EFFECTS OF FERTILIZATION ON ROOTS OF SUGAR MAPLE

(*Acer saccharum* Marsh.)

by

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Abstract

Studies were undertaken to determine the effects of fertilizer and liming materials on soil and fine root chemistry and fine root biomass, and on the starch content of larger diameter sugar maple (*Acer saccharum* Marsh.) roots. Responses in fine root biomass, fine root chemistry, and soil chemistry were observed using root-free ingrowth cores containing an organic based fertilizer (3-4-8 plus dolomitic limestone at a rate of 800 kg/ha), an inorganic fertilizer (0-3-29 plus calcite and dolomite at a rate of 1370 kg/ha), or no fertilizer. The cores were installed in three mature sugar maple stands for one year. Significant differences ($p \leq 0.05$) in many root and soil chemical properties existed among sites. Greatest treatment response in soil and fine root chemistry occurred at the site with the poorest nutrient status. Fine root biomass decreased due to treatment at one site. No other response in fine root biomass was observed.

Larger diameter roots were sampled at two sites from sugarbush fertilization plots treated with base rich fertilizers. At one site, an acidifying treatment was also applied. Significant differences ($p \leq 0.05$) in root starch content were observed between the acidifying treatment and the most base enriched treatments several years following fertilization.

Résumé

Afin de déterminer les effets de l'ajout de matériaux riches en cations basiques et de fertilisants sur l'érable à sucre (*Acer saccharum* Marsh.), des études portant sur la chimie et la biomasse de radicelles, la chimie du sol ainsi que sur le contenu en amidon de racines ont été entreprises. Des cavités de croissance radiculaire ont été utilisées pour observer la réponse de la biomasse des radicelles et la chimie du sol et des radicelles. Les cavités contenaient du sol libre de racines provenant du site même, auxquel était ajouté soit un fertilisant à base organique (3-4-8 plus chaux dolomitique appliqué à un taux de 800 kg/ha), soit un fertilisant inorganique (0-3-29 plus calcite et dolomie, appliqué à un taux de 1370 kg/ha), soit aucun fertilisant. Les sacs ont été installés pour un an dans trois érablières au Québec. Des différences significatives ($p \leq 0.05$) pour plusieurs propriétés chimiques du sol et des radicelles existent entre ces trois sites. La plus importante réponse aux traitements en termes de chimie du sol et des radicelles a été obtenue au site ayant le statut nutritif le plus pauvre. Une diminution de la biomasse des radicelles suite aux traitements a été observée à un des sites; aucune autre réponse au niveau de la biomasse n'a été mesurée.

Des racines de plus grand diamètre ont été échantillonnées pour leur contenu en amidon à deux érablières fertilisées antérieurement. Les différents traitements appliqués étaient à base de cations, mais à un des deux sites un traitement acidifiant avait également été appliqué. Des différences significatives ($p \leq 0.05$) ont été observées entre le contenu en amidon des racines provenant des parcelles traitées à base de fertilisants

riches en cations et celle ayant subi un traitement acidifiant et ce, plusieurs années après la fertilisation.

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Preface

The purpose of this study was to examine the effects of fertilizer treatments on soil and sugar maple fine root chemistry, fine root biomass, and starch content of larger roots. The project was in association with ongoing research into the effects of fertilization on the health of declining sugar maple stands in Quebec. The first chapter is an overview of forest decline and the attributes of sugar maple decline in Quebec. The second chapter is concerned with the effects of fertilizer treatments on soil and fine roots, and the third chapter deals with the effect of fertilization on the starch content of larger diameter roots. The latter two chapters are presented in paper format with introductions pertaining specifically to the experiments. The fourth chapter contains overall conclusions about the research and suggestions for future investigations. The appendices contain soil chemical properties of the study sites and soil and root chemical data not presented in the body of the thesis.

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Chapter 1: Forest Decline

1.1 Introduction

Forest declines are complex diseases involving sequential biotic and abiotic stresses and their interactions (Manion 1981). Declines cause a gradual and progressive deterioration of tree health resulting in the death, or dieback, of the tree canopy and eventually of the entire tree (McLaughlin 1985). At the stand level, dieback results in contiguous trees dying in groups, rather than as individuals within a healthy milieu (Mueller-Dombois 1987).

Decline and dieback have historically occurred in temperate forests, with causes attributed principally to climatic and biotic stress (Cowling 1985a; Rennie 1986; Mueller-Dombois 1987; Smith 1987). However, within the past decade concern about decline and dieback has greatly increased. Declines have rapidly become more extensive in Europe and North America, affecting a number of species simultaneously across ranges of climate, physiography, soil type, stand management, and pollution exposure (McLaughlin 1985). Recent declines ("neuartige Waldschäden" or "novel forest decline") are more intense and systematic than previous decline episodes, and are separable from declines involving only climatic and biotic stresses, specific pollution sources, or silvicultural practices (Krause et al. 1986; Prinz 1987).

Symptoms of current forest declines include reduced growth rate, loss of foliar biomass, branch dieback, foliar discoloration, decreased fine root biomass, decreased incidence of mycorrhizae, abnormal growth, altered photosynthate allocation patterns, altered leaf morphology, excessive seed production, altered water relations, and increased susceptibility to secondary stress (Schütt and Cowling 1985; Hinrichsen

1987; Jakucs 1988). Reduced growth rate is considered to be one of the foremost symptoms of decline, as dendroecological analyses show growth reduction since the late 1950's and early 1960's, well before visible dieback symptoms were observed (Adams et al. 1985; McLaughlin et al. 1987; Nilsson and Duinker 1987).

Both coniferous and deciduous species are currently affected by decline. In Europe, affected species include *Picea abies* (L.) Karst., *Abies alba* Mill., *Larix decidua* Mill., *Pinus sylvestris* L., *Fagus sylvatica* L., *Quercus* spp., *Alnus glutinosa* (L.) Gaertn., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., and *Betula verrucosa* Roth. (Schütt and Cowling 1985; Hinrichsen 1987; Jakucs 1988). In North America, declining species include *Picea rubens* Sarg., *Abies fraseri* (Pursh), *Pinus taeda* Sarg., *P. elliottii* Engelm., *P. echinata* Miller, *Abies balsamea* (L.) Mill., *Acer saccharum* Marsh., and *Quercus rubra* L. (Auclair 1987a; Hinrichsen 1987; Prinz 1987; Bruck et al. 1989; Pitelka and Raynal 1989; Kelly et al. 1990).

1.2 Causes of Forest Decline

1.2.1 Classification of Stress Factors

The classification of causal factors by Manion (1981) has been widely used in investigations of recent declines. Stresses may be categorized as:

1) predisposing: static, permanent stress due to site factors, climate, continuous exposure to air pollution, or limitations of genotypic plasticity,

2) inciting: acute, short-term biological or physical stress due to insect defoliation, climatic extremes or shocks, mechanical injury, or intermittent exposure to air pollution, and

3) contributing: visible, persistent stress factors such as bark beetles, root rots and other pathogenic fungi as well as other disease and decay agents which are ultimately blamed for the death of the tree.

According to Manion's hypothesis, at least one factor from each group is involved in a particular decline syndrome, with the effects being cumulative. This type of classification permits recognition and analysis of all biotic and abiotic stress factors implicated in decline on a case by case basis. However, the flexible nature of this classification may hinder the establishment of clear cause and effect relationships (Blank et al. 1988). Decline symptoms must be considered in the context of the site at which they occur (Manion 1985).

An alternative classification of causal factors may be made by categorizing stress factors as natural or anthropogenic (Klein and Perkins 1988). In the context of recent declines, anthropogenic stress factors refer mainly to atmospheric pollutants although mechanical injury, soil compaction, and management practices may be included in this category (Woodman and Cowling 1987). This classification is useful in considering contemporary declines, as anthropogenic pollutant stress is thought to be involved in decline to a greater (McLaughlin 1985; Schütt and Cowling 1985; Hauhs and Wright 1986; Prinz 1987; Smith 1987; Chevone and Linzon 1988; Schäfer et al. 1988) or lesser extent (Foster 1989; Johnson and Taylor 1989; Pitelka and Raynal 1989; Rehfeuss 1989). The presence of pollution stress may signify the difference between previous and current declines in the capacity of forests to recover (Hendershot and Jones 1989).

Natural stresses include drought, flooding, unseasonable frost, nutrient stress, wind, insect damage, disease, pathogenic fungi, stand aging, competition, and proximity to species climatic limits (Manion 1981; Mueller-Dombois 1987; Woodman and Cowling 1987; Klein and Perkins 1988; Foster 1989). Previous, isolated examples of decline are associated primarily with natural stress factors.

Anthropogenic pollutants include acidic deposition, gaseous pollutants, elevated nitrogen (N) deposition, and heavy metal deposition acting independently or interactively (Klein and Perkins 1988; Johnson and Taylor 1989).

1.2.2 Anthropogenic Pollution Stress

The effects of atmospheric pollutants on forests have been extensively reviewed (Tamm and Cowling 1977; Abrahamsen and Tveite 1983; Morrison 1984; McLaughlin 1985; Kozlowski and Constantinidou 1986; Linzon 1986). The following discussion summarizes the main mechanisms of pollution stress thought to be involved in forest decline.

1.2.2.1 Acidic Deposition

The atmospheric deposition of acidic materials is regional in nature and includes wet (precipitation) and dry (particulate) deposition of sulphuric and nitric acids (Smith 1985). The effects of acid deposition on forests are largely indirect and are related to nutrient cycling through vegetation and soils (Reich et al. 1988).

Acid precipitation may increase foliar leaching of nutrient ions such as potassium (K), calcium (Ca), and magnesium (Mg), predisposing trees to nutrient deficiencies if adequate nutrients cannot be obtained from the soil (Matzner 1986; Hüttl et al. 1990). Increased foliar leaching under acidic precipitation may not occur for all species (Turner and Tingey 1990). Accelerated foliar leaching advances rhizosphere acidification, as protons (H^+) are released with the uptake of replacement cations to maintain electroneutrality at the root surface (Ulrich 1983a; Binkley and Richter 1987).

Elevated acid inputs may cause replacement of base cations on the soil exchange complex with H^+ or aluminum (Al) and increase base cation leaching from the rooting zone of soils, resulting in decreased nutrient supply and exacerbated foliar losses (Ulrich et al. 1980; Matzner and Ulrich 1985). As soil pH decreases, Al solubility and plant availability increases, resulting in: 1) toxicity to fine roots and a subsequent decrease in the uptake of water and other nutrients (Hüttermann 1985; Meyer et al. 1985; 1988; Cronan et al. 1989), and/or 2) physiological interference of nutrient (e.g. Ca or Mg) uptake by Al (Hüttermann and Ulrich 1984; Rehfuess 1987).

Microbial processes such as decomposition, ammonification and nitrification may be inhibited by acidification (Aber et al. 1982; Francis 1982; Berg 1986). Decreased rates of decomposition may result in accumulation of nutrients in soil organic pools, and shifts in microbial populations may occur favoring more acid tolerant communities (Francis 1982; Berg 1986). Mycorrhizal formation and vigor are likely to be reduced under the influence of acidic deposition (Bell 1986; Meyer et al. 1988).

The preceding effects may combine to cause alterations in the rate, pathway, and effectiveness of nutrient cycling in forest ecosystems (Lee and Weber 1983; Johnson et al. 1985; Meiwes et al. 1986; Shulze 1987; Jakucs 1988). The extent to which nutrient cycling is affected by acid deposition is dependent on the magnitude of inputs and the ability of soils and vegetation to buffer inputs over extended periods of time (Johnson et al. 1982). Factors which determine the capacity of forests to buffer acidic inputs include soil cation exchange capacity, soil base saturation, rates of mineral weathering, soil anion adsorption capacity, rates of organic matter mineralization, magnitude of foliar leaching, precipitation buffering by the canopy and forest floor, and rates of uptake by vegetation (Wiklander 1980; Johnson et al. 1982; Tomlinson 1983; Rutherford et al. 1985; Moore and Dubreuil 1987; Hantschel et al. 1990).

The direct effects of acid deposition on mature trees are not well documented but do not occur consistently at rainfall pH above 3.2 (Morrison 1984; Bell 1986). Direct effects to foliage may include damage to protective surfaces, impairment of guard cell function, or disturbance of metabolic processes such as enzyme activity (Tamm and Cowling 1977). Foliar damage may increase susceptibility to water stress or injury by gaseous pollutants (Evans 1982).

1.2.2.2 Gaseous Pollutants

Phytotoxic gasses may have local or regional effects depending on origin. Pollutants arising from a direct emission source, such as sulphur dioxide (SO_2), affect vegetation within close proximity to the source, while secondary pollutants such as ozone (O_3) are formed in photochemical reactions over large areas (Linzon 1986).

The effects of gaseous pollutants on forest vegetation may be both direct and indirect. Direct effects of SO_2 result from its uptake through the stomata of metabolizing tissue and formation of sulphuric acid within the foliage, causing direct injury (Abrahamsen and Tveite 1983; Hinrichsen 1986). Ozone is responsible for the deterioration of cuticular waxes and cell membrane integrity, intensifying foliar leaching of nutrient ions (Prinz 1987; Rehfuess 1987). As described for acidification processes, nutrient deficiencies may be induced where soil nutrient supplies are limiting.

Ozone has been shown to reduce photosynthesis and growth in forest tree seedlings (Reich et al. 1986; 1987). In addition, carbohydrate allocation patterns are altered by priorization of photosynthate for tissue repair and replacement, or by disruption of phloem transport at the expense of root growth, vigor, and disease resistance (Tingey et al. 1976; McLaughlin and Shriner 1980; McLaughlin et al. 1982; Prinz 1987). Mycorrhizal relations may be altered as root carbohydrates become limiting (Stroo et al. 1988).

Tree species vary in their sensitivity to gaseous pollutants with certain species showing relative tolerance (Kozlowski and Constantinidou 1986). However, pollutants seldom occur in isolation and the presence of additional pollutants may result in negative effects at otherwise tolerable doses. The effects of pollution combinations on forest systems are poorly understood at present (Reich et al. 1987).

1.2.2.3 Excess Nitrogen

Deposition of N compounds may occur as ammonia (NH_3), ammonium (NH_4), or nitrate (NO_3) on a regional basis (Nihlgård 1985). Elevated NO_3 levels occur as a result of fossil fuel combustion, while NH_3 and NH_4 arise primarily from livestock production and the manufacturing and use of N fertilizers.

The results of increased N deposition may be partitioned into soil and tree effects (Johnson and Taylor 1989). Soil effects are related to increased rates of nitrification. Where N inputs exceed biological demand, nitrification, and subsequently NO_3 leaching, may be stimulated to eliminate excess N (van Breeman and Jordens 1983; Reuss and Johnson 1986). Nitrification is an acidifying process, and may result in decreased base saturation and increased Al mobilization (Johnson and Taylor 1989; Willison et al. 1990).

Nutrient losses from foliage may be increased as NH_4 is taken up directly through leaf stomata, releasing cations such as Mg or K (Nihlgård 1985). Strong organic acids may also be released, causing direct damage to leaf surfaces and predisposing foliage to further injury or nutrient loss. Nutrient deficiencies may also be induced as tree N status increases with respect to other nutrients (Hüttl 1988; Oren et al. 1988a; Reich et al. 1988).

Increased N uptake by trees results in a strong carbohydrate sink for canopy and volume growth at the expense of root growth (McLaughlin 1985; Nihlgård 1985). Reduced root growth and vigor may increase the susceptibility of trees to mechanical stress and decrease mycorrhizal associations. Nitrogenous compounds may accumulate in foliage, increasing susceptibility to insects and pathogens, and potentially reach toxic levels. Consensus is lacking regarding the role of excess N in decreased frost hardiness in forest trees (Friedland et al. 1984; Nihlgård 1985; Klein et al. 1989).

The net effects of increased N deposition on forest stands are influenced by soil N status, N cycling rates and pathways, availability of other essential nutrients, and magnitude of N inputs (Johnson et al. 1982; Nihlgård 1985; Reich et al. 1987). Forests with adequate N are not adversely affected by additions of fertilizer N; thus concern about N over-supply has been questioned (Miller 1988).

1.2.2.4 Conclusions Regarding Anthropogenic Stress

For individual trees the processes at greatest risk from regional atmospheric pollution include photosynthesis and growth, root metabolism, reproduction, and interactions with pests (Smith 1987). At the ecosystem level nutrient cycling, biomass production, and pathogen population dynamics are likely to be affected. The consistently observed effects of pollution stress on foliage, roots, soils, and nutrient relations as described above emphasize impacts on nutrient cycling.

The effects of air pollutants on forests are difficult to measure against the heterogeneous background of species composition, developmental stage, site conditions, yearly and seasonal variations, natural stress, and management practices, particularly in the absence of unaffected or control sites (Bormann 1982; Smith 1985; Woodman and Cowling 1987; Bruck 1989). Natural variation in long-term soil processes confounds measurements of soil effects (Rennie 1986; Nowak et al. 1989). In addition, inadequate knowledge of pollution effects on individual tree species, nutrient cycling in forests experiencing decline, and forest response to stress other than pollution has been an obstacle to the interpretation of pollutant effects on forests (Foster 1989).

1.2.3 Hypotheses for the Causes of Current Forest Declines

Prinz (1985) suggests that any meaningful hypothesis for explaining decline must meet the following conditions:

1) it must be possible to connect all the specific symptoms of the decline to the causal factor in question,
2) the temporal development of the decline must go along with the temporal development of the causal factor in question, including consideration of accumulation of effects, and
3) the spatial distribution of the decline must largely coincide with the spatial distribution of the causal factor in question.

Observation and documentation of stress factors involved in recent declines has led to the synthesis of several hypotheses to explain declines individually and collectively. The most widely accepted hypotheses at present may be summarized as follows:

1) The multiple stress hypothesis suggests that any of a number of biotic, physical, chemical and competitive stresses, rather than a single cause, are involved in a decline and that the stresses are characterized as predisposing, inciting, and contributing on a site-specific basis (Manion 1981; Cowling 1985b; Dessurault 1985).
2) The acidification-nutrient imbalance hypothesis implicates soil acidification, acceleration of soil and foliar base cation loss,

nutrient deficiencies, and Al toxicity to fine roots (Ulrich et al. 1980; Hüttermann and Ulrich 1984)

3) The O_3 hypothesis describes foliar damage by O_3, foliar nutrient leaching, reduced root growth, and the negative feedback loop of roots attempting to replace nutrients (Krause et al. 1986; Prinz 1987).

4) The climate hypothesis proposes that large-scale weather stress such as drought, frost, and global temperature increase stimulates decline episodes (Auclair 1987b; Rehfuess 1989).

5) The excess N hypothesis suggests that increased atmospheric deposition of nitrogenous compounds is responsible for decline on a regional basis (Nihlgård 1985).

Although a certain degree of overlap exists among these hypotheses, they each provide a framework within which to examine specific symptoms and their possible causes. Individual hypotheses may be more relevant to particular examples of decline than to others.

1.3 Decline of Sugar Maple *(Acer saccharum* Marsh.) in Quebec

The maple sugar industry in Quebec generates an average of $40 million annually as farm income in otherwise marginal areas, and contributes to the diversification and stabilization of rural activity (Ménard 1985; Robitaille 1986). In addition, maple accounts for 23% of the merchantable volume of hardwoods, and 6% of the total volume of Quebec forests.

Decline of sugar maple has occurred periodically in the northeastern United States and southeastern Canada since the late 1940's and early

1950's (Griffin 1965; Cowling 1985a; Auclair 1987a). In Quebec, maple decline had been observed infrequently until 1978, when the first accounts of the current decline originated in the Beauce region south of Quebec City (Bordeleau 1986). By 1982 reports of decline were more numerous, and in 1983 investigations into the extent and causes of maple decline were undertaken by the Ministère de l'Energie et des Ressources du Québec (Carrier 1986). Annual surveys indicated that the incidence and severity of decline was increasing, and by 1985 60% of maple stands were experiencing decline (Bordeleau 1986).

Decline has now been observed throughout the bioclimatic range of sugar maple in Quebec, and has continued to increase in intensity (Bordeleau et al. 1988; Gagnon and Roy 1989). The severity of decline is greatest in stands found on thin, nutrient poor soils at higher elevations; specifically, maple-beech-yellow birch (*Acer saccharum* Marsh.-*Fagus grandifolia* Ehrh.-*Betula alleghaniensis* Britt.) forests on hilltops (Carrier 1986). However, stands on nutrient poor, humid soils in depressions are also among the most damaged (Gagnon et al. 1985).

Trees dying from maple decline are distinguishable from trees dying of normal causes (Gagnon et al. 1986). Visual symptoms of maple decline include: gradual loss of foliage beginning at the outer crown and continuing inward, small, chlorotic leaves which undergo premature fall coloration, reduced rate of taphole healing, radial increment, and twig growth, adventitious branching and tufted foliage, and bark peeling from branches and trunk (Gagnon et al. 1986; Houston et al. 1990). A secondary symptom of declining stands is an abundance of understory species resulting from enlarged canopy gaps.

Examination of possible causes of maple decline in Quebec has identified a number of biotic and climatic stresses to which maple stands have recently been exposed. Between 1978 and 1983 large-scale infestations of forest tent caterpillar (*Malacosoma disstria* Hubner) and Bruce spanworm (*Operophtera bruceata* Hulst) resulted in severe and extensive defoliations of maple and other hardwood forests (Lachance et al. 1981; Benoit et al. 1982, 1983; Lachance et al. 1984). Shoestring root rot fungus (*Armillaria mellea* (Vahl. ex Fr.) Kumm.) was found to be prevalent in severely declining and dead trees (Lachance 1985; Roy et al. 1985).

Additional stress occurred in the form of early summer frost in 1980, February thaw followed by deep frost penetration in March 1981, minimal snow cover in 1981 and 1982, and late frost in 1983, resulting in further damage to foliage and probable damage to roots (Benoit et al. 1983; Lachance et al. 1984; Lachance 1985; Auclair 1987b; Hendershot and Jones 1989). As well, spring and summer droughts occurred on a regional basis in 1982 and 1983 (Roy et al. 1985; Bernier et al. 1989).

Regions subjected to insect defoliation, the 1981 thaw, and the droughts in 1982 and 1983 correspond to the areas most affected by decline (Gagnon et al. 1986). However, these biotic and climatic stresses are not thought to be the exclusive causes of maple decline (Lachance 1985; Roy et al. 1985; Gagnon et al. 1986; Bernier et al. 1989). Shoestring root rot is found only on trees having greater than 51% dieback, and is considered to be a result, rather than a cause of weakened trees (Lachance 1985; Roy et al. 1985). Examination of the role of sugar maple tapping, methods of sap collection, and sugarbush felling practices showed no significant relationship among these factors and decline (Lachance 1985; Gagnon et al. 1986).

Investigations into the nutrient status of maple stands have revealed foliar deficiencies of K, Ca, Mg, and in some instances, phosphorus (P) (Bernier and Brazeau 1988a,b,c; Paré and Bernier 1989a; Hendershot 1990). In addition, 75% of soils sampled in 1968 and again in 1985 have undergone a reduction in the sum of exchangeable cations in humus layers and B horizons (Gagnon et al. 1986). These observations, combined with the inability of biotic and climatic events to entirely account for current decline symptoms (Bernier et al. 1989), suggest that nutrient deficiencies or imbalances are an important factor in maple decline in Quebec (Bernier and Brazeau 1988a,b; Hendershot and Jones 1989). Positive response to fertilization further implies the involvement of nutrient deficiencies (Hendershot 1990).

Foliar nutrient deficiencies and loss of soil base cations have also been observed in declining forests in Europe and elsewhere in eastern North America. In West Germany Ca, Mg, and K, as well as manganese (Mn) and zinc (Zn) have been shown to be deficient in coniferous foliage (Zech et al. 1985; Zöttl and Hüttl 1986; Hüttl and Wisniewski 1987; Hüttl et al. 1990). Histological investigations have demonstrated that the observed needle damage is characteristic of nutrient deficiencies (Zöttl et al. 1989). Decreased soil pH and base cation depletion have been observed over periods of ten years and longer in central Europe and Scandinavia, and are attributable to acid deposition (Berdén et al. 1987; Tamm and Hallbäcken 1988). Site-specific nutrient deficiencies and disturbances are considered to be pivotal components of forest decline in Europe (Krause et al. 1986; Zöttl and Hüttl 1986; Zöttl et al. 1989).

In the northeastern United States nutrient deficiencies have been associated with decline symptoms of red spruce and balsam fir (Friedland et al. 1988; Shortle and Smith 1988; Zöttl et al. 1989). Nutrient deficiencies have been observed in balsam fir and white spruce in Quebec but have not as yet been linked to decline (Bernier et al. 1989). Loss of soil base cations has also occurred and may be ascribed to acidic deposition, as well as to stand uptake and afforestation (Brand et al. 1986; Johnson et al. 1988; Johnson and Taylor 1989).

Nutrient deficiencies observed in declining sugar maple in Quebec have been linked to atmospheric pollution (Bernier and Brazeau 1986; Carrier 1986; Gagnon et al. 1986; Chevone and Linzon 1988). Acid deposition is most strongly implicated for several reasons. First, high loading rates of wet sulphate and NO_3 occur in the regions most affected by decline (Hendershot and Jones 1989). Second, 80% of the soils and bedrock of Quebec have a low potential to reduce acidity and buffer acidic inputs (Gilbert et al. 1985). Third, the occurrence of nutrient deficiencies and reduced soil base saturation are consistent with known effects of soil acidification, and with European observations of acidification induced nutritional disturbances. Finally, data about other possible pollutants such as O_3 does not suggest a direct role. Available information indicates that ambient O_3 levels should not result in acute damage at most locations (Schemenauer and Anlauf 1987). As well, sugar maple is considered to be an O_3 resistant species (Davis and Gerhold 1976).

From the preceding factors a multiple stress hypothesis for the cause of maple decline in Quebec may be generated. Nutrient deficiencies associated with poor soil nutrient status may be a predisposing factor (Gagnon et al. 1986; Hendershot and Jones 1989), severe and recurrent insect defoliations and climatic events may act as inciting factors (Bernier et al. 1989), and pathogenic fungi such as shoestring root rot may be the obvious, contributing factor which eventually kills the tree (Lachance 1985). Explicit relationships among acid deposition, nutrient deficiencies, and maple decline have not to date been demonstrated (Hendershot and Jones 1989; Johnson and Taylor 1989).

1.4 Conclusions

Due to the slow growth, complexity, and high degree of natural variability of forests, tree response to stress is difficult to measure (Smith 1987; Pitelka and Raynal 1989). It is also difficult to separate stress associated with forest decline from normal forest dynamics and natural patterns of mortality (Mueller-Dombois 1987; Pitelka and Raynal 1989). However, this should not give license to presume that decline-related stress, such as atmospheric pollution, will be absorbed into existing forest dynamics. Recent attention has become focused on the indirect effects of atmospheric pollution, which by effecting subtle changes may be indicative of more extensive damage to come (McLaughlin 1985; Johnson and Taylor 1989).

Symptoms of forest decline are most observable at the level of individual trees; however, less visible effects occur at the ecosystem level (Krause et al. 1986). Decline of individual species may result in altered species composition and reduced biomass production over the long term (Adams et al. 1985; Smith 1987). Modelling the response of individual trees to stress associated with decline provides theoretical information about the response of larger systems (McLaughlin 1985; Schäfer et al. 1988).

Decline itself may act as a predisposing stress for forests (Klein and Perkins 1988; Bruck 1989). Gaps in forest canopies will alter wind resistance, light interception, tree water relations, soil moisture, foliar and soil temperature, nutrient cycling, disease resistance, and cold hardiness. Should current concerns about global warming be realized, forests already weakened by decline are less likely to withstand the ensuing stress (Smith 1987).

Chapter 2: Effects of Fertilization on Fine Roots of Sugar Maple

2.1 Introduction

Fine roots comprise up to 20% of the biomass of mature trees and thus represent a significant investment of carbohydrate resources (Persson 1979; Fogel 1985). Decomposition and grazing of fine roots by soil fauna contribute substantial amounts of N to forest soils, and may provide two to five times more organic matter than leaf and branch litter (McClaugherty et al. 1982; Fogel 1983; 1990). As the principal organs of mineral nutrient assimilation, fine roots are of fundamental importance to tree nutrition (Bowen 1984). Biocycling of N, P, Ca, Mg, and K by fine roots is an important component of nutrient cycling in northern hardwood forests containing sugar maple (Wood et al. 1984; Fahey et al. 1988).

The partitioning of carbohydrate resources to roots and shoots is internally controlled, but is influenced by environment and tree age (Hermann 1977; Waring and Schleisinger 1985). Fine root growth normally has priority over stem growth, and should not be limited by carbohydrate supply unless severe loss of photosynthetic capacity has occurred (Persson 1983; Matzner and Ulrich 1985; Waring 1987). Adjustments in the allocation pattern of carbohydrates to roots and shoots may occur under environmental stress, such as limited nutrient availability (Linder and Rook 1984).

Research into the effects of nutrition on fine root growth in temperate forests has focused mainly on N nutrition, presumably because N is most often the growth limiting factor (Mahendrappa et al. 1986). Fine root biomass and turnover (replacement) were found to be greater on nutrient (N) poor sites than on more fertile sites (Keyes and Grier 1981; Vogt et al. 1987). Greater allocation of carbohydrates to fine roots is considered to be a long-term adaptive strategy for acquiring limited nutrient resources (Grier et al. 1981; Vogt et al. 1987). Limited retranslocation of nutrients from fine roots prior to senescence (Nambiar 1987) and rapid turnover of root tissue contribute to the maintenance of a nutrient pool under infertile conditions.

In some investigations greater nutrient availability following fertilization caused a decrease in fine root biomass and a shift in allocation from fine roots to shoots (Vogt et al. 1985; Ahlström et al. 1988). In an experiment examining effects of simulated acid rain on seedling growth, N in acid rain treatments decreased the root/shoot ratio (Reich et al. 1987). Other research indicates a positive response of fine root biomass to fertilization. Alexander and Fairley (1983) determined that N fertilization decreased the turnover of fine roots, but increased biomass after two years. Safford (1974) found that fine root biomass in the northern hardwood forest had increased seven years after application of NPK + dolomitic limestone fertilizer.

High fine root biomass and turnover may also occur on acidic soils as a mechanism for maximizing nutrient acquisition (Ulrich 1983a; Rehfuess 1989). Liming and fertilization treatments on acidic soils in declining West German forests reduced fine root turnover, while biomass increased after seven months (Matzner et al. 1986), or was unchanged several years after fertilization (Murach 1989). Increased fine root biomass following fertilization may result from improved soil chemical conditions, as well as an eventual increase in the overall growth of the tree (Alexander and Fairley 1983; Matzner et al. 1986). A period of constant or decreased root growth may occur while adjustments in carbohydrate allocation take place; thus the timing of biomass measurements relative to fertilization is important.

Fine root turnover rates vary with species, as well as with site, making comparisons among stands tenuous (Joslin and Henderson 1987). Reliable estimates of fine root turnover are difficult to achieve as both production and mortality must be accurately measured (Fairley and Alexander 1985; Kurz and Kimmins 1987). Other aspects of fine root development such as ramification pattern and spatial distribution may also be affected by fertilization, and may not be visible in biomass or turnover measurements (Ahlström et al. 1988; Murach 1989).

A rapid decrease in fine root biomass disturbs the root-shoot balance at the expense of aboveground parts (McLaughlin and Shriner 1980; Schäfer et al. 1988). Root tissue must be replaced to maintain the level of water and nutrient uptake required by the tree (Jakucs 1988). Energy may also be expended as nutrients are translocated within the tree to meet immediate demands (Waring 1985). Where soil nutrient supply is limited greater investments to fine roots must be made to meet demands, or nutrient deficiencies may ensue (Oren et al. 1988a).

Fine root damage is described as "a condition where the mortality rate of fine roots exceeds the regeneration rate with the result that a rapid decrease in fine root biomass may take place" (Meiwes et al. 1986). Fine root damage has been observed frequently in declining stands in West Germany (Schütt and Cowling 1985; Krause et al. 1986; Matzner et al. 1986). A primary hypothesis regarding the cause of acute fine root damage in declining forests implicates the soil chemical environment; specifically, soil solution nutrient imbalances involving Al, Ca and/or Mg resulting from recent soil acidification (Hüttermann and Ulrich 1984; Godbold et al. 1988; Matzner et al. 1986; Meyer et al. 1988). Under acidic conditions soil solution Ca and Mg are frequently low as a result of base cation leaching, and concentrations of exchangeable Al are relatively high. Although direct toxicity to roots by Al (Ulrich et al. 1980; Ulrich 1983b) may occur in very acid soils, it is unlikely to be the prevailing mechanism where soil pH is more moderate or where organic layers promote Al-chelating and detoxification (Krause et al. 1986; Bruck 1989).

The presence of monomeric inorganic Al in soil or nutrient solution is inhibitory to Ca and Mg uptake at low pH (Rost-Siebert 1983, cited in Hüttermann 1985; Jorns and Hecht-Bucholz 1985, cited in Murach and Matzner 1987). The molar Ca/Al or Mg/Al ratio in solution best characterizes the threshold for inhibition or antagonism: a Ca/Al ratio of less than 1.0 and a Mg/Al ratio of less than 0.2 interferes with Ca and Mg uptake, respectively. Due to the pH dependent solubility of Al these ratios are possible only at pH values below 4.2 (Matzner and Ulrich 1985). Aluminum interferes with Ca and Mg uptake by displacing Ca and Mg from root cell wall matrices and reducing the number of exchange sites (Hüttermann 1985; Godbold et al. 1988).

Calcium has important functions in cell division and membrane stability (Clarkson and Hanson 1980). Replacement of Ca by Al restricts meristematic activity and reduces membrane permeability to nutrient ions, both of which may contribute to fine root damage (Cronan et al. 1989; Kelly et al. 1990). Chemical analyses of fine root tissue from declining stands indicate that the Ca/Al ratio of dead roots is lower than that of living roots, and that the Ca/Al ratio of both live and dead roots parallels a decreasing gradient of soil solution Ca/Al ratio with depth (Murach and Matzner 1987). Avoidance of unfavorable soil horizons by fine roots further limits nutrient uptake (Oren et al. 1988c). Matzner et al. (1986) demonstrated that increasing soil pH and Ca/Al ratio by liming treatments improved fine root growth and development.

Poor Mg nutrition is particularly significant to forest decline in Europe (Roberts et al. 1989). The effects of disturbed Mg nutrition on fine roots are different than for Ca. Magnesium deficiencies resulting from inadequate soil supply and/or Al antagonism cause damage to needle phloem cells and prevent downward transport of photosynthate for fine root production (Zöttl et al. 1989; R. Hüttl, pers. comm.). Immobility of photosynthate from foliage under these conditions may also cause feedback inhibition of photosynthesis (McLaughlin and Shriner 1980). Magnesium fertilization resulted in regeneration of phloem tissue and improved fine root growth (R. Hüttl, pers. comm.).

Elemental analyses of fine roots by mass spectrophotometry indicate extremely low quantities of Ca and Mg in the fine roots of declining trees, emphasizing the limited uptake of these elements by fine roots (Bauch 1983; Matzner and Ulrich 1985).

In addition to nutritional disturbances involving Ca, Mg and Al, nutrient imbalances may also be generated from an improper balance of Ca to K in soil solution (Zöttl and Hüttl 1986; Zöttl et al. 1989). At high concentrations of Ca relative to K, Ca may interfere with K uptake and induce K deficiency. Soils low in K, as observed in some declining forests in Europe and North America, are susceptible to high Ca/K ratios and K deficiencies (Zöttl et al. 1989). The effects of K deficiency on fine root development in relation to forest decline have not as yet been investigated; however, K deficiency is known to restrict phloem formation and is thought to impair carbohydrate translocation (Kramer and Kozlowski 1979; Mengel and Kirkby 1987). Histological characteristics of K deficient needles are similar to those deficient in Mg (Zöttl et al. 1989).

To summarize the preceding discussion the following points may be reiterated: 1) fine roots are a critical component of the forest ecosystem, 2) fine root growth is affected by nutrient availability, 3) nutritional disturbances are known to occur in declining forests, and 4) specific effects of the recognized nutrient deficiencies on fine roots are known. The relationships among fine roots and nutrient status emphasize the importance of determining the role of fine roots in forest decline. Models of forest decline processes must include fine root dynamics as major components (Bossel 1986; Schäfer et al. 1988).

The association of nutrient deficiencies with sugar maple decline in Quebec raises interest about the involvement of fine roots in this decline. Nutrient deficiencies associated with maple decline are similar to those observed in Europe, notably Mg, K, and Ca (Bernier and Brazeau 1988a,b,c; Hendershot 1990). Phosphorus deficiencies have been observed in Quebec as well, although the mechanism of deficiency is different than for the base cations, and may be specific for local site properties (Paré and Bernier 1989a,b).

Changes to the fine root system which may have contributed to or resulted from maple decline are unknown, due to the absence of pre-decline data. Nonetheless, based on the results of West German investigations some speculations may be made. Several conditions exist in Quebec sugar maple stands which may increase the potential for Al stress (Cronan et al. 1989), such as high fine root density in surface layers (Fayle 1965), high rates of acidic deposition (Hendershot and Jones 1989), and poor supplies of Ca, Mg, or P (Bernier and Brazeau 1988b; Paré and Bernier 1989a; Hendershot 1990). Although Al is unlikely to be directly toxic to roots in sites studied to date (Paré and Bernier 1989a), Al inhibition of Ca and Mg uptake may be occurring, given the decreased pH and base saturation of Quebec soils, low endemic nutrient supplies, and the observed nutrient deficiencies (Gagnon et al. 1986; Thornton et al. 1986; Bernier and Brazeau 1988b). Hoyle (1971), using solution cultures representing northern hardwood forest soils, found that root growth of yellow birch was inhibited more when Al was superimposed on Ca or Mg deficiencies than with either deficiency alone.

Calcium antagonism to K uptake may be occurring due to low levels of K observed in some Quebec soils (Bernier and Brazeau 1988a). Potassium deficiencies observed in declining sugar maple may originate by this mechanism.

Apart from the nutritional aspects of fine roots in maple decline, another point must be made. The acute climatic stresses to which sugar maple was subjected to in the early 1980's (unseasonable thaw and frost, scant snow cover, and drought) may have caused physical damage to roots. Sugar maple tends to shallow rooting, particularly for fine roots (Fayle 1965). Roots of northern hardwood species are sensitive to cold temperatures and are normally protected by snow cover (Auclair 1987b).

Episodes of deep frost or poor snow insulation may have caused substantial injury. Drought may have also caused damage by root desiccation. Physical damage by climatic stress may have limited the capacity of roots to recover from nutrient stress, or *vice versa*.

Research is currently underway in Quebec to determine the effects of fertilization on the nutrient status of declining sugar maple stands (Bernier et al. 1989; Hendershot 1990). The objective of the following study was to determine the effects of base-rich fertilizer and liming treatments on soil and fine root chemistry and fine root biomass in three mature sugar maple stands in Quebec.

2.2 Materials and Methods

2.2.1 Study Sites

Three geographically distinct sites were chosen to study the effects of fertilization on fine root biomass and chemistry. All sites are located in the Great Lakes-St. Lawrence Forest Region (Rowe 1972). The Tingwick site is located in the Eastern Townships Section of the Region (Rowe 1972), at the ministère de l'Agriculture, des Pêcheries, et de l'Alimentation du Québec (MAPAQ) maple research site 200 km northeast of Montreal. The soils are moderately acid orthic humo-ferric podzols on glacial deposits with moderate to good drainage, loamy sand texture, and little stoniness (Anonymous 1988). The study area is characterized by pit and mound topography and sugar maple-beech stands.

The second site is located in the Laurentian Section of the Region (Rowe 1972) 80 km north of Montreal, at the Station de Biologie de l'Université de Montréal (SBUM) near St. Hippolyte. The soils are acidic orthic ferro-humic podzols on glacial till over precambrian bedrock (Courchesne 1989). The topography is rolling and large boulders are present. Soils are well drained except for depressional areas, and soil texture is sandy loam. The stand contains mature sugar maple, largetooth aspen (*Populus grandidentata* Michx.), and yellow birch.

The third site is located in a commercial sugarbush in the Upper St. Lawrence Section (Rowe 1972) near Vaudreuil, 40 km west of Montreal. The soils are ortstein humo-ferric podzols (Agriculture Canada Expert Committee on Soil Survey 1987) on shallow sand over marine clay. Rocks and boulders are absent and the topography consists of small pits and mounds with good drainage on the mounds and poor drainage in depressions. Soil texture is sand to loamy sand and the stand contains sugar maple, beech and red maple (*Acer rubrum* L.). Selected chemical properties of the study site soils are given in Appendix 1.

2.2.2 Field Layout

Root-free ingrowth cores were used to determine the effects of fertilization on fine root biomass and chemistry (Lund et al. 1970; Matzner et al. 1986; Ahlström et al. 1988). Twenty-one ingrowth cores were installed at each site in October 1988. Three cores were installed 2 m from each of seven trees within the range (across sites) of 18-35 cm diameter at breast height. All trees had low decline ratings based on the evaluation protocol of Millers and Lachance (1988).

The cores consisted of cylindrical 3 mm nylon mesh bags 10 cm diameter by 15 cm depth filled with B horizon soil from the same site which had been previously air dried, sieved to 2 mm, and to which fertilizer treatments had been added. An equal weight of soil (1.41 kg) was placed in each core and the fertilizer rate applied was calculated on a surface area basis. The tops of the cores were level with the upper surface of the first mineral horizon, with the cores extending into the B horizon. Each core contained one of the following treatments:

1) organic based fertilizer 3-4-8 (Maplegro) containing blood, bonemeal, K_2SO_4, and dolomitic limestone at a rate of 800 kg/ha;
2) inorganic fertilizer 0-3-29 containing triple superphosphate, K_2SO_4, calcite and dolomite at a rate of 1370 kg/ha;
3) no fertilizer (control),

with one core of each treatment installed at each tree. The fertilizer treatments were developed for use in other maple fertilization trials, and rates used in this study were derived from previously used plot rates. The cores were left in the ground until October 1989. Following removal, the cores were kept at 5°C until processing was completed. Fine roots (<2 mm) (Fogel 1985) were extracted from the soil by manual separation and wet sieving, washed in distilled water, and dried at 60°C for 24 hr. Soils were air dried and sieved to 2 mm. Fine root biomass, fine root chemistry, and soil chemistry were determined.

2.2.3 Laboratory Analyses

Root tissue was digested in H_2SO_4 and H_2O_2 (Parkinson and Allen 1975). Exchangeable cations in soil were determined after displacement with 0.1 M $BaCl_2$ (Hendershot and Duquette 1986). Analyses of Ca, Mg, K, Mn in tissue and Ca, Mg, K, Mn, and Al in soil were measured by flame atomic absorption spectrophotometry. Total P, N, and Al in tissue were measured colorimetrically (adapted from Murphy and Riley 1962; Mitchell 1972; Wilson 1984). Soil pH was measured in water and 0.01 M $CaCl_2$ (Sheldrick 1984). Total soil carbon was measured with a Leco carbon analyzer. Duplication and quality control procedures were included in each batch of analyses.

2.2.4 Statistical Analyses

Analysis of variance and Duncan's new multiple range test were used to determine significant treatment effects at the 0.05 level for each site. Data from each site were analyzed as a completely randomized block design on Statistical Analysis System (SAS) (SAS Institute Inc. 1982). Tests for homogeneity of variance were done for all analyses and data transformations were carried out where necessary (Sokal and Rohlf 1973; Bhattacharyya and Johnson 1977). Data are presented in non-transformed form. Appendix 2 shows the data requiring transformation and the transformations used. Where criteria for homogeneity of variance could not be met no further data analysis was done.

Regression analysis and multiple linear correlation were carried out with root biomass as the dependent variable and selected root chemical properties as independent variables. SYSTAT and SYGRAPH were used to generate regression equations and plot root weight against the independent variables (Wilkinson 1988,1989).

2.3 Results

2.3.1 Soil Analyses

Results of selected chemical analyses of soil removed from ingrowth cores following the one year field installation period are presented in Tables 2.1, 2.2, and 2.3. Soil chemical data not presented in Tables 2.1 to 2.3 may be found in Appendix 3.

Significant differences ($p \leq 0.05$) in exchangeable Ca due to treatment were observed at two sites. At Tingwick Ca values were different among all treatments, with greatest values observed in the organic 3-4-8 treatment, intermediate values in the inorganic 0-3-29 treatment, and lowest values in the control (Table 2.1). At St. Hippolyte, Ca values were greater in the two fertilizer treatments than in the control, with no difference between fertilizer treatments (Table 2.2). Greater exchangeable Ca values were observed in the fertilizer treatments than in the control treatment at Vaudreuil as well; however, differences were not statistically significant (Table 2.3).

Significant differences in exchangeable Mg due to treatment occurred at Tingwick only. Magnesium values were greater in the 3-4-8 treatment than in the other two treatments, with no significant difference between the inorganic treatment and the control. Exchangeable Mg also increased in the fertilizer treatments at St. Hippolyte and Vaudreuil although Mg values in those treatments were not statistically different from those in the control.

Table 2.1: Mean values of selected soil chemical properties, Tingwick (n=7)

TREATMENT	Ca	Mg	K	CEC	pH
	cmol(+)/kg				H_2O
3-4-8	0.66a	0.13a	0.09a	7.01a	4.45ab
	(11.68)ǂ	(15.76)	(7.16)	(3.44)	(0.53)
0-3-29	0.55b	0.09b	0.09a	6.61b	4.48a
	(9.92)	(7.88)	(8.02)	(5.44)	(1.24)
CONTROL	0.43c	0.08b	0.09a	6.35b	4.42b
	(16.10)	(8.84)	(11.37)	(8.99)	(0.78)

TREATMENT	base saturation	Al	Ca/K	Ca/Al	Mg/Al
	%		molar ratio		
3-4-8	12.62a	85.82b	3.57a	0.17a	0.03a
	(8.51)	(1.34)	(11.91)	(10.33)	(16.92)
0-3-29	11.09b	87.21ab	2.94b	0.14b	0.02b
	(9.11)	(1.17)	(6.68)	(11.27)	(12.00)
CONTROL	9.40c	88.21a	2.47c	0.11c	0.02b
	(12.16)	(1.53)	(18.71)	(16.74)	(9.31)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

ǂ Coefficients of variation (%) are given in parentheses.

Table 2.2: Mean values of selected soil chemical properties, St. Hippolyte (n=7)

TREATMENT	Ca	Mg	K	CEC	pH
	cmol(+)/kg				H_2O
3-4-8	2.22a	0.25a	0.05a	5.03a	5.33a
	(16.71)ǂ	(46.30)	(17.57)	(3.19)	(1.18)
0-3-29	2.22a	0.17a	0.07a	5.09a	5.25b
	(9.96)	(24.18)	(12.92)	(5.31)	(1.63)
CONTROL	1.81b	0.13a	0.06a	4.67b	5.23b
	(14.26)	(17.81)	(42.95)	(8.95)	(1.01)

TREATMENT	base saturation	Al	Ca/K	Ca/Al	Mg/Al▾
	%		molar ratio		
3-4-8	50.05a	49.06a	24.09a	1.41a	0.16
	(16.93)	(17.54)	(20.94)	(27.75)	(53.08)
0-3-29	48.31a	50.79a	16.78b	1.29a	0.10
	(5.86)	(5.43)	(17.66)	(11.67)	(23.49)
CONTROL	42.59a	56.47a	17.98b	1.03a	0.07
	(7.33)	(5.50)	(37.14)	(14.14)	(11.94)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

▾ Data failed to meet homogeneity of variance criteria and was not analyzed further.

ǂ Coefficients of variation (%) are given in parentheses.

Table 2.3: Mean values of selected soil chemical properties, Vaudreuil (n=7)

TREATMENT	Ca	Mg	K	CEC	pH
	cmol(+)/kg				H_2O
3-4-8	1.60a	0.43a	0.07a	4.92a	5.06a
	(17.02)‡	(24.12)	(25.58)	(4.02)	(2.01)
0-3-29	1.59a	0.36a	0.08a	4.84a	5.04ab
	(7.95)	(14.06)	(22.25)	(5.55)	(0.90)
CONTROL	1.44a	0.32a	0.07a	4.95a	4.95b
	(7.87)	(16.96)	(16.84)	(4.36)	(1.11)

TREATMENT	base saturation	Al	Ca/K	Ca/Al	Mg/Al
	%		molar ratio		
3-4-8	42.70a	56.88a	11.41a	0.89a	0.24a
	(18.27)	(13.77)	(21.70)	(30.47)	(35.93)
0-3-29	42.02a	57.49a	10.63a	0.86a	0.20a
	(4.67)	(3.62)	(17.67)	(11.44)	(11.82)
CONTROL	37.01a	62.58a	10.80a	0.70a	0.16a
	(7.72)	(4.58)	(19.05)	(11.75)	(18.61)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

‡ Coefficients of variation (%) are given in parentheses.

No differences in the amount of exchangeable Al due to treatment were observed at any site. Alternatively, the percentage of the soil cation exchange capacity (CEC) occupied by Al (%Al) was used as a measurement of soil Al status. Differences in %Al due to treatment occurred at Tingwick only, where %Al values are very high (control=88.2%) (Table 2.1). Percent Al decreased in the 3-4-8 treatment compared to the control. A pattern of decreased %Al in the fertilizer treatments relative to the control was observed at all sites.

The molar ratio of exchangeable Ca/Al increased significantly due to fertilizer treatment at Tingwick as a result of both increased Ca and decreased Al (Table 2.1). The molar ratio was greatest in the 3-4-8 treatment and lowest in the control, reflecting the highest Ca and lowest %Al values for that treatment. The increase in exchangeable Ca due to treatment without a decrease in %Al at St. Hippolyte did not result in a significant increase in the Ca/Al ratio.

Treatment differences in the Mg/Al molar ratio also occurred only at Tingwick. The Mg/Al ratio increased in the 3-4-8 treatment relative to the other two treatments, which were not different from each other. As with the Ca/Al ratio, the increased Mg/Al ratio in the 3-4-8 treatment may be attributed to increased Mg and decreased %Al.

No differences in exchangeable K due to treatment were observed at any site. However, increased Ca at Tingwick and St. Hippolyte resulted in an increased molar ratio of exchangeable Ca/K due to treatment at these sites (Tables 2.1 and 2.2). The Ca/K ratio was different among all treatments at Tingwick with greatest values in the 3-4-8 treatment and lowest in the control. At St. Hippolyte the Ca/K ratio was also greatest in the organic treatment with no difference between the 0-3-29 and the control.

Fertilizer treatment increased soil CEC at the Tingwick and St. Hippolyte sites. At Tingwick CEC was greater in the 3-4-8 treatment with no significant difference between the other treatments. Cation exchange capacity at St. Hippolyte was greater in the two fertilizer treatments than in the control, with no difference between fertilizers. Percent base saturation was significantly different among all treatments at Tingwick. Values were greatest in the 3-4-8 treatment and lowest in the control.

Soil pH (H_2O) increased in the 3-4-8 treatment at St. Hippolyte and Vaudreuil (Tables 2.2 and 2.3). At St. Hippolyte, pH in the organic treatment was greater than in the other treatments with no differences between the inorganic treatment and the control. At Vaudreuil, pH in the 3-4-8 treatment was greater than in the control but not different from the 0-3-29 treatment. At Tingwick, greatest pH values were observed in the 0-3-29 treatment (Table 2.1).

2.3.2 Fine Root Analyses

Results of selected fine root chemical analyses and fine root dry weight from ingrowth cores are presented by site in Tables 2.4, 2.5, and 2.6. Fine root chemical data not given in Tables 2.4 to 2.6 are presented in Appendix 4.

No significant differences in fine root Ca due to treatment were observed at any site (Tables 2.4 to 2.6). Significant differences in root K occurred only at Tingwick (Table 2.4). Potassium was lower in the 3-4-8 treatment compared to the other treatments. Potassium values in the

Table 2.4: Mean values of selected fine root chemical properties and fine root dry weight, Tingwick (n=7)

TREATMENT	Ca	Mg	K	Al
	mg/g			
3-4-8	1.01a	4.15a	6.05b	4.32a
	(22.14)ǂ	(24.84)	(18.09)	(17.58)
0-3-29	0.99a	2.31b	7.81a	3.95a
	(16.98)	(22.04)	(17.00)	(15.16)
CONTROL	0.93a	2.37b	7.83a	4.17a
	(13.42)	(10.79)	(26.63)	(7.35)

TREATMENT	Ca/Al	Mg/Al	Ca/K	dry weight (g)
	molar ratio			
3-4-8	0.17a	1.06a	0.17a	2.92a
	(34.64)	(15.76)	(20.51)	(20.63)
0-3-29	0.17a	0.66b	0.13b	2.70a
	(18.37)	(20.88)	(15.26)	(24.16)
CONTROL	0.15a	0.63b	0.12b	2.83a
	(17.02)	(12.32)	(28.56)	(15.74)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

ǂ Coefficients of variation (%) are given in parentheses.

Table 2.5: Mean values of selected fine root chemical properties and fine root dry weight, St. Hippolyte (n=7)

TREATMENT	Ca	Mg	K	Al
	mg/g			
3-4-8	2.11a	5.86a	5.87a	2.70a
	(5.16)ǂ	(26.69)	(20.02)	(15.95)
0-3-29	2.21a	4.71ab	7.19a	2.77a
	(15.01)	(25.31)	(26.54)	(7.39)
CONTROL	2.13a	3.67b	8.00a	2.70a
	(15.61)	(23.66)	(22.54)	(16.45)

TREATMENT	Ca/Al	Mg/Al	Ca/K	dry weight
	molar ratio			(g)
3-4-8	0.54a	2.41a	0.36a	1.99a
	(13.62)	(25.75)	(17.92)	(37.18)
0-3-29	0.55a	1.93ab	0.33a	2.20a
	(14.94)	(30.96)	(37.82)	(33.38)
CONTROL	0.55a	1.51b	0.27a	1.63a
	(28.71)	(18.20)	(21.85)	(37.76)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

ǂ Coefficients of variation (%) are given in parentheses.

Table 2.6: Mean values of selected fine root chemical properties and fine root dry weight, Vaudreuil (n=7)

TREATMENT	Ca	Mg	K	Al
	mg/g			
3-4-8	2.04a	6.04a	7.86a	1.87b
	(13.35)ǂ	(18.68)	(47.21)	(9.34)
0-3-29	2.17a	5.59a	7.13a	2.13a
	(15.36)	(30.04)	(35.31)	(16.92)
CONTROL	2.18a	5.14a	7.70a	2.18a
	(10.09)	(22.01)	(38.26)	(8.60)

TREATMENT	Ca/Al	Mg/Al	Ca/K	dry weight
	molar ratio			(g)
3-4-8	0.75a	3.65a	0.28a	1.33b
	(16.25)	(25.44)	(24.34)	(26.00)
0-3-29	0.73a	2.97a	0.32a	1.56b
	(36.81)	(28.27)	(24.62)	(30.58)
CONTROL	0.69a	2.64a	0.30a	2.01a
	(15.75)	(21.14)	(27.04)	(33.43)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

ǂ Coefficients of variation (%) are given in parentheses.

0-3-29 treatment and the control were not significantly different from each other.

The molar ratio of Ca/K in root tissue was greater in the 3-4-8 treatment at Tingwick than in the other treatments, as a result of increased soil Ca/K and decreased root K in this treatment. Increased soil Ca/K in the 3-4-8 treatment at St. Hippolyte did not result in greater root Ca/K.

Differences in root Mg were observed at Tingwick and St. Hippolyte. Highest values were observed in the 3-4-8 treatment at both sites. At Tingwick root Mg in the organic treatment was significantly greater than in the other treatments with no difference between the inorganic fertilizer and the control. At St. Hippolyte Mg was also significantly greater in the 3-4-8 treatment than the control, but not significantly greater than in the 0-3-29 treatment. Root Mg values were greater in the fertilizer treatments than in the control at Vaudreuil as well, although differences were not significant.

Significant differences in root Al were observed at Vaudreuil only (Table 2.6). Aluminum was lower in the 3-4-8 treatment than in the other treatments, and the two other treatments were not significantly different from each other. No response in the Ca/Al molar ratio was observed at any site. The molar ratio of Mg/Al increased in the 3-4-8 treatment at Tingwick and St. Hippolyte, following the same pattern in each case as observed for Mg.

Significant differences in root biomass due to treatment were observed at Vaudreuil only (Table 2.6). Root weight was lower in the 3-4-

8 and the 0-3-29 treatments than in the control. There was no significant difference in root weight between the two fertilizer treatments.

2.3.3 Regression Analysis

Multiple linear correlation was used to compare observed and predicted values of fine root biomass generated from regression equations using selected root chemical properties as independent variables. Regression equations, correlation coefficients, and plots of root weight *vs.* independent variables are shown in Figures 2.1 and 2.2. Figure 2.1 indicates a negative relationship between root Mg concentration and root weight, and Figure 2.2 indicates a positive relationship between root Al concentration and root weight.

2.4 Discussion

2.4.1. Comparisons Among Sites

Fertilizer response varied over the three sites used in this study. Most of the significant treatment responses in measured parameters occurred at Tingwick, while similar, non-significant patterns in response were observed at the other two sites. Soil nutrient status was poorest at Tingwick, as illustrated by the lowest observed values of soil exchangeable Ca and Mg, % base saturation, Ca/Al and Mg/Al ratios, and pH, and highest values of exchangeable Al and %Al. The highest CEC and lowest base saturation values at Tingwick indicate the greatest potential for response to base-rich treatments by replacement of Al with base cations. Fewer responses in root and soil chemistry were observed at St. Hippolyte, where % base saturation was greatest, than at Tingwick. Very little

Figure 2.1: Root weight (g) *vs.* root Mg concentration (mg/g)

root weight = 3.05+(-0.21)(root Mg)

correlation of observed *vs.* predicted values:

$R^2=0.20$, $p<0.001$

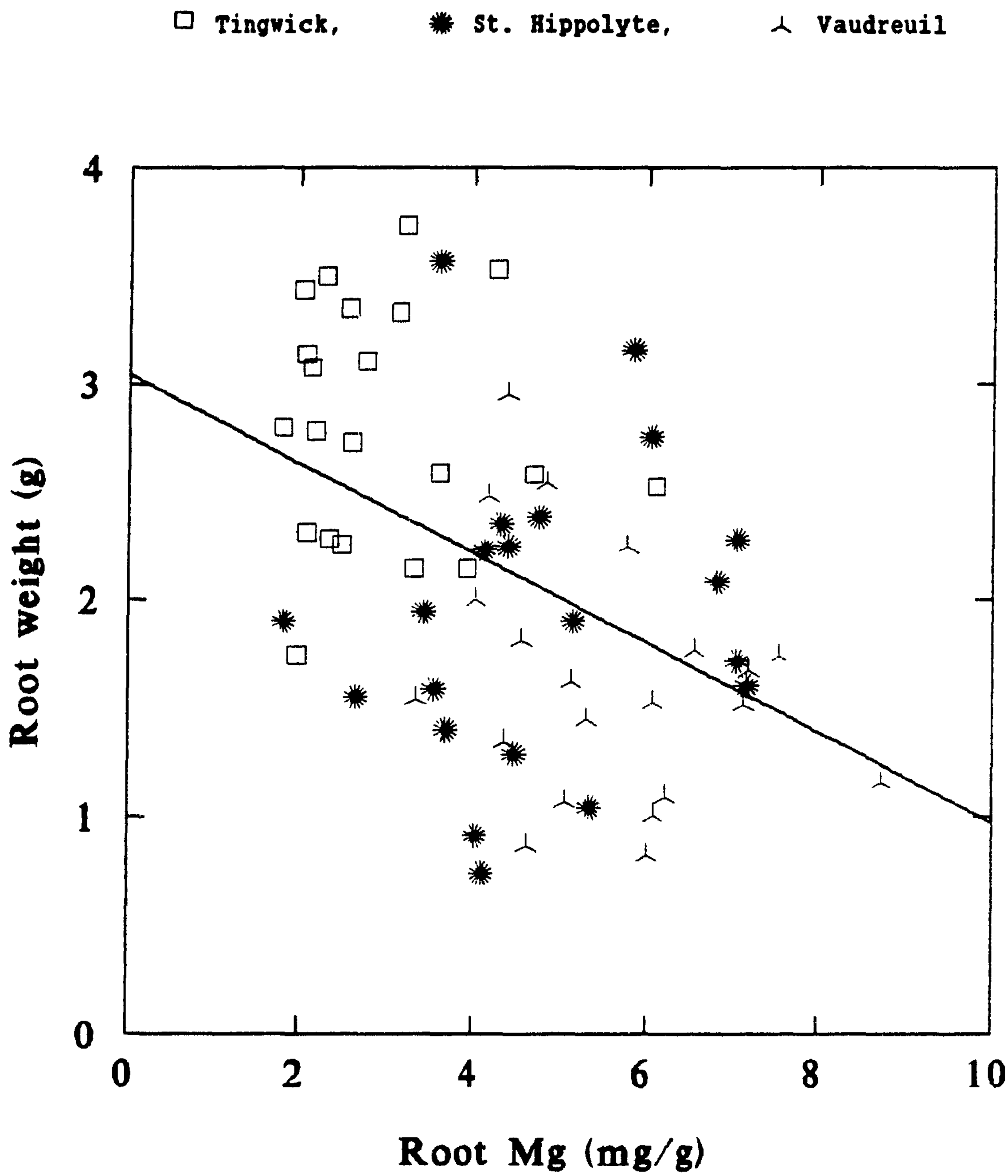


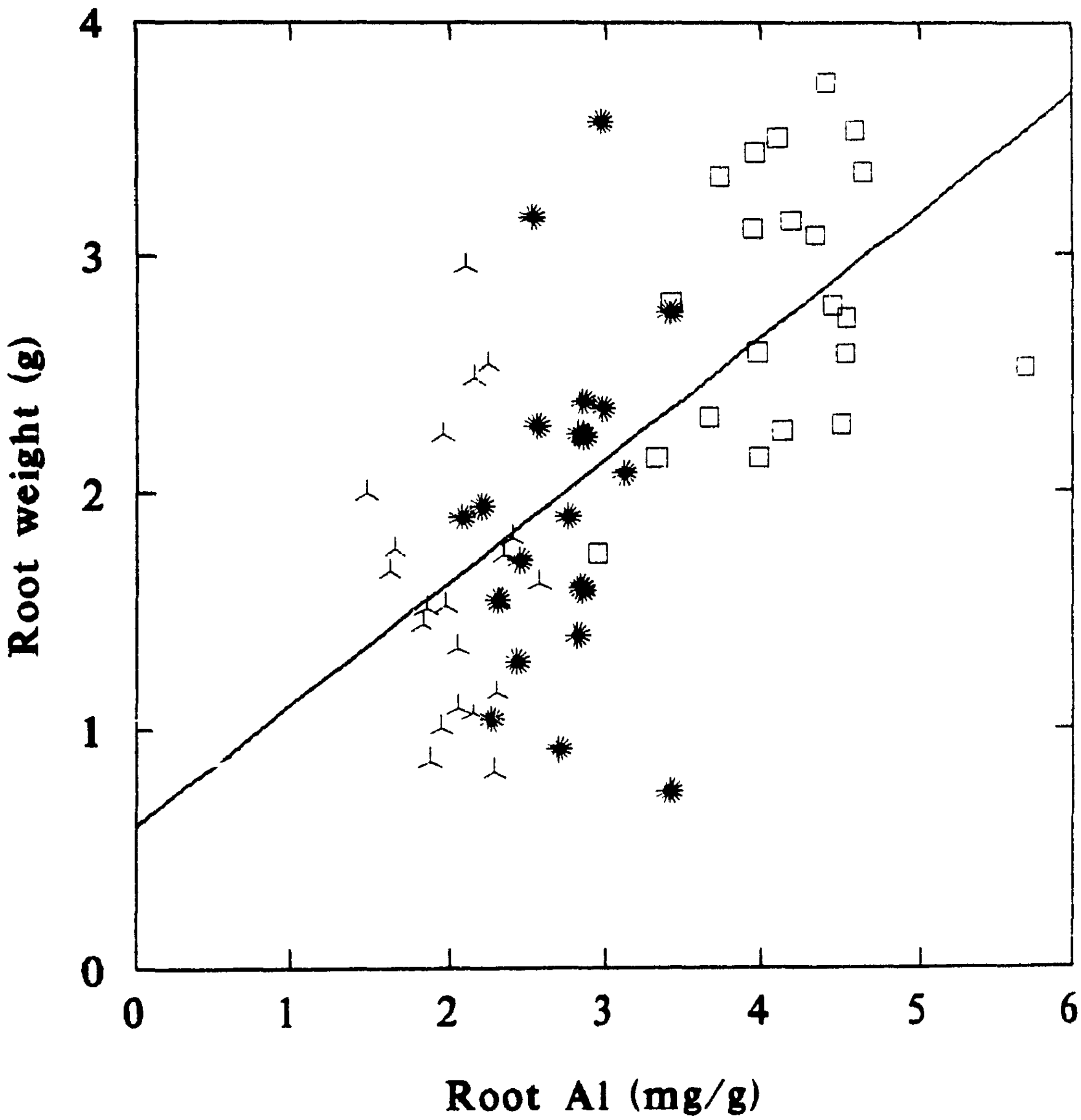
Figure 2.2: Root weight (g) *vs.* root Al concentration (mg/g)

root weight = 0.59+(0.52)(root Al)

correlation of observed *vs.* predicted values:

$R^2=0.41$, $p<0.001$

□ **Tingwick,** ✱ **St. Hippolyte,** ⅄ **Vaudreuil**



response of soil and fine root chemistry to fertilizer treatment was observed at the Vaudreuil site.

2.4.2 Response Patterns Within Sites

Fertilizer treatments had significant effects on root and soil chemical properties at all sites and on fine root biomass at one site. Fertilizer response most frequently followed one of three patterns. The first type of response involved significant differences among all treatments with greatest values occurring in the organic 3-4-8 treatment and lowest values in the control. This response was observed at the Tingwick site in soil exchangeable Ca, Ca/Al ratio, Ca/K ratio and % base saturation. A second response resulted in a significant difference between the fertilizer treatments and the control, with no difference between the two fertilizer treatments, as was observed in soil Ca and CEC at St. Hippolyte and root weight at Vaudreuil. The third response resulted in a significant difference between the 3-4-8 treatment and the other treatments, with no difference between the 0-3-29 treatment and the control. This response was consistently observed in measurements involving Mg (soil exchangeable Mg and Mg/Al ratio and root Mg and Mg/Al ratio) at Tingwick, as well as for root Al at Vaudreuil and root K at Tingwick. A significant difference between the 0-3-29 treatment and the two other treatments was observed only for soil pH at Tingwick.

2.4.3 Soil Chemical Response

Fertilizer treatment generally improved soil chemical conditions by increasing soil Ca, Mg, Ca/Al and Mg/Al ratios, CEC, % base saturation, and pH, and by decreasing %Al on the exchange complex. An adverse treatment response was an increase in soil Ca/K ratio at Tingwick and St. Hippolyte resulting from increased exchangeable Ca in the fertilizer treatments without a corresponding increase in exchangeable K. Lack of K response to treatment is unexpected, particularly in the high K (0-3-29) treatment. The high mobility of K in soils likely resulted in uptake or leaching of fertilizer K within the year following fertilization. Decreased root K and increased root Ca/K ratio in the organic fertilizer treatment at Tingwick likely resulted from increased soil Ca and Ca/K in this treatment.

2.4.4 Root Chemical Response

Favorable treatment response in fine root chemistry was limited to increased Mg and Mg/Al ratios at Tingwick and St. Hippolyte, and decreased Al at Vaudreuil. Response in root Mg and Mg/Al ratio to fertilizer treatment at Tingwick and St. Hippolyte suggests the possible involvement of Mg in nutrient imbalances at these sites, where soil exchangeable Mg and Mg/Al ratios are lowest. However, increased root Mg and Mg/Al ratios did not result in an increase in root biomass as would be expected following alleviation of Mg deficiencies (Zöttl et al. 1989). Figure 2.1 shows root weight values plotted against root Mg values.

Root tissue Ca/Al ratios are greater at all sites than threshold values for living fine roots of Norway spruce (0.10) and European beech (0.06) found in West Germany (Murach and Matzner 1987). Adequate Ca/Al ratios and lack of response in root Ca or Ca/Al to increased soil Ca at

Tingwick and St. Hippolyte indicate that Ca is not limiting for roots at these sites.

Limited changes in fine root mineral nutrient concentration following fertilization have been observed elsewhere (Ahlström et al. 1988). The element concentration of fine roots is representative of fluctuating soil conditions and is not as consistent an indicator of nutrient status as foliar nutrient concentrations (Zöttl and Hüttl 1986; Oren et al. 1988c).

2.4.5 Root Biomass Response

Greatest fine root biomass in the control treatment was observed at Tingwick. This finding is consistent with observations that fine root biomass and turnover are greater on nutrient poor and acidic soils than on fertile soils (Keyes and Grier 1981; Rehfuess 1989). Although fine root turnover generally decreases with fertilization, the response of fine root biomass is variable (Vogt et al. 1985; Matzner et al. 1986) and is closely related to the timing of measurement relative to fertilization (Alexander and Fairley 1983). Three phases of response in root biomass to fertilization may be anticipated. First, an initial increase in fine root biomass may occur in the short term from improvement of adverse soil chemical conditions (Matzner et al. 1986; Kishchuk and Hendershot 1989). Second, within a period of one or two years a decrease in fine root biomass may occur as turnover decreases, less root volume is maintained for soil exploitation, and more carbohydrates are partitioned to foliage production (Alexander and Fairley 1983). Finally, an increase in fine root biomass may result from an overall augmentation of tree biomass.

In this study fine root biomass was measured once without estimates of turnover, permitting only a static view of the effects of fertilization on fine roots. The assumption is made that ingrowth core sampling represents localized root fertilization and is unlikely to bring about long-term changes in tree biomass. A decrease in root biomass occurred only at Vaudreuil, the site showing the least response in soil base cation properties, indicating that the decrease in fine root biomass has not resulted directly from an increase in soil base cations.

Decreased root biomass at Vaudreuil was accompanied by a decrease in root Al in one treatment. Investigations of Al toxicity in trees are largely limited to seedling studies, which indicate inconsistent or weak negative correlations between root tissue Al and root biomass (Joslin and Wolfe 1988; DeWald et al. 1990; Raynal et al. 1990). In this study, a positive relationship between root Al and root biomass was found. The correlation of observed and predicted values of root biomass estimated from root Al is significant ($p<0.001$) (Figure 2.2). Decreased root biomass at Vaudreuil in the 3-4-8 treatment seems more related to decreased root Al than to an increase in soil base cations.

Root biomass alone may not be an adequate indicator of response to Al (Kelly et al. 1990). Aluminum causes changes in root branching and morphology resulting in thicker roots with swollen apices (Andersson 1988; Cronan et al. 1989), which may confound biomass measurements. In solution culture Al treatments, Schier (1985) found that decreased root length was compensated for by increased root diameter, resulting in no net biomass change. Root elongation was found to be more sensitive to Al than biomass (Raynal et al. 1990), and both decreased lateral root number and increased root length were observed at some solution Al concentrations (Sucoff et al. 1990). The number of living root tips was negatively correlated with soil Al in forest soils (Meyer et al. 1988). Root responses to Al which result in decreased absorptive surface area, such as decreased elongation and increased diameter, are more functionally important than changes in biomass (Andersson 1988; Kelly et al. 1990). Mycorrhizae are generally not considered in Al toxicity studies but may also be important in altering nutrient absorption properties of fine roots (Keltjens and van Loenen 1989; Raynal et al. 1990).

The positive relationship between root Al and root biomass in this study suggests that Al may be directly affecting root biomass, possibly through changes in morphology or ramification pattern. This is supported by highest root Al concentration and root biomass values at Tingwick where soil Al is greatest. Aluminum treatment did not cause changes in the appearance or morphology of sugar maple roots in solution culture (Thornton et al. 1986). Root measurements other than biomass such as root tip number or root length, some of which may be correlated with root biomass (Joslin and Wolfe 1988), would provide more specific information about the effects of soil chemistry on fine root biomass in forest conditions.

Decreased root Al due to treatment only at the Vaudreuil site is unexpected, as this response would be most anticipated where soil Al is high and % base saturation is low. Replacement of Al on soil exchange sites by fertilizer base cations results in lower Al concentrations in fine root tissue (Murach 1989). Treatment response in root Al was absent at Tingwick, where highest values of soil exchangeable Al and %Al and lowest values of % base saturation were found.

Replacement of exchangeable Al with base cations in the fertilizer treatments likely occurred at all sites. However, due to the higher CEC and very high %Al at Tingwick the reduction of Al in the rooting environment was less than at Vaudreuil and not sufficient to decrease root Al uptake significantly. The smaller quantity of exchangeable Al and the coarser texture of the Vaudreuil soil contributed to more effective leaching of Al displaced from soil exchange sites into soil solution, resulting in less uptake by fine roots. Decreased root biomass at Vaudreuil occurred in both fertilizer treatments, although root Al was decreased only in the 3-4-8 treatment. The addition of organic materials in the 3-4-8 treatment may have increased Al-organic matter binding and further decreased Al uptake (Joslin et al. 1988).

2.5 Conclusions

Response of fine root and soil chemistry to fertilizer treatment was observed at all sites investigated in this study, with effects varying among sites. Greatest treatment response in soil and fine root chemistry occurred at Tingwick, where soil nutrient status was generally improved by base cation fertilization. Fertilizer induced nutrient imbalances, such as an increased Ca/K ratio, are most likely to occur at sites such as Tingwick where soil nutrient status is very poor.

Calcium does not appear to be limiting for fine roots of sugar maple at any site, as root Ca and Ca/Al ratios were unaffected by increased soil Ca. Increased root Mg and Mg/Al ratios indicate that Mg may be limiting at Tingwick and St. Hippolyte. Increased root Mg coincident with decreased soil Al suggests that Al may be inhibiting Mg uptake at Tingwick. Fertilizer treatment had no effect on soil K at any site.

Both the organic 3-4-8 and the inorganic 0-3-29 fertilizer treatments had effects on root and soil chemistry. Of the two fertilizers, the 3-4-8 most often resulted in significant treatment differences, particularly for parameters of root and soil Mg. The reason for more treatment response in the 3-4-8 treatment is not known, but may be related to a higher Mg/Ca ratio in this fertilizer than in the 0-3-29. The addition of N, or of P in organic rather than inorganic form, may also have affected treatment response.

Fine root biomass may be influenced by both soil nutrient status and soil Al. The effects of these properties on biomass must be separated in order to determine the response of fine roots to fertilization. The response of fine roots to Al under field conditions must be evaluated, particularly with respect to alterations in fine root morphology and function which may interfere with nutrient assimilation. As well, the effects of increased base cation status on roots in the absence of Al stress must be known. Deviations from the expected response in the presence of Al may then instigate investigation of the interactions between soil nutrient status and Al. Use of a fine root response parameter other than biomass would further clarify the effects of fertilization on fine roots.

Ingrowth cores are a means of measuring the response of a spatially limited subsample of fine roots to fertilization under field conditions. The method does not provide information about the effects of whole-tree or stand fertilization on the rooting system. To fully understand the response of fine roots to fertilization, entire trees or stands must be considered in order that changes in tree biomass production and carbohydrate allocation to fine roots may be determined. Measurement of fine root turnover rates before and after fertilization, in addition to characterization of the effects of soil chemistry on fine roots, would provide more comprehensive information about the response of fine roots to fertilization.

Connecting Paragraph

In the preceding experiment, the effects of base-rich fertilizer and liming treatments on fine root and soil chemistry and fine root biomass in sugar maple stands were determined. Another response of sugar maple roots to improved nutrient status by fertilization may be expected to occur in the starch content of larger diameter roots. In the second part of this study, the effect of fertilization on the starch content of structural roots was measured.

Chapter 3: Effect of Fertilization on Root Starch Content of Sugar Maple

3.1 Introduction

Carbohydrates produced by plants in excess of demands for structure, maintenance, and growth are stored as reserves (Glerum 1980). In trees, carbohydrate reserves accumulate mainly in the bole, stump, and roots >0.5 cm diameter, and occur primarily as starch (Edwards et al. 1977; Glerum 1980; Waring and Schlesinger 1985). The principal role of reserve carbohydrates is to provide energy and materials for metabolic activity when photosynthate is not being produced (Kramer and Kozlowski 1979). As well, stored carbohydrates facilitate recovery from defoliation, increase resistance to pathogen attack, and function in the cold acclimation of certain species (Manion 1981; Ostrofsky and Shigo 1984; Gregory et al. 1986).

Reserve carbohydrates such as starch are particularly important in deciduous species for metabolism during the leafless winter period and for growth of shoots and roots prior to leaf emergence (Kramer and Kozlowski 1979; Waring and Schlesinger 1985). Starch accumulation in large roots of hardwoods preceding radial growth represents a mechanism for ensuring adequate energy reserves in the spring (Wargo 1979).

Starch reserves exhibit seasonal variation in deciduous trees (Glerum 1980; Bonicel 1987). Generally for northern hardwoods, starch begins to accumulate in late summer as growth slows, reaches a maximum with leaf fall, declines slightly through the winter, and decreases rapidly in the spring as shoot growth begins (Glerum 1980). The ability of deciduous species to maintain seasonal patterns of carbohydrate depletion and accumulation are important in competitive and successional strategies (McLaughlin et al. 1980).

Starch content is an index of the physiological condition and performance, or vigor, of a tree: high starch content indicates good vigor; conversely, low starch content is indicative of poor vigor (Wargo 1981). A symptom of declining trees is low reserve carbohydrate content (Manion 1981). In relation to forest decline, the starch status of trees has been studied mainly where insect defoliation and climatic stress have been primary causal factors. Examining the effects of defoliation, Wargo et al. (1972) found that sugar maple root starch levels decreased with increasing frequency and severity of defoliation. Mortality of defoliated sugar maple was associated with xylem starch depletion caused by late season defoliation (Gregory and Wargo 1986). Starch content of conifer twigs was found to be a useful predictor of post-defoliation survival (Webb 1981).

The effects of climatic stress on root starch content have also been investigated. Parker and Patton (1975) showed that drought alone reduced root starch levels of black oak (*Quercus velutina* Lam.), and reductions were greater in combination with defoliation. Gregory et al. (1986) found that cold stress following late season defoliation of sugar maple caused carbohydrate depletion in shoots and roots, poor cold acclimation resulting from low starch reserves, and contributed to decline.

In the preceding examples, reduced starch content resulted from inciting or acute stresses associated with decline, as described by Manion (1981). In sugar maple, declining starch levels may then stimulate contributing stress factors such as shoestring root rot (Wargo 1972). The breakdown of starch in sugar maple is accompanied by an increase in the reducing sugars glucose and fructose, which are favorable substrates for the fungus (Wargo 1972; Parker and Houston 1974). Bioassays indicated that fungus growth was greatest on tissue from defoliated trees, and corresponded to the tissue undergoing the most starch conversion.

The extent to which storage carbohydrates become depleted is influenced by environmental factors other than the inciting stress (McLaughlin and Shriner 1980). Starch reduction following defoliation in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was greater on poor sites than on more productive sites (Webb and Karchesy 1977). Recovery of sugar maple following defoliation was also related to site quality (Gregory and Wargo 1986). Ozone pollution also causes reductions in root carbohydrates (Tingey et al. 1976; McLaughlin et al. 1982); O_3 exposure in combination with other stresses which reduce carbohydrates may result in serious depletion of starch reserves (Gregory et al. 1986).

Many of the current forest declines in Europe and North America are associated with nutrient deficiencies or imbalances (Zöttl et al. 1989). As with fine roots, research into the effects of nutrient status on starch content has focused mainly on N nutrition, as well as that of P. Under conditions of low nutrient availability, nonstructural carbohydrates accumulate as growth is limited by elements other than carbon (Matson and Waring 1984; McDonald et al. 1986). Improvement of nutrient status by fertilization reduces carbohydrate reserves as the demand by growing parts, or sink strength, increases (Ericsson 1979; Shaver and Chapin 1980). In contrast to defoliation or climatic stress, N or P limitation would thus be expected to increase starch content relative to unstressed trees. The net result of simultaneous nutrient stress, defoliation, and/or climatic stress does not appear to have been investigated.

The effects of nutrient deficiencies other than N or P on carbohydrate storage has not been well documented. A recent study of carbon relations in West German stands indicates that declining trees accumulate less storage carbohydrate than healthy trees (Oren et al. 1988b). As well, carbohydrates in declining trees were utilized at a lower rate and growth was less than in healthy trees. Differences could not be attributed to climate, competition, or stand structure. Lower rates of photosynthesis resulting from needle damage, and low sink strength of declining trees due to deficiencies of nutrients such as Mg or K were suggested as reasons for lower rates of carbohydrate accumulation and utilization. Deficiencies of nutrients other than N or P may therefore decrease root starch content indirectly through carbon assimilation processes.

The starch content of sugar maple has been investigated previously in relation to insect defoliation (Wargo et al. 1972; Parker 1974; Gregory and Wargo 1986; Gregory et al. 1986). In hardwoods, the starch content of roots is a reliable indicator of starch status (Wargo 1978). The starch content of roots is three to five times that of stems, making fluctuations easier to detect. Root starch is less subject to temperature induced biochemical reactions than stem starch and is therefore more stable. Wargo (1976, 1981) found that roots of similar diameter and sampled at the same distance from the trunk showed little variation in starch content, and that single root samples were representative for a tree.

The seasonal pattern of sugar maple starch content is regular and predictable, thus deviations from normal patterns are readily detectable (Wargo 1971). Root starch in sugar maple was found to be a better indicator of physiological condition than crown condition or twig growth, and indicated reductions in tree vigor which were subsequently manifest as canopy dieback (Carroll et al. 1983).

Research is currently being carried out in Quebec to determine the effects of fertilization on the health of declining sugar maple stands (Bernier et al. 1989; Hendershot 1990). The objective of this study was to determine the effect of fertilization treatments on the root starch content of mature sugar maple trees.

3.2 Materials and Methods

3.2.1 Study Sites

Two sites established for sugar maple fertilization trials and foliar analysis were sampled for root starch. Both sites are located in the Great Lakes-St. Lawrence Forest Region (Rowe 1972). The first site is located in the Eastern Townships Section near Cookshire, 175 km east of Montreal. The stand is in a previously exploited sugarbush on a dystric brunisol (Agriculture Canada Expert Committee on Soil Survey 1987). The second site is in the Laurentian Section of the Region (Rowe 1972), 80 km north of Montreal at the Station de Biologie de l'Université de Montréal (SBUM) near St. Hippolyte. The plots sampled for root starch at the SBUM are adjacent to the ingrowth core study area (Chapter 2.2.1).

3.2.2 Sampling and Laboratory Analysis

The Cookshire site contains eight plots fertilized in June 1987 with the following treatments: 1) $CaCO_3$; 2) K_2SO_4 3) organic based 4-4-8 (blood, bonemeal, K_2SO_4, and dolomitic limestone); 4) $CaMg(CO_3)_2$ + K_2SO_4,

5) $CaCO_3 + K_2SO_4$; 6) control; 7) $CaMg(CO_3)_2$; and 8) $(NH_4)_2SO_4$. Four hundred kg/ha of each material was applied; thus treatments 4 and 5 each received 800 kg/ha of fertilizer. The treatments were designed to test the hypothesis that maple dieback was related to deficiencies of base cation nutrients. Ammonium sulphate was used to determine the effects of an acidifying treatment on foliar nutrient status.

The St. Hippolyte site contains six plots, half of which were fertilized in June 1989 with a mixture of K_2SO_4, $CaCO_3$, and $CaMg(CO_3)_2$ at a rate of 500, 250, and 250 kg/ha respectively. The remaining plots were not fertilized.

Sampling was done in November 1988 and November 1989, following the methodology of Renaud and Mauffette (1989). Four mature sugar maple trees per plot at Cookshire and six trees per plot at St. Hippolyte were sampled. Two root sections 0.5 to 1.0 cm diameter and 15 cm length were taken at opposite sides of each tree 2 m from the trunk. Samples were taken from the B horizon. The roots were de-barked and kept on ice until transported to laboratory facilities. Roots were immediately rinsed in distilled water and oven dried at 60°C for 24 hr. Samples were ground and the two samples per tree combined. Analysis for starch content was done by high pressure liquid chromatography (HPLC) (Renaud and Mauffette 1989).

3.2.3 Statistical Analyses

All statistical analyses of root starch data were carried out using SYSTAT (Wilkinson 1989). Analysis of variance and Tukey's test were used to determine treatment effects at the Cookshire site in each sampling year. Homogeneity of variance was tested prior to analysis by Bartlett's test. Paired t-tests were used to determine differences between treatment means of the two years.

For the St. Hippolyte site, analysis of covariance to determine treatment effects was performed with the pre-fertilization root starch content as the covariate. A t-test was performed to test treatment differences in 1989 data.

3.3 Results and Discussion

Results of starch content analysis of roots at the Cookshire site are presented in Table 3.1. Values from the control treatment are similar to those found for sugar maple by Renaud and Mauffette (1989). No differences due to fertilizer treatment were observed in 1988, while some treatment differences were observed in 1989.

For 1989 data, root starch contents of the 4-4-8, $CaMg(CO_3)_2$ + K_2SO_4, $CaCO_3$ + K_2SO_4, and $CaMg(CO_3)_2$ treatments were significantly greater ($p \leq 0.05$) than the $(NH_4)_2SO_4$ treatment. No differences were observed between the control and any other treatments. Lower rates of carbon uptake and storage carbohydrate accumulation may result from foliar damage caused by nutrient (e.g. Mg) deficiencies (Oren et al. 1988b; Zimmermann et al. 1988). In this study, lower starch content in the $(NH_4)_2SO_4$ treatment may have resulted from decreased carbon assimilation arising from acidification induced nutrient deficiencies. Decreased root starch content in the $(NH_4)_2SO_4$ treatment may also have resulted from increased carbohydrate demand by other plant parts following N fertilization (Ericsson 1979; Shaver and Chapin 1980); however, starch content was

Table 3.1: Mean values of root starch content, Cookshire (% dry weight)

	TREATMENT			
	$CaCO_3$	K_2SO_4	4-4-8	$CaMg(CO_3)_2$+K_2SO_4
1988	11.77a	11.22a[1]	11.16a	15.34a
	(19.73)ǂ	(11.52)	(24.40)	(17.76)
1989	15.61ab	14.51ab	17.31a	16.65a
	(11.26)	(10.36)	(24.65)	(17.64)

	TREATMENT			
	$CaCO_3$ + K_2SO_4	CONTROL	$CaMg(CO_3)_2$	$(NH_4)_2SO_4$
1988	11.10a	12.69a	12.88a	9.08a
	(39.26)	(8.01)	(26.82)	(16.77)
1989	16.08a	14.20ab	16.61a	8.87b[1]
	(8.99)	(24.52)	(13.54)	(33.25)

Values from the same year followed by the same letter are not statistically different ($p \leq 0.05$).

n=4 except where indicated by [1] n=3

ǂ Coefficients of variation (%) are given in parentheses.

Table 3.2: Mean values of root starch content, St. Hippolyte (% dry weight)

	PLOT	
	FERTILIZED	UNFERTILIZED
1988 (pre-fertilization)	12.86[2]	13.21[2]
	(20.80)ǂ	(26.11)
1989 (post-fertilization)	14.69[1]	14.35[2]
	(17.36)	(26.84)

[1] n=17; [2] n=18

ǂ Coefficients of variation (%) are given in parentheses.

increased in the other N-containing (4-4-8) treatment. No other measurements of carbon metabolism were made in this study.

Increased root starch content in the treatments receiving the doubled rate of fertilizer material, the dolomitic limestone treatment, and the base-enriched organic treatment implies that root starch content is related to soil base cation status. Lack of significant differences between the base-rich treatments and the control, and the acidifying treatment and the control, indicates that the soils at this site are neither sufficiently depleted of base cations to respond to low rates of enrichment, nor are they significantly different from the acidified treatment. Correlations between soil chemistry and root starch content may clarify these relationships; however, soil chemistry was not measured in this study.

Absence of treatment effects in 1988 demonstrates that a response in root starch content to fertilization may take several years to occur. With the exception of the $(NH_4)_2SO_4$ treatment, mean values of 1989 starch content are greater than 1988 values for the same treatment. Paired t-tests of 1988 and 1989 treatment means show that the differences between the two years are not significant. However, the appearance of treatment differences in 1989 indicates that changes in starch content have occurred between 1988 and 1989. Further sampling would determine whether treatment differences are maintained.

Mean values of root starch content of samples from St. Hippolyte are presented in Table 3.2. Analysis of covariance was carried out on post-fertilization (1989) data using the pre-fertilization (1988) starch content as the covariate. No significant difference between the root starch content of fertilized and unfertilized trees was found. As well, no significant difference between the starch content of fertilized and unfertilized trees was observed in the 1989 data alone using a t-test.

Post-fertilization sampling was done approximately five months following fertilization. Based on the Cookshire results, it is likely that this was insufficient time for a response to occur. Further sampling at this site as well should provide evidence of treatment differences within several years.

3.4 Conclusions

Significant differences in root starch content among fertilizer treatments were observed at the Cookshire site two and a half years following fertilization. The lower starch content observed in the $(NH_4)_2SO_4$ treatment may have resulted from base cation deficiencies induced by soil acidification. More supporting information, such as soil chemistry and carbon assimilation data is necessary to derive conclusive results about the relationship between nutrient status and starch content of sugar maple.

Results of fertilization at both Cookshire and St. Hippolyte indicate that response in root starch content to fertilization may take several years. Starch content measurements should be continued in these stands, in conjunction with soil chemistry and carbon metabolism investigations.

Chapter 4: Conclusions

4. Conclusions

Nutrient deficiencies associated with decreased soil base cation status are thought to be involved in the decline of sugar maple in Quebec. Changes in soil chemistry occurring prior to or coincident with decline cannot be verified without pre-decline data. Fertilizer treatments provide a means of observing the response of soil and plant tissue to improved soil nutrient status. In the research presented in preceding chapters, effects of fertilizer treatments on fine root chemistry and biomass and on the starch content of larger roots were evaluated.

In the fine root study, significant differences existed among sites, and consequently response to treatment varied with site. Effects of Al on fine roots in these stands do not appear to involve direct toxicity; however, further investigation is required to determine the role of Al in nutrient uptake under field conditions. Understanding of the effects of both Al and base cation nutrition on fine roots will facilitate interpretation of fine root response to altered soil chemistry.

The method used in this study places limitations on the information which may be obtained. Investigations of fine root response to fertilization should include data regarding changes in carbohydrate allocation patterns of trees and fine root turnover rates. To assess the effects of fertilization on entire trees, entire trees or stands should be treated.

Responses in fine root turnover and fine root chemistry or physiology to fertilization should initially be segregated, and integrated only after individual effects have been determined. The ingrowth core method should be effective in estimating fine root turnover if large numbers of cores are installed and sampled at intervals. This method reduces the heterogeneity associated with alternative methods of fine root sampling for biomass and turnover, such as conventional soil cores.

Investigations involving the effects of soil chemical parameters on fine roots should be done in as natural an environment as possible. The disturbance of soil horizons involved in ingrowth core establishment reduces the validity of this method for evaluating the effects of soil chemistry on fine roots. For these investigations, undisturbed soil cores should be considered.

In the root starch study, circumstantial evidence indicates that the root starch content of sugar maple was influenced by soil chemical conditions several years following fertilization. Correlation of root starch data with soil chemical data would permit testing of the hypothesis that the root starch content of sugar maple is decreased under conditions of low soil base cation status. Data on the influence of fertilization on carbohydrate allocation patterns would provide more information with which to evaluate responses in starch content.

The results of both studies indicate that more comprehensive information about the response of trees to improved nutrient status is necessary to evaluate the effects of fertilization on roots. Specifically, responses in carbohydrate production and allocation to a range of nutrient conditions must be known in order to recognize effects resulting from fertilization. Linking carbohydrate response with soil and tissue chemical response is necessary to interpret the effects of fertilization on sugar maple roots. Integration of the responses of other ecosystem components to fertilization will eventually permit better understanding of the role of forest nutrition in maple decline.

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Appendices

Appendix 1: Selected chemical properties of study site B horizons

	Tingwick	St. Hippolyte	Vaudreuil
horizon	Bf	Bhf	Bf
pH H_2O	4.69	5.16	5.36
pH $CaCl_2$	4.20	4.42	4.56
CEC cmol(+)/kg	2.52	2.51	1.03
% base saturation	11.47	32.67	26.77
% Fe (Na-pyrophosphate extractable)	1.04	1.00	0.19
% Al (Na-pyrophosphate extractable)	0.74	0.95	0.22
% C	▲	5.39	0.98

▲ Data not available

Appendix 2: Data transformations (root ingrowth core study)

SITE	DATA	TRANSFORMATION
Tingwick	root Mg concentration	log
St. Hippolyte	root Ca concentration	log
	soil exchangeable Mg	1/x
	soil exchangeable Al	log
	soil % K saturation	log
	soil % Al saturation	log
Vaudreuil	soil % base saturation	1/x
	soil % Al saturation	1/x
	soil exchangeable Ca/Al molar ratio	log
	soil exchangeable Mg/Al molar ratio	1/x

Appendix 3: Mean values of soil chemical properties (n=7)

SITE	TREATMENT	C %	Mn —cmol(+)/kg—	Al	pH $CaCl_2$
Tingwick	3-4-8	5.14a	0.11b	6.02a	3.83b
		(21.57)ǂ	(15.75)	(3.17)	(0.77)
	0-3-29	5.66a	0.11b	5.77a	3.89a
		(7.98)	(14.57)	(6.16)	(0.97)
	CONTROL	5.09a	0.15a	5.60a	3.84b
		(7.92)	(15.06)	(10.14)	(0.89)
St. Hippolyte	3-4-8	5.51a	0.04a	2.46a	4.53a
		(3.57)	(22.63)	(15.36)	(1.58)
	0-3-29	5.68a	0.05a	2.58a	4.49a
		(9.01)	(18.88)	(4.78)	(0.86)
	CONTROL	5.73a	0.04a	2.63a	4.47a
		(7.52)	(35.75)	(8.69)	(0.75)
Vaudreuil	3-4-8	4.18a	0.02a	2.80a	4.22a
		(12.23)	(28.16)	(14.27)	(2.30)
	0-3-29	4.37a	0.02a	2.78a	4.22a
		(8.46)	(35.17)	(7.87)	(0.86)
	CONTROL	4.43a	0.02a	3.10a	4.14a
		(15.44)	(27.16)	(6.23)	(1.51)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

ǂ Coefficients of variation (%) are given in parentheses.

Appendix 3 (continued): Mean values of soil chemical properties (n=7)

SITE	TREATMENT	Ca	Mg	K	Mn
		%			
Tingwick	3-4-8	9.47a	1.82a	1.33a	1.56b
		(9.26)ǂ	(15.91)	(7.01)	(15.97)
	0-3-29	8.34b	1.32b	1.42a	1.70b
		(10.04)	(11.24)	(8.60)	(16.76)
	CONTROL	6.74c	1.25b	1.38a	2.39a
		(15.40)	(8.39)	(13.77)	(22.37)
St. Hippolyte	3-4-8	44.13a	4.98▾	0.94a	0.89a
		(14.55)	(44.59)	(15.23)	(21.61)
	0-3-29	43.59a	3.39	1.33a	0.90a
		(6.19)	(19.10)	(12.98)	(16.79)
	CONTROL	38.65a	2.68	1.25a	0.94a
		(8.84)	(10.50)	(48.68)	(28.66)
Vaudreuil	3-4-8	32.55a	8.68a	1.48a	0.42a
		(17.14)	(24.41)	(26.73)	(26.56)
	0-3-29	32.90a	7.52a	1.60a	0.48a
		(7.69)	(13.66)	(21.80)	(35.78)
	CONTROL	29.13a	6.50a	1.40a	0.40a
		(7.01)	(14.44)	(20.08)	(28.36)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

▾ Data failed to meet homogeneity of variance criteria and were not analyzed further.

ǂ Coefficients of variation (%) are given in parentheses.

Appendix 4: Mean values of fine root chemical properties (n=7)

SITE	TREATMENT	N	P	Mn
			mg/g	
Tingwick	3-4-8	13.81a	1.32a	0.76b
		(12.32)‡	(11.74)	(35.50)
	0-3-29	13.93a	1.47a	0.77b
		(13.66)	(18.24)	(32.63)
	CONTROL	14.23a	1.39a	1.19a
		(9.82)	(8.23)	(25.01)
St. Hippolyte	3-4-8	11.96a	1.33a	0.22b
		(7.26)	(11.51)	(27.86)
	0-3-29	11.98a	1.34a	0.22b
		(5.46)	(13.19)	(20.37)
	CONTROL	12.39a	1.39a	0.31a
		(9.86)	(15.35)	(29.98)
Vaudreuil	3-4-8	11.15a	1.22a	0.15a
		(10.32)	(7.41)	(25.25)
	0-3-29	11.34a	1.20a	0.15a
		(10.59)	(9.08)	(32.04)
	CONTROL	11.41a	1.26a	0.17a
		(10.87)	(6.17)	(31.84)

Values within elements followed by the same letter are not statistically different ($p \leq 0.05$).

‡ Coefficients of variation (%) are given in parentheses.