). Highest suckering capacity was variable within each time although in July, mixedwood only suckered half as much as no and low decline and less than a third in September. Overall, the low decline had the highest suckering capacity. The heavy decline had lowest sucker number except in September 1996 when sucker number was highest. Overall, the no decline had the highest number of suckers. Mean sucker weight was generally highest for the no decline treatment within sampling times overall, sucker weight was similar for the low, heavy and mixedwood.

Mean number of leaves per cutting was generally highest in the no decline treatment within sampling time and overall (Table B.3). Mean leaf number was lowest in the heavy decline overall because no leaves were produced in May and there were fewer leaves in September. Leaf area per leaf was similar between the no and low decline. Leaf area per cutting was generally higher for the no decline within each time and overall.

3.2.2 Effects over time

Suckering capacity over time varied with treatment (Table B.2). The no decline and mixedwood had highest suckering capacity in May 1996, whereas the low and heavy decline where highest in September 1996. Mean sucker number was highest in July 1996 for the no and low decline. For mixedwood, mean sucker number was highest in May, and for heavy decline it was highest in September 1996. Generally, mean sucker weight was consistent over time for each treatment except for the no decline where a substantial decrease in mean sucker weight occurred in July 1996.

Mean number of leaves per cutting was generally lowest in July for all treatments (Table B.3). Mean leaf number was substantially lower for no decline in July and September, whereas the low decline increased in leaf area from May to September. Mixedwood was highest in May and similar in July and September 1996. This trend was also observed in the leaf area per cutting.

3.2.3 Comparison of suckers grown in light verses dark

Suckering capacity and number of suckers m^{-1} root for no decline was generally higher for each sampling time except in the September 1996 sampling time (Table B.2). The suckering capacity for low decline was lower when grown in the light in May 1996. Heavy decline was highest in suckering capacity when grown in the dark for May and July 1996, but in September 1996, it was three times as high when grown in the light. Sucker weight for no decline was higher when grown in the light and the other treatments were similar to suckers grown in the dark.

For mean number of leaves and mean leaf area, no decline, low decline and mixedwood were higher for each sampling time (Table B.3). Heavy decline did not produce suckers in the light for May and July 1996, however, in September 1996, the suckers grown in the dark produced more leaves on average, but mean leaf area was lower. Leaf area per cutting was higher for treatments grown in the light for all sampling times and overall.

3.3 Carbohydrates

Generally, the heavy decline had the lowest amount of starch, sugar and glucose within a sampling time and overall (Table B.4). Over time, September 1996 had the highest amounts of starch and glucose. Sugar did not have consistent results over time. There was a decrease in starch, sugar and glucose after suckers were growing in the light (Table B.5) compared to roots sampled before planting (Table B.4).

Generally starch was lowest in July 1996 and highest in September (Table B.4) for all treatments. For sugar, there was no trend over time. Overtime, all treatments had highest amounts of glucose in September 1996.

3.4 Development of Suckers

Only suckers that grew were used in the analysis. For May and July 1996, roots began to sucker approximately 25 days after planting, whereas September 1996 suckers appeared approximately 30 days after planting (Figure B.1). The no decline treatment generally had more suckers in May than in July and September 1996. There was no suckering in the heavy decline in May and July 1996, however, in September 1996, some suckering was observed. The low decline treatment grew between 3 to 4 suckers by about 30 to 35 days after planting for each time and generally did not increase in sucker number. The mixedwood gradually increased in sucker number reaching maximum number of suckers about 40 to 45 days after planting (about 3 to 4 suckers) in May and July 1996. In September, the mixedwood only reached about 1 to 2 suckers per cutting by the end of the growing period.

All suckers observed were at stage 5 for all treatments immediately after suckers reached the surface of the sand (Table B.6). This was different from suckers grown in the dark (Figure 2.2) in that there was a gradual increase to stage 5 and suckers generally did not reach this stage until about 40 to 45 days after planting when grown in the dark. There were no trends in average length of suckers over time or between treatments (Figure B.2). However, in May 1996 the no decline suckers were taller than in July and September, whereas the low decline was the shortest overtime compared to July and September 1996. There were no trends in number of leaves over time or between treatments (Figure B.3). However, number of leaves developed over time was between 4 and 12 leaves per cutting.

Suckers grown in the light reached only about half the length (Figure B.2) of the roots that grew under no light conditions (Figure 2.3).

4.0 DISCUSSION

Although amount of dead roots found in the mixedwood was high in May 1996, percent of dead roots was only 16%, whereas in the heavy decline dead roots accounted for 38% of the root length. In the no and low decline treatments, percent dead roots in May were 25 and 7%, respectively. Overall, the percent of dead roots found in the heavy decline was 53% compared with the no, low and mixedwood stands which were 13, 18 and 11%, respectively. Thus, as hypothesized, higher amounts of dead root length were found in the heavy decline, thus, live root length was also lowest.

It is interesting that although no suckers grew in May and July in the heavy decline, there was still a drop in the carbohydrate content. Although the roots are not part of an intact root system, there are still indications of root respiration used possibly for the development of new suckers. One difference observed in the roots is the decrease in starch, sugar and glucose after the suckers were growing in the light indicating that photosynthates produced by leaves were not being translocated to the roots and used for sucker growth.

Generally, the May 1996 cuttings seemed to give more suckers for the no and low decline and mixedwood treatments. Heavy decline treatment suckers seemed to do best in September 1996 cuttings.

Although suckering capacity was variable between suckers grown in light and dark, there were higher sucker numbers per cutting for suckers grown in the dark in the September 1996 sampling time. At this time carbohydrates were highest. The higher number of leaves and leaf area for suckers grown in the light indicate production of photosynthates for leaf development. Suckers also reached stage 5 immediately after reaching the surface when growing in the light. The length of suckers grown in the light where shorter than those under no light conditions indicates elongation occurred in shoots grown in the dark as they try to reach light.

Table B.1 Root length in the no decline, low decline, high decline and mixedwood treatments from May to September 1996.

	May 1996	July 1996	September 1996	Overall
Root Class	Mean	Mean	Mean	Mean
Dead Roots (cm)				
No Decline	339	95	43	159
Low Decline	160	469	566	398
Heavy Decline	231	561	606	466
Mixedwood	1008	124	327	486
Live Roots (cm)				
No Decline	1334	1101	1151	1195
Low Decline	2122	1180	2297	1866
Heavy Decline	376	922	1351	883
Mixedwood	5389	2323	4400	4038
Live Roots 0.5 to 2.0 cm Diameter (cm)				
No Decline	652	392	349	464
Low Decline	861	448	1244	851
Heavy Decline	190	388	685	421
Mixedwood	1368	849	1398	1205

Table B.2 Suckering capacity, number of suckers and average sucker weight in the no decline, low decline, high decline and mixedwood treatments from May to September 1996 from roots collected from site 2 and 4 and grown in the light and dark.

	May 1996		July 1996		September 1996		Overall	
Root Class	Mean		Mean		Mean		Mean	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark
Suckering Capacity (suckers m^2)								
No Decline	198	133	363	37	131	207	231	126
Low Decline	267	523	318	270	343	329	309	374
Heavy Decline	17	120	0	70	434	144	150	111
Mixedwood	278	351	152	187	48	264	159	268
Sucker Number Suckers m^{-1} Root								
No Decline	3.0	2.1	9.3	1.2	3.8	6.2	5.4	3.3
Low Decline	3.1	6.3	7.1	5.7	2.8	6.3	4.3	6.2
Heavy Decline	0.9	3.7	0.0	6.0	6.3	8.6	2.4	5.3
Mixedwood	2.0	2.8	1.8	2.1	0.3	2.0	1.4	2.3
Sucker Weight (gm)								
No Decline	0.19	0.06	0.08	0.05	0.18	0.09	0.15	0.07
Low Decline	0.06	0.09	0.06	0.04	0.10	0.10	0.07	0.08
Heavy Decline	0.08	0.18	0.00	0.04	0.07	0.10	0.07	0.14
Mixedwood	0.08	0.07	0.05	0.05	0.06	0.03	0.06	0.05

Table B.3 Number of leaves and leaf area in the no decline, low decline, high decline and mixedwood treatments at three different times from May to September 1996 from roots collected from site 2 and 4 and grown in the light and dark.

	May 1996		July 1996		September 1996		Overall	
Root Class	Mean		Mean		Mean		Mean	
	Light	Dark	Light	Dark	Light	Dark	Light	Dark
Mean Number of Leaves per Cutting								
No Decline	10.3	4.3	6.0	5.5	13.6	4.7	10.0	4.7
Low Decline	7.8	4.0	6.8	4.2	8.9	6.3	7.8	4.7
Heavy Decline	0.0	5.5	0.0	7.7	4.3	11.4	2.2	7.6
Mixedwood	5.4	4.7	5.3	4.9	7.3	2.2	6.0	3.8
Mean Leaf Area (cm^2 $leaf^{-1}$)								
No Decline	2.4	0.7	1.3	0.2	1.4	0.7	1.7	0.6
Low Decline	0.7	0.2	1.4	0.1	3.1	0.3	1.7	0.2
Heavy Decline	0.0	0.2	0.0	0.1	2.1	0.7	1.1	0.4
Mixedwood	1.2	0.5	1.0	0.2	1.0	0.5	1.1	0.4
Leaf Area (cm^2 $cutting^{-1}$)								
No Decline	34.8	4.3	16.5	2.4	27.7	5.8	26.4	4.6
Low Decline	10.0	2.0	22.2	0.9	26.9	3.4	19.7	2.1
Heavy Decline	0.0	1.7	0.0	1.1	24.4	3.9	12.2	2.3
Mixedwood	14.8	3.0	8.3	1.8	9.1	3.8	10.7	2.8

Table B.4 Total starch, sugar and glucose in aspen roots from the no decline, low decline, high decline and mixedwood treatments at three different times from May to September 1996 before suckers were grown in the light.

	May 1996	July 19966	September 1996	Overall
Root Class	Mean	Mean	Mean	Mean
Starch (gm gm^{-1})				
No Decline	0.047	0.053	0.195	0.098
Low Decline	0.047	0.048	0.115	0.070
Heavy Decline	0.036	0.014	0.136	0.062
Mixedwood	0.067	0.061	0.107	0.078
Sugar (gm gm^{-1})				
No Decline	0.109	0.100	0.116	0.108
Low Decline	0.114	0.129	0.119	0.210
Heavy Decline	0.088	0.109	0.099	0.099
Mixedwood	0.145	0.117	0.164	0.142
Glucose (gm gm^{-1})				
No Decline	0.155	0.153	0.311	0.206
Low Decline	0.160	0.177	0.234	0.190
Heavy Decline	0.124	0.122	0.235	0.160
Mixedwood	0.212	0.177	0.271	0.220

Table B.5 Total starch, sugar and glucose in aspen roots from the no decline, low decline, high decline and mixedwood treatments at three different times May to September 1996 after suckers were grown in the light.

Root	May 1996		July 1996		September 1996		Overall	
Class	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Starch (gm gm^{-1})								
No Decline	0.004	0.002	0.006	0.004	0.069	0.057	0.026	0.043
Low Decline	0.013	0.005	0.006	0.001	0.032	0.017	0.017	0.015
Heavy Decline	0.013	0.003	0.005	0.003	0.034	0.007	0.017	0.013
Mixedwood	0.025	0.006	0.007	0.006	0.057	0.001	0.029	0.023
Sugar (gm gm^{-1})								
No Decline	0.068	0.011	0.094	0.023	0.092	0.016	0.085	0.019
Low Decline	0.090	0.017	0.094	0.016	0.076	0.011	0.087	0.015
Heavy Decline	0.053	0.014	0.083	0.016	0.101	0.023	0.079	0.026
Mixedwood	0.105	0.021	0.087	0.010	0.110	0.025	0.101	0.020
Glucose (gm gm^{-1})								
No Decline	0.072	0.012	0.100	0.019	0.161	0.070	0.111	0.054
Low Decline	0.103	0.022	0.101	0.016	0.108	0.021	0.104	0.018
Heavy Decline	0.066	0.013	0.088	0.019	0.135	0.031	0.096	0.036
Mixedwood	0.130	0.022	0.093	0.015	0.167	0.024	0.130	0.037

Table B.6 Average stage of sucker development from root cuttings collected in May, July and September 1996.

	Treatments							
	No Decline		Low Decline		Heavy Decline		Mixedwood	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Days After Planting								
May 1996								
26	NA[1]	NA	5.00	0.00	0.00	0.00	5.00	NA
30	NA	NA	5.00	0.00	0.00	0.00	5.00	NA
37	5.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00
44	4.71	0.59	5.00	0.00	0.00	0.00	5.00	0.00
51	5.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00
July 1996								
25	NA	NA	NA	NA	0.00	0.00	NA	NA
33	5.00	0.00	5.00	0.00	0.00	0.00	4.86	0.38
40	5.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00
53	5.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00
September 1996								
34	5.00	0.00	5.00	0.00	5.00	NA	NA	NA
42	5.00	0.00	5.00	0.00	5.00	0.00	5.00	NA
49	5.00	0.00	5.00	0.00	5.00	0.00	5.00	0.00

[1] NA – Not applicable

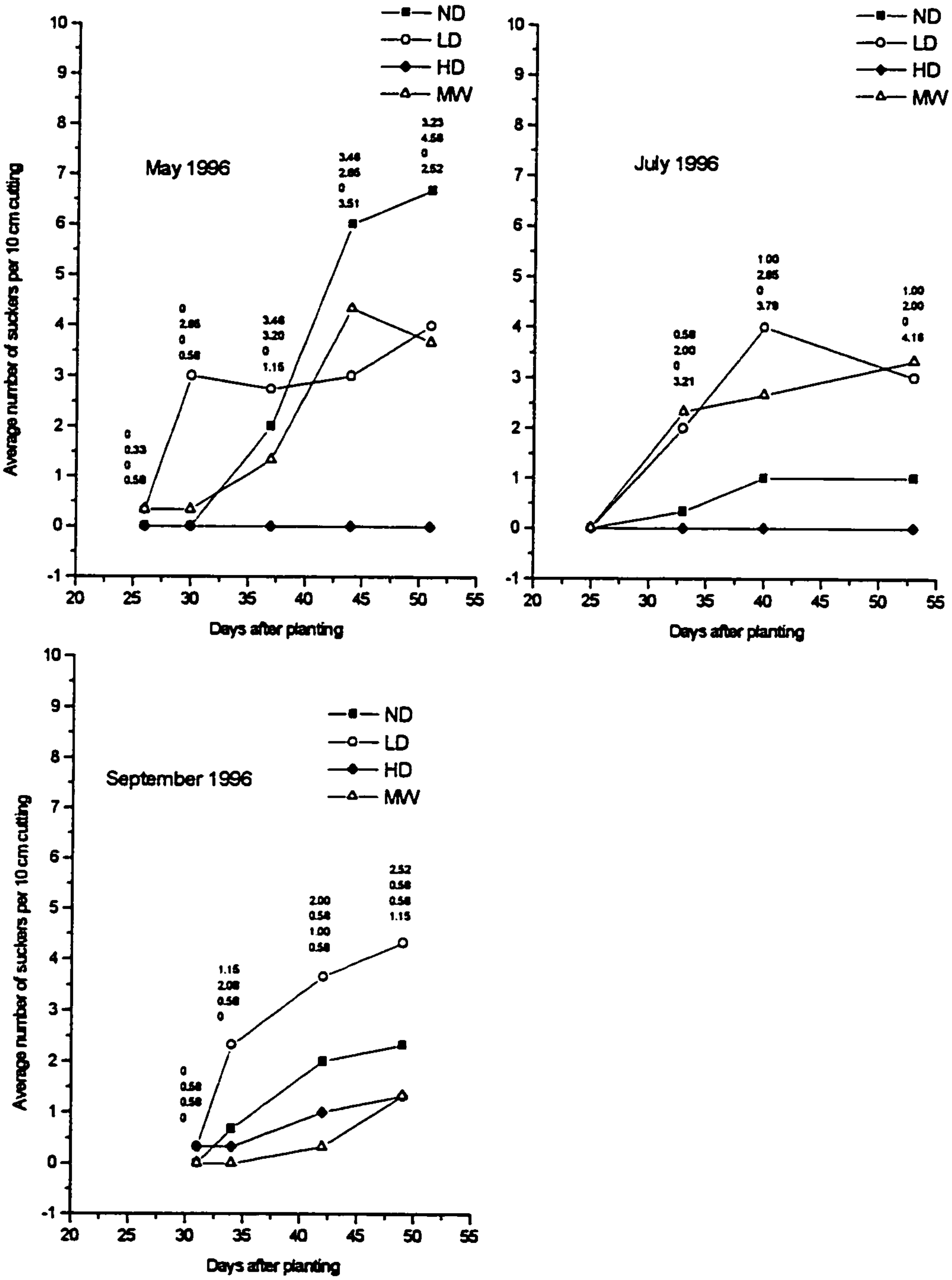


Figure B.1 Average number of suckers per treatment from aspen root cuttings collected in May, July and September 1996 and grown in the light. Numbers at each point are standard deviations in the order of treatments on the legend.

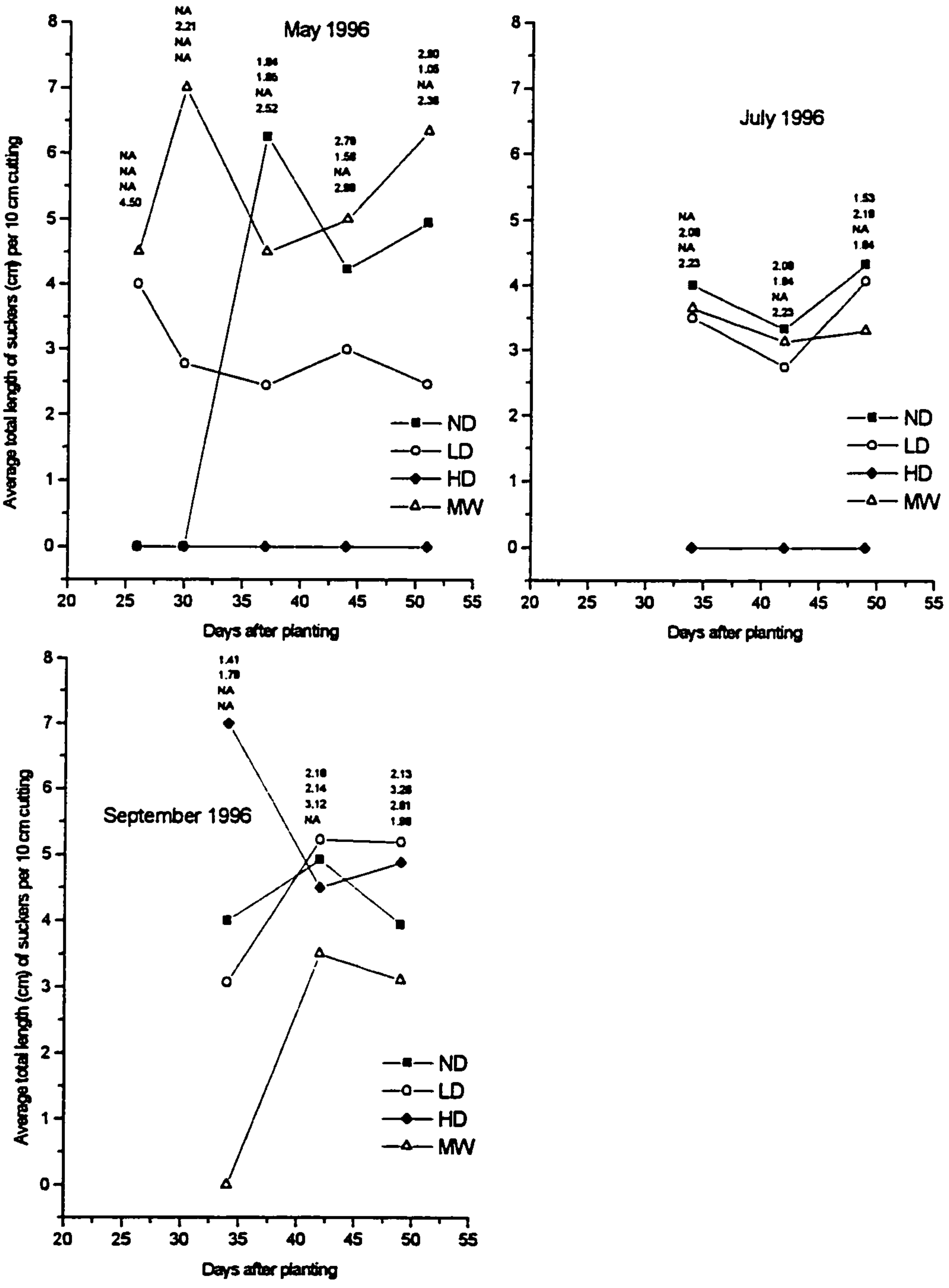


Figure B.2 Average total length of suckers per treatment from aspen root cuttings collected in May, July and September 1996 and grown in the light. Numbers at each point are standard deviation in the order of treatments on the legend.

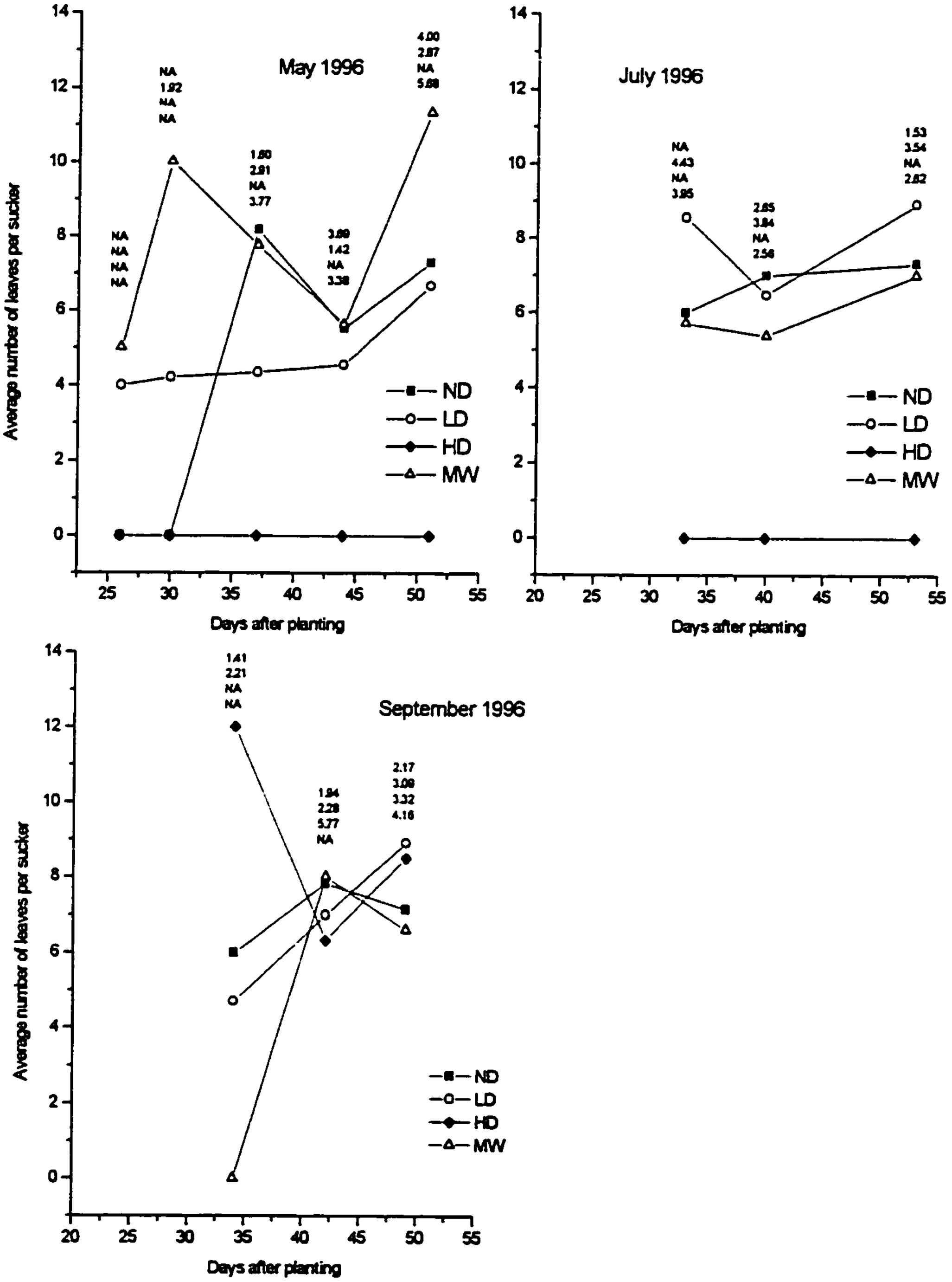


Figure B.3 Average number of leaves per treatment from aspen root cuttings collected in May, July and September 1996 and grown in the light. Numbers at each point are standard deviations in the order of treatments on the legend.

APPENDIX C

VEGETATION

Table C.1 Average number of species found in each treatment.

	No Decline		Low Decline		Heavy Decline		Mixedwood	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<u>Forbs/Grasses</u>								
Site 1	12.3	1.2	14.7	1.2	13.0	5.9	6.3	2.5
Site 2	14.0	3.0	11.7	3.5	11.7	3.1	10.3	1.2
Site 3	11.0	3.0	11.0	2.0	10.3	3.8	10.7	4.5
Site 1-3 (4-6 MW)	12.4	2.6	12.5	2.7	11.7	4.0	9.1	3.4
<u>Shrubs</u>								
Site 1	3.7	0.6	5.7	1.2	4.7	0.6	5.3	1.5
Site 2	5.7	1.5	4.0	1.7	5.3	0.6	2.3	1.2
Site 3	4.7	0.6	5.7	0.6	6.3	1.5	3.4	0.6
Site 1-3 (4-6 MW)	4.7	1.2	5.1	1.4	5.4	1.1	3.9	1.5

Table C.2 Vegetative characteristics from the aspen decline and mixed wood stands. Ground cover assessments of vegetation, litter, moss and bareground.

	No Decline		Low Decline		Heavy Decline		Mixedwood	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<u>Ground Cover</u>								
Vegetation								
Site 1	8.3	0.6	16.0	2.7	19.3	3.2	79.7	3.0
Site 2	11.3	2.1	10.7	2.1	13.0	1.7	12.3	1.2
Site 3	7.3	4.5	13.7	2.5	12.3	2.5	8.0	1.5
Site 1-3 (4-6 MW)	9.0	3.1	13.4	3.1	14.9	4.0	5.3	2.9
<u>Litter</u>								
Site 1	90.7	1.5	81.7	1.5	79.3	3.2	79.7	0.6
Site 2	88.7	2.1	87.7	3.1	84.7	1.5	97.3	1.2
Site 3	92.7	4.5	84.3	4.2	87.7	2.5	94.3	2.1
Site 1-3 (4-6 MW)	90.7	3.1	84.6	3.8	83.9	4.3	90.4	8.3
<u>Moss</u>								
Site 1	1.0	1.7	2.3	4.0	1.3	2.3	12.3	3.1
Site 2	0.0	0.0	1.7	2.9	2.3	2.5	0.0	0.0
Site 3	0.0	0.0	2.0	1.7	0.0	0.0	0.3	0.6
Site 1-3 (4-6 MW)	0.3	1.0	2.0	2.7	1.2	2.0	4.2	6.3
<u>Bare Ground</u>								
Site 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Site 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Site 3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Site 1-3 (4-6 MW)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table C.3 Vegetative characteristics from the aspen decline and mixed wood stands. Average height of forbs, grasses, shrubs and tall shrubs.

	No Decline		Low Decline		High Decline		Mixedwood	
Average heights	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Forbs (m)								
Site 1	0.37	0.12	0.40	0.18	0.40	0.13	.	.
Site 2	0.72	0.06	0.65	0.00	0.65	0.13	0.45	0.26
Site 3	0.67	0.10	0.61	0.09	0.59	0.15	0.22	0.04
Site 1-3 (4-6 MW)	0.59	0.19	0.55	0.15	0.55	0.17	0.33	0.21
Grass (m)								
Site 1	0.79	0.07	0.27	0.13	0.50	0.22	.	.
Site 2	0.68	0.28	0.70	0.00	1.12	0.90	0.49	0.33
Site 3	0.72	0.10	0.72	0.37	0.53	0.13	0.47	0.15
Site 1-3 (4-6 MW)	0.73	0.16	0.56	0.29	0.72	0.55	0.48	0.23
Shrubs (m)								
Site 1	0.78	0.04	0.76	0.14	0.79	0.09	.	.
Site 2	0.81	0.32	1.25	0.00	0.78	0.03	0.32	0.08
Site 3	0.61	0.09	0.65	0.01	0.67	0.18	0.80	0.09
Site 1-3 (4-6 MW)	0.73	0.19	0.89	0.28	0.75	0.11	0.56	0.27
Tall Shrubs (m)								
Site 1	2.29	0.70	2.34	0.09	2.13	0.30	.	.
Site 2	2.24	0.23	1.73	0.00	1.93	0.47	.	.
Site 3	1.63	0.32	2.03	0.32	2.44	0.00	1.83	0.00
Site 1-3 (4-6 MW)	2.05	0.51	2.03	0.31	2.17	0.36	1.83	0.00

Table C.4 Species list of forbs and grasses.

Latin Name	Common Name
Achillea millefolium L.	Yarrow
Agropyron sp. Gaertn.	Wheatgrass sp.
Aralia nudicaulis L.	Wild sarsparilla
Artemisia campestris L.	Wormweed
Aster conspicuus Lindl.	Showy aster
Aster laevis L.	Smooth aster
Aster sp. L.	Aster sp.
Bromus inermis Leyss.	Smooth brome
Calamagrostis canadensis Beauv.	Marsh reed grass
Campanula rotundifolia L.	Common harebell
Carex sp. L.	Sedge sp.
Cornus canadensis L.	Bunchberry
Disporum trachycarpum S. Wats.	Fairybells
Elymus innovatus Beal	Hairy wild rye
Epilobium angustifolium L.	Fireweed
Equisetum arvense L.	Horsetail
Fragaria virginiana Duchesne	Wild strawberry
Galium boreale L.	Northern betstraw
Galium sp. L.	Bedstraw sp.
Galium triflorum Michx.	Sweet-scented bedstraw
Geranium sp. L.	Geranium sp.
Graminae sp.	Grass sp.
Lactuca sp. L.	Lettuce sp.
Lathyrus ochroleucus Hook.	Creamy-coloured vetchling
Lathyrus venosus Muhl.	Peavine
Ledum groenlandicum Oeder	Common labrador tea
Linnaea borealis L.	Twin-flower
Maianthemum canadense Desf.	Wild lily-of-the-Valley
Mitella nuda L.	Bishop's cap
Mushroom sp.	Mushroom sp.
Oryzopsis sp. Michx.	Rice grass
Petasites sagittatus (Pursh) A. Gray	Arrow-leaved coltsfoot
Plantago major L.	Common plantain
Poa compressa L.	Canada bluegrass
Pyrola sp. L.	Wintergreen
Rubus pubescens Raf.	Running raspberry
Smilacina stellata Desf.	False solomon's-seal
Sphagnum sp.	Sphagnum sp.
Taraxacum officinale Weber	Dandelion
Thalictrum sp. L.	Western meadowrue
Trifolium hybridum L.	Alsike clover
Trifolium repens L.	White clover
Vicia americana Muhl.	American vetch
Viola adunca J.E. Smith	Early blue violet
Viola renifolia A. Gray	Kidney-leaved violet
Viola sp. L.	Violet sp.

Table C.5 Species list of trees and shrubs.

Latin Name	Common Name
Alnus sp Mill.	Alder sp.
Amelanchier alnifolia Nutt.	Saskatoon
Arctostaphylos uva-ursi (L.) Spreng	Common bearberry
Betula papyrifera Marsh.	Paper birch
Corylus cornuta Marsh.	Beaked hazelnut
Ledum groenlandicum Oeder	Common labrador tea
Lonicera dioica L.	Twining honeysuckle
Lonicera involucrata (Richards.) Banks	Bracted honeysuckle
Picea glauca (Moench) Voss	White spruce
Populus balsamifera L.	Balsam poplar
Populus tremuloides Michx.	Trembling aspen
Ribes triste Pall.	Wild red currant
Rosa woodsii Lindl.	Common wild rose
Rubus idaeus L.	Raspberry
Salix sp. L.	Willow sp.
Shepherdia canadensis (L.) Nutt.	Buffalo-berry
Symphoricarpos albus (L.) Blake	Snowberry
Symphoricarpos occidentalis Hook.	Buckbrush
Viburnum edule Raf.	Low-bush cranberry