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EFFECTS OF URBAN ENVIRONMENTAL CONDITIONS ON THE SYMBIOSIS BETWEEN VESICULAR-ARBUSCULAR MYCORRHIZAL FUNGI AND SILVER MAPLE (*ACER SACCHARINUM* L.)

by

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PREFACE

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ABSTRACT

Roots of silver maple (*Acer saccharinum* L.) trees from downtown Montreal and the municipal nursery in Terrebonne were sampled to determine their vesicular-arbuscular mycorrhizal (VAM) colonization levels. Soil was analyzed to determine the concentration of various soil nutrients, pH, and bulk density. It was found that trees from downtown Montreal grow in soils with lower phosphorus and magnesium, and higher copper, zinc, sodium, pH and bulk density than nursery trees. Downtown tree health, in terms of % dieback, was positively correlated with soil phosphorus, potassium, calcium, the phosphorus:copper ratio and negatively correlated with soil copper, zinc, bulk density and tree age. It is suggested that tree health and survival are associated with tree location. Older and healthier trees grow on streets that provide larger soil volumes. Downtown trees had significantly higher VAM colonization levels (44.9%) than those from the nursery (36.1%). The colonization level in downtown trees was positively correlated with the phosphorus:copper ratio and tree age, and negatively correlated with soil potassium. It is hypothesized that downtown trees living under the most stress will be those with the highest VAM colonization. Under controlled conditions 81.5% of the variability of % VAM infection of silver maple seedlings could be explained by soil zinc, phosphorus, copper, sodium, and potassium. Zinc, phosphorus and copper negatively affected VAM colonization, while a slight positive effect of sodium and potassium was found. This suggests that VAM colonization in downtown trees may be affected by soil factors, but the effects may be masked by other conditions, such as water stress, light, or size of root systems.

RÉSUMÉ

Des échantillons de racines d'érable argenté (*Acer saccharinum* L.) ont été prélèvés dans le centre-ville de Montréal ainsi qu' à la pépinière municipale de Terrebonne, afin de mesurer leur niveau de colonisation par des champignons mycorrhiziens a vésicules et arbuscules (MVA). Les sols ont été analysés pour les concentrations de minéraux, le pH et la densité par volume. Les résultats de ces analyses démontrent qu'au centre ville, les arbres poussent dans des sols contenant moins de phosphore et de magnésium mais plus de cuivre, de zinc et de sodium et ayant un pH et une densité plus élevé que le sol de la pépinière. La quantité de potassium dans le sol ainsi que l'âge de l'arbre ont une influence positive sur l'état de santé de l'arbre. L'état de santé des arbres semble être associé au volume de terre dans lequelle ils poussent. Les arbres du centre-ville avaient un niveau de colonisation de MVA supérieur (44,9%) à celui de la pépinière (36,1%). La proportion entre le phosphore et le cuivre, ainsi que l'âge de l'arbre étaient corrélés positivement avec le niveau de colonization dans les arbres du centre-ville. Une corrélation negative existait entre le niveau de potassium dans le sol et la colonisation racinaire. Ces résultats suggèrent que les arbres du centre-ville vivant dans des conditions de stress élevé développent des niveaux plus élevés de mycorhization. Dans des conditions de laboratoire, 81,5% de la variabilité du % d'infection de MVA des jeunes érables argentés était lié directement aux concentrations de zinc, phosphore, cuivre, sodium, et potassium du sol. Le zinc, le phosphore et le cuivre étaient associés négativement avec la colonisation de MVA, tandis que le sodium et le potassium avaient une influence positive. Ceci indique que la colonisation de MVA des arbres du centre-ville peut être affectée par les conditions du sol. Cependant, cet effet peut varier car d'autres conditions, tel que le volume des racines, l'éclairage ou la sécheresse pourraient aussi influencer le niveau de colonisation des arbres.

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CHAPTER 1

GENERAL INTRODUCTION

Increasing attention is being given to improving urban life with plants. Although this use of plants is relatively easy in suburban areas, it is much more difficult in the urban centres of most large cities. European cities are renowned for their boulevards lined with large, old, healthy trees. The situation in North American cities, on the other hand, is much more bleak. American street trees live on average 7 to 10 years, with trees in containers living only 2 to 5 years (Moll and Urban, 1989). Clark and Kjelgren (1989), estimated that 80% of unirrigated newly planted street trees died within two years in Seattle. The state of Montreal urban trees is very similar. Michel Labrecque (1993) determined that downtown Montreal trees, on average, live 4 to 5 years. Furthermore, only 4% of trees live beyond 10 years. When the economic component is factored into this situation, the problem becomes more apparent. It costs the city of Montreal $500 to $600 to produce and transplant one tree. Each year 400 to 500 trees are planted in Montreal , 20% of which do not survive beyond their first year. Hence, $40,000 to $60,000 is being spent on replacing dead trees each year.

1. Factors affecting urban tree survival

In natural environments trees tend to grow in habitats to which they are well adapted. On the other hand, trees in urban environments are planted for their aesthetic contribution, often with little or no consideration of the suitability of the environment. As a result of the arbitrary selection of planting, trees in urban environments are often subjected to stresses that are more severe than those encountered by trees growing in forests (Kramer, 1987). Thus, urban trees are often in poor health and have a shorter life expectancy than would normally be expected for forest trees. Clearly, tree species that are more tolerant of these stresses are needed; but first the stresses need to be identified, and the way urban trees are affected by them must be understood.

1.1 Restricted soil volumes

Inadequate soil rooting space can be one of the more important factors in the premature mortality of trees in urban areas (Lindsey and Bassuk, 1991). There is a basic conflict between the biological needs of trees, whose root systems are generally near the surface and spread laterally, and the small, confined areas to which they are relegated in the design of streets in our urban areas. The typical street tree pit is "sandwiched" in a narrow strip between the road and sidewalk, which places severe limitations upon healthy tree growth and development. The small volumes of soil in these areas often do not hold water sufficiently to meet transpirational demand, resulting in the tree experiencing periodic to prolonged water deficits (Krizek and Dubik, 1987).

Thus far, there has been no widely applicable method for determining the optimum size of a tree pit or container. Most researchers base their estimates on a tree's water requirements and the waterholding capacity for a particular soil. Kramer (1987) estimated that a 10.5 metre tree with an actual leaf surface area of 200 m^2 might lose up to 130 litres of water a day. Vrecenak and Herrington (1984) estimated 950 litres each day for a tree with a 19 metre canopy diameter of average density. In comparison, a typical Montreal street tree pit of 1.5 m^3 having an available waterholding capacity of 12% could hold approximately 170 litres of water, which a large tree would use in 1 to 2 days.

Most urban trees fare poorly since they get too large for the planting pits and eventually die unless they move out of this constraining volume of soil into amenable soils nearby (Labrecque, 1993; Kramer, 1987). Yet, it is uncertain whether tree roots can eventually develop outside the planting hole; hence, it is increasingly assumed that street trees are forced to stand in a pot-like confinement for their entire lifetime. In these circumstances, the dimensions of the planting hole and the quality of the growth substrate determine the tree's ultimate size and also greatly influence the utility and aesthetic value of the mature tree (Kopinga, 1991).

1.2 Soil

Urbanization contributes unique amendments and contaminants to soil that are not usually present in a natural environment. Bidwell and Hole (1964) discussed the beneficial and detrimental human effects on soils. Beneficial effects include addition of nutrient materials, addition of water through irrigation, and removal of excess water by artificial drainage. However, the detrimental effects such as removal of more plant nutrients than are replaced, addition of toxic materials, and subjecting soil to excessive heat, wind and compaction far outweigh the beneficial effects.

Some general characteristics of urban soil have been outlined by Craul (1985). They include modified soil structure leading to compaction, restricted aeration and water drainage, elevated pH levels, interrupted nutrient cycling leading to poor soil fertility, and presence of high levels of contaminants. These properties distinguish urban soils from most natural soils.

1.2.1 Soil fertility

Urban soils generally lack organic matter cycling due to the removal of all organic matter. Individual trees in sidewalk pits suffer maximum effects of this interrupted cycling unless fertilized, which is usually not done in large cities such as Montreal. In addition, most urban soils do not rest on parent material or bedrock, and do not receive the benefits of nutrients released from inorganic mineral weathering (Craul, 1992). These two factors produce poor soil fertility and have been related to unhealthy urban trees.

The decline of urban sugar maple in Boston has been related to a lack of or poor availability of nitrogen, elevated soil and foliar sodium levels, and low concentrations of foliar nitrogen, calcium, magnesium and potassium (Dyer and Mader, 1986). Kelsey and Hootman (1990) studied urban street tree soils in Illinois and discovered significantly higher sodium and lower phosphorus levels than occur in native soils. Close, et al. (1996a), determined that foliar nitrogen, potassium, calcium, manganese, boron and sodium were less favorable for street trees than for forest trees in East Lansing, Michigan. This was a contributing factor to a slow growing, low-density root system resulting in low vitality and reduced growth rates in street trees.

1.2.2 pH

Many urban soils tend toward elevated pH levels. Craul and Klein (1980) found that pH levels for streetside soils of Syracuse were on average 8.0. Ware (1990) also found an elevated pH level of about 7.6 in urban Philadelphia soils. There are many explanations for the elevated pH values of urban soils. First is the application of calcium or sodium chlorides in street and sidewalk de-icing salts (Craul, 1992). The second deals with the release of calcium carbonate from the weathering of concrete structures (Kelsey and Hootman, 1990; Messenger, 1986). The irrigation of urban soils with calcium-enriched water is a third cause (Craul, 1992).

Although it is known that a high pH reduces the availability of many plant nutrients, there have not been many studies to show this in urban trees. A high pH has been shown to contribute to manganese deficiency in chloritic urban sugar and red maples. Most chlorotic trees grew on soils with pH above 6.8 (Smiley, et al., 1986).

1.2.3 Contaminants

Sources of contaminants are numerous, including de-icing salts, pesticides, paints, plastics, batteries, fertilizers, galvanized metals, burning of fossil fuels, brass and rubber products, electroplating, and wet and dry air deposition (Brady, 1990). The presence of heavy metals may cause reduced vigor and increased mortality of urban trees. Large concentrations of de-icing salts containing sodium, calcium or chloride cause nutrient ion imbalance leading to one or more nutrient deficiencies.

Studies to date have dealt less with the effects of contaminants on urban tree health, and more on the actual presence of these contaminants. A detailed investigation of the Washington D.C. Mall found the soils contained greater amounts of heavy metals (lead, zinc, nickel, copper) than nearby undisturbed soils (Short, et al., 1986). Lagerwerff and Specht (1970) sampled heavy metals in soils from several roadside locations near Baltimore, Washington, Platte City and Cincinnati. They found that concentrations of cadmium, nickel, lead and zinc decreased with distance from traffic. Hence trees planted along streets, as is the case in Montreal, would theoretically be growing in heavy metal contaminated soils. More recently, Amrhein and Strong (1990) reported elevated concentrations of lead ranging from 14 to 939 ppm, zinc from 50 to 1950 ppm, nickel from 5.5 to 47 ppm, and copper from 16 to 191 ppm in roadside soils. A major cause of sugar maple decline along roadsides has been attributed to de-icing salts (Kotheimer et al., 1967). These salts have been shown to cause progressive root destruction and dieback, as the diminishing root system was unable to sustain top growth of sugar maples (Guttay, 1976).

1.2.4 Compaction

Most conditions present in the urban situation tend to destroy soil structure which leads to compaction (Day and Bassuk, 1994). Most urban soils have been transported from natural settings, which partially destroys their structure. Organic matter, an aggregating, structure-forming agent, is lacking, which results in a limited soil organism population and activity. Furthermore, urban soil surfaces are subjected to various physical activities, such as foot and vehicle traffic and vibrational forces from vehicles, which also contribute to the destruction of soil structure (Craul and Klein, 1980).

Soil compaction leads to a reduction in pore space (Foil and Ralston, 1967), a shift of some of the macropore space into micropore space, a reduction of aeration and water infiltration, mechanical obstruction to nutrient absorption by plant roots (Craul, 1992), decrease of organic matter decomposition (Brady, 1990) and a reduction in the number and activity of soil animals (Craul, 1992).

There have been numerous studies on the effects of soil compaction on root growth and plant vigor, especially in agricultural and forest situations, of which only a few will be mentioned. Duffy and McClurkin (1974) observed a direct relationship between soil compaction and planting failure of loblolly pine. Planting success decreased from 100% at bulk densities of 1.25-1.34 g/cm^3 to 0% at bulk densities greater than 1.65 g/cm^3. Root growth of yellow poplar and sweet gum seedlings was found to be reduced at bulk densities of 1.40 to 1.55 g/cm^3 (Simmons and Pope, 1988). Vepraskas (1988) found that maximum values for increase of root number and yield of corn were 1.66, 1.61, 1.60, and 1.58 g/cm^3, and root concentrations were zero at bulk densities of 1.85,1.82, 1.81, and 1.80 g/cm^3 for sand, loamy sand, sandy loam and sandy clay loam textures, respectively.

Similar observations have been made for urban trees. Rooting space for street trees planted in tree pits or narrow parkways is already restricted. Compacted soil, however, creates an additional, more immediate space limitation as roots are unable to penetrate dense soils encountered beyond the planting hole (Day and Bassuk, 1994). A comparison of healthy and declining oaks in an urban environment revealed that soil aeration in the upper soil strata was critical to tree vigor (MacDonald, et al., 1993). Patterson (1977) found that urban Washington trees in poor health were growing in extremely compacted clay soils with bulk densities ranging from 1.7 to 2.2 g/cm^3. Compaction was indicated as a primary factor in sugar maple decline in some urban areas (Ruark, et al., 1983). Shoot growth of other urban tree species has also been shown to be adversely affected by soil compaction (Pan and Bassuk, 1985; Alberty, et al., 1984).

1.3 Water stress

Soil water deficits, and the plant water stress which accompanies them, are significant limiting factors in the growth of urban trees. Observations across a wide geographic range have demonstrated that the onset of water stress caused by water deficits is one of the principal limiting factors controlling the growth of urban trees (Roberts and Schnipke, 1994). It has been shown that newly transplanted street trees die if supplemental water is not provided, and mature trees may die during relatively mild, periodic droughts (Clark and Kjelgren, 1990).

The rate of absorption of soil water usually lags behind the rate of transpirational water loss from tree crowns. In urban trees, absorption of water is often impeded by low soil moisture content, a small or slow-growing root system, poor soil aeration, high atmospheric temperatures and a high concentration of salts in soil water (Kozlowski, 1987). Such adverse conditions, which characterize most urban soils, cause an increase in the lag of water absorption behind transpiration, thus inducing dehydration of tree crowns (Close, et al., 1996b; Krizek and Dubik, 1986; Spirn, 1984; Berrang and Karnosky, 1983; Steiner, 1980; Tattar, 1980). Despite this apparent consensus, observations of tree water status under actual street conditions are largely absent. The aforementioned studies which have addressed urban tree water relations have involved simulated urban environments or have been relatively short term.

Labrecque (1993) determined that sugar maple, hackberry, and green ash from downtown Montreal were quite often under water stress in 1992. It was determined that the health of these trees was significantly affected by this water stress. Close, et al. (1996b) also concluded that water stress was the most important factor adversely influencing the growth and vitality of sugar maple in East Lansing, Michigan. These trees had significantly lower predawn water potential, osmotic potential and stomatal conductance than those in natural habitats. These results were significantly correlated with low soil moisture levels of the street site. Chronically low stomatal conductances can have a serious effect on tree vitality, in that there will be significant limitations in photosynthesis due to the greatly reduced diffusion of carbon dioxide through the stomata. This can result in reduced food production for maintenance and growth. Without adequate amounts of carbohydrates produced throughout the season, growth rates are impaired and sufficient reserves may not be stored, predisposing the tree to further environmental or biological stresses, as is quite often the case in urban trees (Freedman, 1995).

Other investigators have indicated that soil moisture is not limited in urban conditions and that predawn water potentials are similar to those found in natural conditions (Whitlow, et al., 1992; Karnosky, 1985). A New York City study actually found excess soil moisture to be the cause of death of street trees (Berang, et al., 1985). These studies indicate the great site variability that can exist in urban conditions; this variability often leads to discrepancies in published data.

A well-branched root system is essential for effective water uptake in tree planting pits with or without adequate soil moisture (Krizek and Dubik, 1987; Watson and Himelick, 1982). However, because of the small soil volume given to urban trees, the high degree of soil compaction and the general poor quality of urban soils, root systems are usually poorly developed in urban trees. Poorly developed root systems not only cause poor growth, but also reduce water uptake in urban trees (Keever, et al., 1985). Watson and Himelick (1982) reported that the volume of soil containing roots of transplanted trees amounted to only 2% of the total soil volume from which the roots absorbed water before the trees were transplanted. Transplanting success was greatly reduced in these trees.

Poor soil aeration in compacted soils, as previously mentioned, reduces root growth. It may also decrease the capacity of roots for absorbing water by causing decay of roots and inhibiting root formation and elongation (Kozlowski, 1987). Root growth is often decreased more than leaf growth by poor soil aeration; hence, the small root system cannot absorb water fast enough to replenish the water lost in transpiration, causing dehydration of tree crowns (Kozlowski, 1984, 1985).

Many urban trees exist in isolated conditions as opposed to the continuous canopy frequently found in forests. This isolation creates a different set of microclimatic conditions surrounding the tree, and increases the atmospheric water loss. The stomatal behaviour of isolated trees may be more closely coupled to atmospheric demand than that of closed-canopy forest trees, resulting in greater water use (Clark and Kjelgren, 1990). Trees located close to the street were found to suffer from water deficits more than those located in unpaved areas. This was found to be caused by the intense amount of heat reflected from parked cars and pavement (Krizek and Dubik, 1987). Isolated urban trees are also quite often desiccated by high winds, develop abiotic leaf scorch and are more likely to succumb to dieback (Hammerschlag, et al., 1986).

Dehydration of tree crowns has also been shown to be related to the application of de-icing salts (Levitt, 1980). This response often is attributed to reduced water absorption because of the osmotic effects of the salts. Hence, a tree may be subjected to physiological drought even if the soil water is at field capacity. Reduced absorption of water in saline soils may also be associated with a decrease in root permeability caused by dehydration, increased suberization and inhibition of root growth. High salt concentrations in the soil may also injure young feeder roots, especially those of trees growing on sandy soils, further decreasing the absorption of water (Kozlowski, 1987).

1.4 Light intensity

The potential contributions of the urban climate to limiting tree growth in cities have not been widely investigated. Information on tree responses to low light situations, such as that found on the north side of buildings, has been particularly limited. The amount of potential radiation received on a street is defined by street aspect, planting location, height and number of buildings, street width, and building setback (Clark and Kjelgren, 1989). Most downtown areas generally receive a fraction of the total radiation available, perhaps only 4 to 6 hours of direct sun per day (Whitlow and Bassuk, 1988), or 20% of total seasonal potential irradiance (Harris and Bassuk, 1993).

Labrecque (1993) determined that 104 (17%) downtown Montreal trees do not receive any direct sunlight, while 370 (60%) receive three hours or less direct sunlight per day. Furthermore, the healthiest trees were those receiving the most direct sunlight, while the trees receiving little direct sunlight were in poor health and did not survive long. Low light levels have been shown to effect potential photosynthesis by significantly reducing the rate of carbon fixation (O'Rourke and Terjung, 1981). Kjelgren and Clark (1992) also reported reduced photosynthesis and trunk growth in sweetgum at an irradiance level of 44% of full sun.

The effect of reduced irradiance depends on the shade tolerance and acclimation of tree species. Kjelgren (1995) found that low light levels caused a significant reduction in Norway maple trunk growth and crown density. However, these trees were also found to have large specific leaf areas, which indicated shade acclimation. Specific leaf area is considered to be a sensitive indicator of foliar shade acclimation (Bjorkman, 1981). Photosynthesis was maximized by these trees by allocating a limited supply of carbohydrates to fewer and thinner leaves to increase illumination and decrease self-shading. This resulted in greater specific leaf areas, lower crown density, and fewer carbohydrates available for trunk growth. Consequently, these stress responses need not be considered negative effects of the reduced irradiance. In spite of that, reduced growth becomes a problem when other stresses or diseases exist, which is very often the case in urban environments.

1.5 Temperature

Although the incoming radiation may be less in the city because of increased haze or the presence of large buildings, the amount of heat absorbed and reflected by building and street surfaces is greater than by vegetation, raising both daytime and night-time urban air temperatures (Landsberg, 1981). Typically, the mean annual temperature in an urban centre is 1 to 2°C higher than in outlying areas. When only night-time temperatures are considered this difference may exceed 10°C (Graves, 1994).

Although there are few published studies dealing with the impact of urbanization on soil temperatures, the general belief is that urbanization causes an increase in soil temperatures, especially where underground utilities as well as asphalt and concrete surfaces are present. Graves and Dana (1987) reported the mean soil temperature at several downtown street tree planting sites were significantly higher than at urban sites away from streets, street-side sites in residential areas, and at a site in a nearby native woodland. Furthermore, there was little difference in soil temperature at depths of 5 to 50 cm at the downtown street tree sites, whereas there was a steady decrease in temperature with increasing soil depth in the forest. They also noted that trees in one sidewalk planting pit in Indianapolis did not survive long due to the soil temperature often reaching 69°C because of heat from an underground utility steam line. Halverson and Heisler (1981) found that an asphalt surface increased soil temperature at a 15 cm depth by 7°C in a parking lot in New Jersey.

Growth of woody plants is very sensitive to temperature and a change of only a few degrees Celsius often leads to a change in the rate of growth (Freedman, 1995). Optimal temperatures for trees vary, but rarely exceed 25 to 30°C for temperate species. Further increases in temperature cause very rapid decreases in reaction rates and growth (Hale and Orcutt, 1987). Graves, et al. (1991) reported a reduction in water uptake and transport, lower root and shoot dry matter accumulation, smaller root-to-shoot biomass ratios, and reduced leaf area in tree-of-heaven with root zones at 34°C. Although honeylocust was able to sustain growth at root-zone temperatures above 32°C, abundant soil water was necessary. Many urban sites lack adequate moisture, particularly during times of unusually high temperatures, and irrigation is rarely supplied; hence, honeylocust would probably fare poorly at elevated soil temperatures in actual urban sites. At 35°C, growth reductions and chlorosis were observed in *Amur maackia* and Japanese pagoda. It was suggested that the chlorosis was caused by a reduction in nutrient uptake and translocation, particularly iron (Graves and Green, 1993; Graves, 1991).

1.6 Air pollution

At the present time there are no published studies on the effects of air pollution on the growth of urban street trees. Whether air pollution is a significant factor in determining the survival of these trees is not known. Air pollutants such as sulfur dioxide, ozone, nitrogen oxides and peroxyacetylnitrate are known to inhibit chlorophyll synthesis and photosynthesis and alter stomatal aperture, permeability of cell membranes, amounts of stored carbohydrates and proteins, and activity of enzymes of forest trees (Freedman, 1995). However in the urban environment, there are many interacting stresses contributing to the overall stress in trees, this makes it difficult to quantify the effects of air pollution. Most researchers suggest that water stress and restricted soil volumes are the major factors causing premature death of urban trees, while air pollution is usually considered a minor stress (Labrecque, 1993).

2. Vesicular-arbuscular mycorrhizae

It has been estimated that associations involving vesicular-arbuscular mycorrhizal fungi (VAM) occur on 90% of all vascular plants (Kendrick and Berch, 1985). In most deciduous ornamental trees, VAM fungal associations are the rule, while uncolonized roots are the exception. The symbiosis is named for the two conspicuous fungal structures found inside the host plant cells: arbuscules (the site of exchange of materials) and vesicles (resting spores or storage sites). These two structures plus the extramatrical hyphae, extending away from the plant root into the surrounding soil, are the observable manifestations of the symbiosis. The plant roots themselves are little changed, and colonization cannot be determined by simple visual examination.

Since these symbiotic associations have been shown to enhance growth and vigor of host plants (Harley and Smith, 1983), it may be seen that there are significant implications of mycorrhizae to urban plants, especially in light of the known shortcomings of urban soil. Some of the beneficial aspects of VAM fungi to urban trees as well as the urban conditions unfavorable to mycorrhizal colonization will be discussed.

2.1 Host photosynthesis

In general the higher plant provides reduced carbon derived from photosynthesis, while the fungus provides soil minerals, particularly those of low soil mobility, and sometimes water. Published studies have estimated that between 2% and 30% of photoassimilated carbon is allocated by plants to VAM (Jakobsen and Rosendahl, 1990; Van Veen, et al., 1989; Whipps, 1987). Since the growth of mycorrhizae requires plant carbohydrates, any stress that reduces plant photosynthesis and the export of carbohydrates to the roots is also likely to inhibit colonization of VAM (Kozlowski, 1991).

Low levels of light can reduce photosynthesis, resulting in reduced VAM development (Nemec, 1987; Furlan and Fortin, 1977; Gerdemann, 1968). The effect of light on VAM seems to depend on the photosensitivity of the species of host plant. At low light levels, VAM colonization of shade tolerant species is higher than that of shade intolerant species (Bagyaraj, 1991).

Air pollutants may also reduce mycorrhizal populations, often because of the reduced flow of assimilates from leaves to roots (Kasana and Mansfield, 1986). SO_2 reduced the number of infected roots and the percentage of infection of red oak seedlings with mycorrhizal fungi (Clapperton, et al., 1990; Reich, et al., 1985). High concentrations of O_3 have also been shown to reduce total infection of red oak (Reich, et al., 1986) and number of arbuscules in sugar maple seedlings (Duckmanton and Widden, 1994).

2.2 Phosphorus

The absorbing surface of most root systems is greatly increased by the presence of mycorrhizal roots from which fungal hyphae extend out into soil not penetrated by roots or root hairs. The hyphae also can enter spaces between soil particles that are too small to be penetrated by roots. This is very important for absorption of relatively immobile elements such as phosphorus (Kozlowski, 1991).

Only one tenth as much phosphorus as nitrogen is contained in plant tissues. However, the most common form of phosphorus in soil is phosphate, which is about one hundredth as mobile as the common form of nitrogen (nitrate). This low mobility causes the area next to root surfaces to be depleted in phosphorus in a very short time, while the remainder of the soil volume is unexploited with regard to phosphorus. In the mycorrhizal symbiosis the proliferation of fungal hyphae, reaching over 10 cm from the root surface, provides a way to exploit the soil volume between roots. The rate of phosphorus uptake from soil is three to four times higher in mycorrhizae than for uninfected roots (Stribley, 1987; Harley and Smith, 1983). Li, et al. (1991) found that mycorrhizal inoculations doubled P concentration in shoots and roots of white clover irrespective of P levels. Jakobsen (1986) also reported that a large proportion of phosphorus uptake by field-grown pea was attributed to VAM. Thus in low phosphorus urban soils, VAM may provide urban trees with required phosphorus much more efficiently than the tree roots.

Some studies have shown a negative association between the amounts of extractable phosphate in soils and abundance of VAM fungi as assessed by infection (Abbott and Robson, 1991; Morita and Konishi, 1989; Son and Smith, 1988). Amijee, et al. (1989) observed that the density of hyphae and arbuscules was greatly reduced when phosphorus application was increased from 150 ppm to 750 ppm. Abbott, et al. (1984) also detected a reduction in the length of infected root and the length of external hyphae per cm of infected root when phosphorus application was increased from 33 ppm to 150 ppm.

Frequently, however, there is little quantitative association between concentrations of extractable soil phosphate and the extent of mycorrhizal colonization in plants. For example, sites with large amounts of extractable phosphate may have high levels of infection, whereas sites with small amounts of extractable phosphate may have low levels of infection (Jeffries, et al., 1988; Gianinazzi-Pearson, et al., 1980). In these cases factors other than phosphorus may be more important in explaining VAM infection levels. Koide and Li (1990) found that VAM infection rates increased as phosphorus applications increased from 0 ug/ml to 0.94 ug/ml. DeMars and Boerner (1995) found that VAM development did not increase with decreasing phosphorus availability. However, it was determined that VAM development was significantly correlated with moisture. VAM development was lower in moister topographic positions and higher in drier positions. To date, no research has been conducted on the effects of phosphorus levels in urban soils on VAM infection rates.

2.3 pH

Since pH affects many soil characteristics and processes, it is often difficult to determine the specific effects of pH on the symbiosis (Sylvia and Williams, 1992). The effect of pH seems to be more important in spore germination than in the actual physiological processes of VAM fungi. High levels of infection have been observed over a wide range of soil pH. Some species of VAM fungi are restricted to either acid or alkaline soils, whereas others occur in both acid and alkaline soils (Robson and Abbott, 1989; Young et al., 1985). *Glomus mosseae* and *G. epigeum* have been reported to germinate optimally between pH 6 and 9 (Bagyaraj, 1991), while *Gigaspora* sp. and *Acaulospora laevis* optimally germinate in the 4 to 6 range (Porter, et al., 1987). This indicates that the high pH levels found in urban soils should not be a problem for VAM colonization of urban trees. However, there have been no observations on the VAM species distribution in high pH urban soils.

2.4 Soil contaminants

2.4.1 Salt

Sodium and chloride ions have been shown to inhibit spore germination of VAM fungi (Gildon and Tinker, 1983a). In a Utah salt playa with varying sodium concentrations of 10,000, 3100, 1300, and 153 ppm, per cent colonization of VAM in roots of grasses was found to be 0, 3.8, 9.2, and 34.2, respectively (Kim and Weber, 1985). Johnson-Green, et al. (1995) determined that >40% of roots of grasses and shrubs in an inland boreal salt pan site in north-central Manitoba were colonized by VAM fungi where salt concentrations were low. However in areas with high salt concentrations, VAM fungal colonization was <2%. Gupta and Krishnamurthy (1996) also found a reduction in VAM colonization when 5% NaCl was applied to soils on which peanut plants were growing as compared to soils when 1% NaCl was applied. Stahl and Williams (1986) demonstrated that increasing the salinity of the soil solution markedly changes the species distribution among VAM fungi, but does not change the overall infection levels.

There has been one study dealing with the effects of salt on VAM of street trees. Guttay (1976) conducted an experiment to investigate the status of VAM in salt-damaged sugar maples along Connecticut highways. Soils from trees with low mycorrhizal levels had significantly more sodium (180 ppm vs. 7 ppm) and chloride (44.5 ppm vs. 2.5 ppm) than soils from trees with high mycorrhizal levels. It was determined that VAM colonization was significantly lower in the severely damaged trees than in those trees rated as undamaged.

2.4.2 Heavy metals

It is becoming widely accepted that VAM can increase the uptake of relatively immobile minerals other than phosphorus, such as copper or zinc, when these micronutrients are at low concentrations. Copper and zinc concentrations are generally higher in mycorrhizal than nonmycorrhizal plants. Li, et al. (1991) determined that copper uptake by mycorrhizal hyphae ranged from 53% to 62% of total copper uptake of white clover. Results from a study conducted by Gildon and Tinker (1983b) indicated that *Glomus mosseae* VAM fungi can increase the supply of copper to leeks. Timmer and Leyden (1990) also concluded that the supply of copper to sour orange seedlings was increased by infection of VAM fungi. Zinc uptake has been shown to be increased by VAM fungi in corn (Faber, et al., 1990), peanut (Bell, et al., 1989), wheat (Thompson, 1990), a grass species (*Lygeum spartum*) and a legume species (*Anthyllis cytisoides*) (Diaz, et al., 1996).

While enhancement of copper and zinc uptake is increased by a factor of two to three in the presence of VAM fungi and is likely to be beneficial, these micronutrients are toxic at higher concentrations. Mycorrhizal colonization can be delayed, reduced and even eliminated by high concentrations of copper, zinc, nickel or cadmium (Weissenhorn and Leyval, 1995; Koomen, et al., 1990; McGee, 1987). Mycorrhizal infectivity and *Glomus mosseae* spore germination were found to be negatively correlated with extractable metals. VAM spores germinated at a rate of 70.9, 20.7 and 3.7% in soils containing 70, 575 and 24,410 ppm zinc, and 13, 30 and 1630 ppm copper, respectively (Leyval, et al. 1995). Gildon and Tinker (1983a) determined that the degree of infection of onions with VAM was strongly reduced by additions of zinc and copper. When zinc was added to the soil at rates of 0, 20, and 75 ppm, the root length infected by VAM was 55, 39, and 0%, respectively. For copper, rates of 0, 15, and 75 ppm, produced VAM infection rates of 51, 34 and 0%, respectively. Graham, et al. (1986) also found colonization by the VAM fungus *Glomus intraradices* to be reduced logarithmically with increasing copper concentrations. Copper concentrations up to 300 ppm were added to soil, but the minimum toxic amounts to VAM fungi ranged from 19 to 34 ppm.

Researchers have shown that some VAM fungi are able to tolerate high concentrations of zinc. It has been suggested that in these cases mycorrhizal infection may play a role in heavy metal resistance of the plants (Dehn and Schuepp, 1989). When zinc was applied to a soil at a rate of 309.7 ppm, it was found that mycorrhizal lettuce plants had higher root zinc concentrations but lower shoot concentrations. In this situation VAM were acting as a filter for toxic concentrations of zinc by providing an enhanced root/shoot barrier for the host plant (Dehn and Schuepp, 1989). Shetty et al. (1994) also found an increased retention of zinc in roots. It was suggested that in roots heavily colonized by VAM, heavy metal accumulation was increased not only by a larger metal adsorption capacity, but also by a more effective mechanism for binding metal in the hyphae or fungal cell walls. This has even been found when total infection was reduced by heavy metals (Baath, 1989). Hence, VAM may restrict heavy metal transport to the shoots, thereby providing a mechanism for heavy metal tolerance of plants.

2.5 Soil compaction

VAM fungi are aerobic, hence soil compaction, and the reduced aeration and soil moisture associated with compaction, has a considerable impact on their distribution and effectiveness (Sylvia and Williams, 1992). It is generally understood that spore germination rate and frequency decline with soil compaction due to lower soil moisture (Wilson, 1984; Tommerup, 1983). However, there is a large difference in the effects of soil water between VAM species. *Gigaspora* sp. will not germinate below a soil water potential of about -10 bars, while those of *Glomus* sp. will germinate down to about -30 bars (Don Smith, pers. comm., March, 1995). Le Tacon, et al. (1986) demonstrated that low levels of oxygen can inhibit spore germination and hyphal growth of *Glomus mosseae*. Entry et al. (1996) and Douds et al. (1995) found that in agricultural systems mycorrhizal infection was reduced due to compaction . Simmons and Pope (1988) studied the interaction of soil compaction with mycorrhizal inoculations of sweetgum and yellow-poplar. Their results indicated that for yellow-poplar compaction effects outweighed mycorrhizal benefits at a bulk density of 1.55 g/cm^3. However, for sweetgum the effects of compaction were alleviated by inoculation with *Glomus fasciculatum*. This observation could have promising applications for urban trees growing on compacted soil. However, no studies have been conducted to test the effects of VAM on alleviating the effects of soil compaction, or the effects of soil compaction on VAM infection rates in urban soils.

2.6 Water

VAM infection has been found to improve the water relations of many plants. The mechanism by which VAM fungi increase water uptake is similar to that for phosphorus uptake. As well as having VAM hyphae that penetrate beyond water depletion zones occurring around the root surface during periods of low soil moisture, mycorrhizal roots have greater surface absorbing areas because of their greater root length and increased branching (Cooper, 1984). Several studies have demonstrated that a large proportion of plant water uptake is supplied by VAM hyphae (Ruiz-Lozano and Azcon, 1995; Faber, et al., 1991; Hardie, 1985). Mycorrhizal plants have also been found to have a lower resistance to water flow than nonmycorrhizal plants (Koide, 1985; Safir and Nelson, 1981).

VAM have also been reported to increase resistance of plants to water stress (Puppi and Bras, 1990; Bethlenfalvay, et al., 1988). Improved drought resistance by VAM fungi can be directly attributed to increased water uptake, as discussed above, independent of any improvement in phosphorus nutrition; or it can be attributed to the indirect influence of VAM on improved phosphorus nutrition. Improved phosphorus nutrition alters membrane permeability, thereby influencing water transport (Puppi and Bras, 1990). VAM infection has been shown to cause an improvement in leaf water and turgor potentials, maintenance of stomatal opening and transpiration (Auge, et al., 1987a,b), osmotic adjustment (Auge, et al., 1986) and changes in cell-wall elasticity (Sanchez-Diaz and Honrubia, 1994). These changes in plant physiology indirectly caused by VAM infection have been reported to increase drought resistance.

Regardless of whether VAM directly or indirectly improve plant survival through periods of drought, it is apparent that VAM can perform an important role in urban situations. It is surprising to find a lack of published studies on the relation between VAM and use of the water supply by urban trees, even though urban street trees are often subjected to long periods of water stress.

3. Summary and Project Objectives

In spite of the fact that $40,000 to $60,000 is wasted each year on replacing dead trees in Montreal, research on identifying which stresses exist, how they interact, and how they affect urban trees is lacking. Furthermore, research on VAM associations of urban trees is virtually non-existent, despite the theoretical evidence that VAM can improve the living conditions of street trees.

The urban environment is a complex system involving a combination of a variety of stresses. It is reasonable to assume that the factors affecting VAM in agricultural settings, or the benefits of VAM to agricultural or other annual plants, may not be the same as those of ornamental deciduous tree species used for urban planting.

This thesis reports on a preliminary examination of VAM and silver maple tree health in downtown Montreal. The study objectives were as follows:

1. To characterize the soil on which downtown Montreal silver maple street trees grow.
2. To determine to what extent the soil characteristics affect the health and survival of these trees.
3. To determine the level of colonization of VAM on these trees.
4. To determine the factors affecting VAM development.
5. To investigate, under controlled conditions, the effect of typical urban soils on VAM development of silver maple seedlings.

CHAPTER 2

VAM INFECTION LEVELS AND SOIL PROPERTIES OF SILVER MAPLE TREES GROWING IN DOWNTOWN MONTREAL

1. Introduction

Silver maple (*Acer saccharinum* L.) is one of the most planted species in downtown Montreal. It is relatively fast growing and is considered to be tolerant to many of the stresses that exist in the urban environment. However, silver maple (as well as all other tree species) planted in downtown Montreal have short life spans of, on average, four to five years. The inability of trees to grow large and survive to their natural lifespans is not only a biological problem, but also has economic and social consequences. In these times of fiscal restraint, the $40,000 to $60,000 the city of Montreal spends to replace dead trees each year is considered to be a problem. Socially speaking, the necessity of having large, healthy trees in urban centres to improve the living conditions in these areas is increasingly being acknowledged. Clearly, it is essential to not only identify, but also to understand which downtown Montreal conditions affect street trees.

In 1991 and 1992 Michel Labrecque of the L'Institut de Recherche en Biologie Végétale conducted a study to determine the environmental factors that best explained the health and survival of street trees growing in downtown Montreal. The factors that were studied included tree species, street type, irrigation, light levels, physical injury, and water stress. However, of the 622 trees studied, only 20 soils were sampled to determine pH, sodium and compaction. Consequently, there were no firm conclusions on the effects of the soil on the health and survival of downtown Montreal street trees. Hence, the first part of this chapter reports on a preliminary examination of the effects of various soil variables on the health of downtown Montreal silver maples.

Numerous experiments have demonstrated that plants with vesicular-arbuscular mycorrhizal (VAM) associations are more efficient in acquiring relatively immobile nutrients, such as phosphorus (Li, et al., 1991; Furlan and Bernier-Cardou, 1989; Stribley, 1987; Jakobsen, 1986), copper and zinc (Diaz, et al., 1996; Faber, et al., 1990), than non-mycorrhizal plants . It has also been demonstrated that VAM can improve the drought and heavy metal resistance of plants (Sanchez-Diaz and Honrubia, 1994; Shetty, et al., 1994; Puppi and Bras, 1990; Dehn and Schuepp, 1989; Bethlenfalvay, et al., 1988). In consideration of the beneficial aspects of VAM and with an understanding of the inferior quality of urban soils, it may be seen that there are significant advantages that urban trees can derive from VAM. On the other hand, some of the conditions unfavorable to urban tree growth may also be unfavorable to VAM development. Low light levels or air pollution may reduce photosynthesis in urban trees, thereby reducing VAM infection. Low soil aeration, as well as high salt and heavy metal concentrations, may directly inhibit VAM from developing.

Observations on the effects of these urban conditions on the growth of VAM are relatively non-existent since most of the information on VAM comes from research involving crop and other plants that are not used in urban situations. Furthermore, the city of Montreal has inoculated trees with VAM. These trees are currently growing at the municipal nursery and are intended to be transplanted in downtown Montreal areas in 1999. Any information on the status of VAM in downtown Montreal will be helpful to improve the success of the inoculations and future survival of VAM. Thus, the second part of this chapter reports on a preliminary examination of the status of VAM populations and the affect of soil and other environmental factors on the development of VAM in silver maple street trees.

2. Materials and Methods

2.1 Study Site

The study area was located in downtown Montreal and was bounded by Peel St. on the west, Bleury St. on the east, Sherbrooke to the north, and René-Lévesque to the south. Only those trees growing along city streets next to the sidewalks were included in the survey. Trees growing in parks, church lawns, or mall courtyards were not sampled. All silver maple trees without protective steel grates were sampled. There were a total of 73 trees. Tree health was assessed by visual analyses of the percent of crown dieback. Crown dieback was divided into 10% classes. An additional 10 silver maple trees were randomly selected and sampled at the Montreal nursery located in Terrebonne, approximately 30 minutes north-east of Montreal.

Streets were grouped into four types using the system developed by Labrecque (1993). Street type 1 was defined as running east/west, narrow, and heavily used both above and below ground. Streets of type 2 are the same as type 1 except that they run north/south. Type 3 streets are larger and less used both above and below ground, while type 4 streets are very large and heavily used streets. Tree age was used to assess which street type provided the best survival conditions.

2.2 Soil sampling

At each tree, two samples were collected at randomized compass points at the furthest edge of the soil surface, which was approximately 0.5 to 1.0 m from the base of the tree. Each sample consisted of a 10 x 20 cm (deep) core, since most feeder root growth occurs at this depth (Brundrett et al., 1990). These cores were used to measure root colonization, soil pH, dry bulk density, and exchangeable phosphorus, potassium, calcium, magnesium, sodium, copper, and zinc. Samples were taken on August 9 and 10, and on September 18 and 25, 1995. All samples were bagged and stored at 5°C until they could be processed.

2.3 Staining and quantification of VAM

Maple feeder roots identified by their characteristic beaded appearance were washed from the soil samples and then cleared by autoclaving for 30 minutes in a 10% potassium hydroxide solution. Root samples were then rinsed three times with distilled water, bleached in 35% hydrogen peroxide for 1 h, acidified in 1% hydrogen chloride, and stained using a 0.01% solution of acid fuchsin (Kormanik and McGraw, 1982). The samples were left in the stain for 24 h and stored in a solution of equal volumes of lactic acid and glycerin. The quantification of VAM infection was performed using a Wild M3C dissecting microscope with a magnification of 40 x. The percent of infection for each sample was estimated using the grid-line intersect method (Giovannetti and Mosse, 1980), by evaluating 100 intersects for each sample. The thickness of the grid-lines was approximately 0.5 mm. The number of intersects where vesicles, arbuscules, or internal mycelium were found was defined as total infection.

2.4 Soil variables

2.4.1 pH

With 15 ml of distilled water, 7.5 g of soil was added to a beaker and stirred for 30 minutes. The mixture was then left to stand for one hour to allow most of the suspended clay to settle. A combination electrode was carefully immersed into the solution to measure soil pH (Black, et al., 1965).

2.4.2 Dry bulk density

The exact volume of the soil core was measured. Soil samples were oven dried at 60°C for 24 hours, weighed and then divided by the volume of the soil core to obtain the dry bulk density measured in g/cm^3 (Miller and Donahue, 1990).

2.4.3 Nutrient concentrations

Phosphorus, potassium, calcium, magnesium, sodium, zinc and copper levels were determined using the Mehlich III extractant (Mehlich, 1984). Phosphorus and potassium concentrations were measured using the Quik Chem AE flame photometer (Lachat Instruments). A Perkin-Elmer 2380 Atomic Absorption Spectrophotometer was used to measure all other nutrient concentrations.

2.5 Statistical analysis

Correlation and regression analyses were performed using the SAS System for Windows (version 6.10) computer program (SAS, 1990) to examine relationships between VAM infection, tree health and soil parameters ($P=0.01$ and $P=0.05$). ANOVA were performed using the Microsoft Corporation Excel (version 5.0) computer program (Microsoft Corp., 1994) to examine effects of grouping data by street type and tree age ($P=0.05$). Scheffé post-hoc comparisons ($P=0.05$) were used to determine individual differences between groups.

An exploratory regression analysis was performed to determine which, if any, nutrient ratios (i.e. P:K, P:Ca, Mg:Cu, etc...) had a significant effect on % VAM colonization. Only P:Cu was found to have a significant effect ($P<0.05$).

3. Results

3.1 Soil factors and tree health

Soil nutrient concentrations and physical characteristics for the street and nursery sites are listed in Table 1. Street soils had significantly lower concentrations of phosphorus and magnesium, but higher values of sodium, copper, zinc, pH, and bulk density ($P<0.05$) than nursery soils. There was no significant difference for calcium and potassium.

Downtown street trees had, on average, 12.7 % dieback. No significant effect of any soil variables on tree health was found by a multiple regression analysis ($R^2=0.18$; $P>0.05$). However, simple correlation coefficients showed that % dieback was positively correlated with potassium and phosphorus/copper ($P<0.01$) and to a lesser extent with calcium and phosphorus ($P<0.05$) (Table 2). Copper, zinc, and bulk density were negatively correlated with percent dieback ($P<0.05$) (Table 2). Tree age was negatively correlated with phosphorus, phosphorus/copper and % dieback ($P<0.01$), and positively correlated with copper, zinc, and bulk density ($P<0.01$) (Table 2). Younger trees had significantly higher % dieback than older trees ($P<0.05$).

Significant differences in % dieback between trees of different street types were found in the present study. Street type 3 trees had significantly less dieback than type 4 trees ($P<0.05$), whereas street type 1 and type 2 trees were intermediate in percent dieback (Figure 1). Street type 3 also had significantly older trees ($P<0.05$), while street type 4 had the youngest trees but was significantly different than the age of trees on street types 1 and 2 (Figure 2).

3.2 VAM infection rates

On average, street trees were infected by VAM at a rate of 45.0% which was significantly higher than the nursery tree average VAM colonization of 36.1% ($P<0.05$). Nursery tree % infection was negatively correlated with phosphorus ($r = -0.723$) ($P<0.01$). No significant effect of any soil variables was found by a multiple regression analysis ($R^2=0.12$; $P>0.05$). However, simple correlation coefficients showed that street VAM infection rates were negatively correlated with tree age ($P<0.01$) and potassium ($P<0.05$), and positively correlated with phosphorus/copper ($P<0.05$) (Table 2).

Street type 4 had significantly more VAM infection than type 3 ($P<0.05$), while street types 1 and 2 were intermediate in VAM infection (Figure 3).

	P* (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg* (mg/kg)	Cu* (mg/kg)	Zn* (mg/kg)	Na* (mg/kg)	P:Cu*	pH*	B. Dens.* (g/cm^3)
STREET SOIL	50 ± 4	234 ± 10	573 ± 38	175 ± 8	31 ± 2	96 ± 11	197 ± 24	2.7 ± 0.4	8.08 ± 0.04	1.55 ± 0.02
NURSERY SOIL	159 ± 6	266 ± 10	400 ± 22	340 ± 16	6 ± 0.1	13 ± 0.7	73 ± 2	28.5 ± 1	6.97 ± 0.02	1.13 ± 0.01

Table 1: Soil parameters of street and nursery trees

Means and standard errors are shown (n=73 for street; n=10 for nursery).

*=soils are significantly different ($P<0.05$).

	% VAM INFECT.	% DIEBACK	TREE AGE
PHOSPHORUS	0.050	0.195*	-0.459**
POTASSIUM	-0.217*	0.300**	-0.079
CALCIUM	-0.021	0.196*	-0.034
MAGNESIUM	-0.004	0.101	0.007
COPPER	-0.110	-0.241*	0.271**
ZINC	0.054	-0.214*	0.310**
SODIUM	0.131	0.001	-0.153
P:CU	0.226*	0.326**	-0.489**
pH	0.038	-0.083	-0.118
BULK DENSITY	-0.101	-0.195*	0.319**
% VAM INFECT.	1	0.055	-0.444**
% DIEBACK	0.055	1	-0.308**
TREE AGE	-0.444**	-0.308**	1

Table 2: Correlation coefficients (r) between % VAM infection, % dieback, tree age and soil parameters

n=73.

**=P<0.01; *=P<0.05.

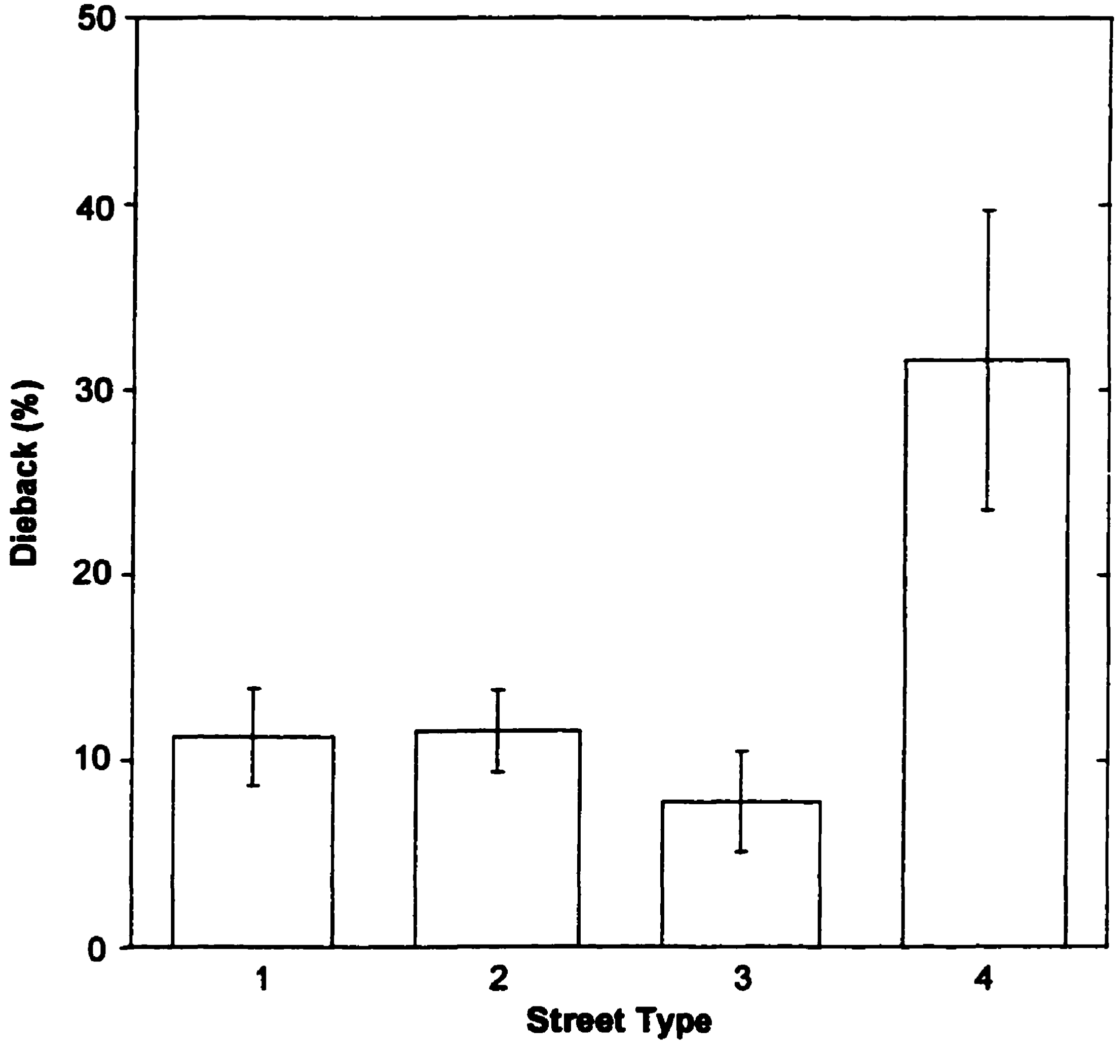

Figure 1: Percent dieback of trees growing on different street types

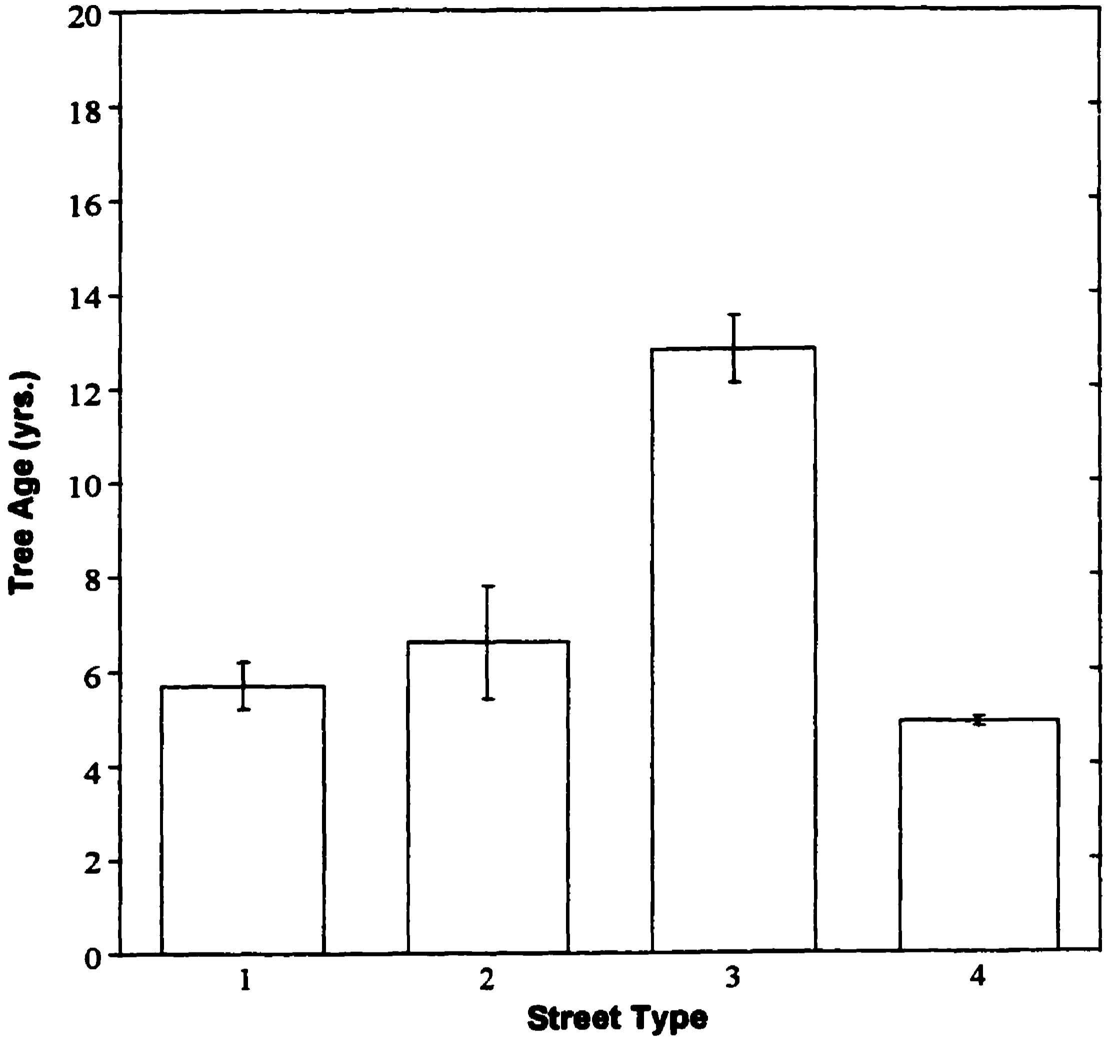

Figure 2: Age of trees growing on different street types

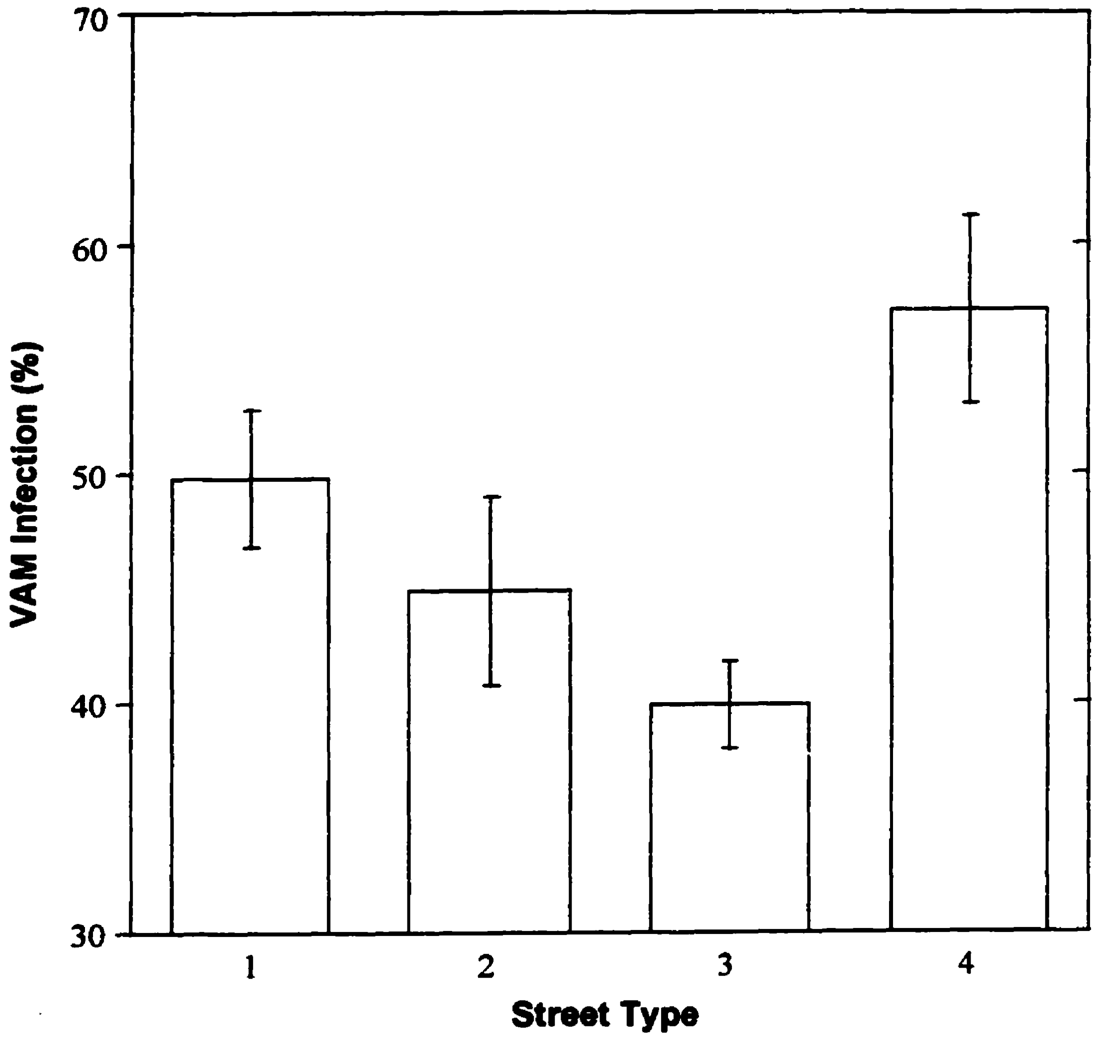

Figure 3: VAM infection rates of trees growing on different street types

4. Discussion

4.1 Tree health

4.1.1 Sodium, potassium and calcium

The soils sampled from downtown Montreal follow the general trend of most other urban soils. The high sodium concentration, due to the use of de-icing salts which contain NaCl, is one of the reasons for the elevated pH level. The direct transport of excessive sodium to the above-ground tissue may result in dieback and lack of vigor in street trees (Hofstra, et al., 1979). Soil sodium can also directly damage trees by reducing water uptake by plant roots. The trees subsequently exhibit scorched foliage due to desiccation of the tissue, and finally crown dieback occurs (Hootman, et al., 1994). Despite the knowledge of the relationship between sodium and tree dieback, no direct correlation was observed between sodium and % crown dieback of silver maples in the study area (Table 2). Although the elevated level of sodium (197.3 ppm) was found to be significantly higher than the nursery soil, it was still below the 250 ppm threshold which is considered to be excessive for most trees (Hootman, et al., 1994). Only 14% (10 trees) of the silver maples in the study area had sodium concentrations above the 250 ppm threshold.

Although no direct relationship between soil sodium and % dieback was observed, indirect effects may still be occurring. Sodium is known to compete with potassium, calcium, magnesium and other cations, potentially reducing nutrient uptake in trees (Miller and Donahue, 1990). A significant positive correlation between % dieback and soil potassium and calcium was observed. It is conceivable that, although sodium may not be directly harming trees, it may be indirectly affecting trees by competing with potassium or calcium. The high soil potassium and calcium concentrations of trees exhibiting crown dieback may be a result of the reduced potassium and calcium uptake caused by the elevated sodium concentrations.

A common factor seen in declining forests is the presence of nutrient imbalances in forest soils which is reflected in the tree foliage. Bernier and Brazeau (1988a,b) found high negative correlations between sugar maple decline and foliar potassium and calcium. Cramer, et al (1985) demonstrated that sodium was replacing calcium on the root cell membranes, thereby impairing their essential functions. Thus, it is essential to measure foliar and root nutrient concentrations and ratios of downtown trees to confirm whether an interaction between sodium and potassium or calcium is occurring in these soils.

4.1.2 Copper, zinc and bulk density

The high copper and zinc concentrations found in the street soils, as compared to the nursery soils, is most likely due to the contamination of the soils by pollutants. The higher bulk density of street soils was also not unexpected, since it is common knowledge that urban soils are highly compacted (Day and Bassuk, 1994; Craul, 1992; Ruark, et al., 1983). It is interesting to note that copper, zinc and bulk density were positively correlated with tree age (Table 2). Over time, soils from older trees become increasingly compacted due to the constant application of stress from foot traffic or vibrational forces from vehicle traffic. In the case of copper and zinc there are two reasons that may cause these metals to accumulate in these soils. First, the continual input of these metals; and second, the high pH, which causes these metals to be bound in forms that become immobile (Foth, 1990).

4.1.3 Phosphorus

The situation with phosphorus is the opposite to that of copper and zinc. As a tree uses the supply of phosphorus in soil, phosphorus will be depleted over time. In a natural setting, there is a constant input and recycling of phosphorus as organic matter decays; however, in downtown Montreal organic matter recycling is absent, nor is there an input of phosphorus in the form of fertilizer (which takes place in the municipal nursery). This can explain why soils under older trees had less phosphorus than soils under younger trees in this study area. It is not known whether the depletion of phosphorus over time can harmfully affect trees.

4.1.4 Other factors

The data suggest that sodium, and the possible associated effects it has on reducing potassium and calcium uptake, may be involved in affecting tree health in terms of % dieback. However, the multiple regression analysis indicated that soil factors did not significantly affect % dieback of silver maples in downtown Montreal (r^2=0.18; P>0.05). It is conceivable that the observed dieback is related to environmental factors such as temperature, light, or the small volumes of soil in which these trees are allowed to establish their root systems. The following discussion will try to shed some light on the effects of these factors.

Younger trees had significantly more dieback than older trees. It is reasonable to assume that the younger trees may still be going through a period of adjustment; thus, the higher dieback may be directly or indirectly related to transplantation shock. On the other hand, the older trees have been able to establish themselves and survive since they either had fewer stresses to deal with or they are tolerant of the stresses. In either case, the older trees are under less stress, and this is outwardly exhibited in the fact that they have lower crown diebacks. Although this interpretation is based on circumstantial evidence, there is a general trend in downtown Montreal whereby the healthiest and oldest trees grow in areas that have the best environmental conditions in terms of water, light or soil volumes.

As previously indicated, Labrecque (1993) defined four street types in downtown Montreal. He concluded that trees on street type 3 were in good health because of more direct sunlight reaching these trees, fewer physical injuries since fewer people use type 3 streets, and most importantly because of the assumed larger soil volumes afforded to these trees, since there are fewer utility pipes or electrical conduits underground. Trees on street types 1 and 4, on the other hand, were found to be in the poorest health due to either reduced amounts of direct sunlight, more physical injuries, or an assumed small soil volume. Street type 2 was determined to be intermediate in terms of tree health.

The results of the present study are similar to those of Labrecque (1993). Trees growing on street type 4 had the most crown dieback, while street type 3 trees had the least. (Street type 1 was not found to be significantly different than type 2, contrary to the findings of Labrecque (1993); this could be due to the fact that the present study was a relatively small one of only 73 trees, while that of Labrecque (1993) was larger with 622 trees.) Since there were no significant correlations between street types and soil characteristics, it is sensible to conclude that tree health is more likely a function of the specific conditions of the street types rather than soil parameters.

Labrecque (1993) estimated the number of hours of direct sunlight trees receive in early and late summer. He found that type 3 streets, such as Bleury, Phillips, or Union, receive on average more direct sunlight (6.6 hr/dy) than types 1 and 4 (4.8 hr/dy), and type 2 (3.4 hr/dy). The lower dieback levels for type 3 streets (Figure 1) may be associated to the higher amounts of direct sunlight these trees receive which may allow these trees to have photosynthetic rates high enough to support growth. No data have yet been collected on photosynthetic rates of various trees growing in downtown Montreal to see if the rates are significantly different for different light levels. Nevertheless, results from previous research on street trees from other cities suggest that the lower light levels of some downtown Montreal streets can produce lower photosynthetic rates (Kjelgren and Clark, 1992; O'Rourke and Terjung, 1981).

Although Labrecque (1993) determined that type 4 street trees receive less direct sunlight per day than type 3 streets, the difference was not found to be significant. Type 4 streets, such as René-Lévesque, Sherbrooke, or University south of Cathcart, are extremely wide and are characterized as wind tunnels (Michel Labrecque, pers. comm., March,1995). Since these trees are planted in isolation, they could be desiccated by high winds, develop abiotic leaf scorch and are more likely to succumb to dieback (Hammerschlag, et al., 1986). Moreover, isolation creates a different set of microclimatic conditions surrounding the tree, and increases the atmospheric water loss. The stomatal behaviour of isolated trees is known to be more closely coupled to atmospheric demand than that of closed-canopy forest trees, resulting in greater water use (Clark and Kjelgren, 1990).

Coupled with the greater water use of trees growing on street type 4 is the assumed small soil volume available to these trees. Over the past 20 years large skyscrapers and hotels have been constructed on type 4 streets (especially René-Lévesque and Sherbrooke); hence more underground space has been taken up by municipal service pipes. The small soil volumes available to trees planted on these streets may eventually lead to small root systems that can not support the larger water needs of these trees; as a result these trees may show symptoms of decline.

Type 4 streets can be contrasted to type 3 streets. Most buildings on type 3 streets are 30 to 40 years old, and large scale construction projects have not taken place near them in the past 30 years. Consequently, underground utility conduits have essentially not been upgraded, and the soil has been left relatively undisturbed. Thus type 3 trees are assumed to have larger soil volumes that can support increased water needs in drought situations. This may result in smaller crown diebacks for type 3 street trees.

From this standpoint the question of the minimal dimensions of rootable soil that are necessary to sufficiently meet a tree's growth requirements may arise. In natural forest environments it has been estimated that a tree, depending on its size at maturity, generally roots in a soil volume of 25 to 300 m^3 (Helliwell, 1986). For urban trees, the minimum soil volume needed has been estimated to be 6 m^3 (Lindsey and Bassuk, 1991; Arnold, 1989; Cervelli, 1986; Kopinga, 1985). Clearly the typical Montreal planting pits, which are usually no more than 2 m^3, are insufficient. Given that the larger soil volume estimates are unattainable for a city such as Montreal, trees that are smaller at maturity and need smaller soil volumes could be planted. Evans, et al. (1990) suggest the best alternative would be to connect planting pits under paved areas and then cover them with permeable paving. This paving would help ensure vital oxygen diffusion and water infiltration through the soil.

Since it is virtually impossible to quantify the size of street tree root systems, no studies have been conducted to estimate the size of root systems for downtown Montreal street trees. The size of root systems can be estimated by visually inspecting the immediate surroundings and by analyzing the past large scale construction projects. Although this can only provide presumptive evidence of the effects of soil volumes and root systems on tree health, it is a useful procedure to use in the absence of other information.

4.2 VAM infection rates

4.2.1 Phosphorus

Due to the high phosphorus concentration of the nursery soil as compared to the street soils, it was not unexpected to find nursery VAM infection rates to be lower than the rate for street trees. The negative correlation observed between VAM infection and soil phosphorus concentration of nursery trees is consistent with other published findings (Abbott and Robson, 1991; Morita and Konishi, 1989; Son and Smith, 1988). However, the negative correlation between VAM infection and soil phosphorus was not observed in street soils. DeMars and Boerner (1995) also found that VAM infection did not increase with decreasing phosphorus availability. Similarly, the results from the present study suggest that one or more factors other than phosphorus may be more important in regulating VAM infection.

4.2.2 Phosphorus:copper ratio

There is a lack of information regarding the combined effects of phosphorus and copper on VAM infection. In spite of this, several studies have been conducted to investigate the separate effects of copper and phosphorus which are useful in explaining the positive effect of the phosphorus:copper ratio in the present study.

The data from the present study indicate that VAM infection increases as the concentrations of copper decrease and phosphorus increase. Research conducted by Leyval, et al. (1995), and Gildon and Tinker (1983a) also indicated that VAM infection will increase with decreasing levels of copper. In addition, Mosse (1978) hypothesized that VAM infection should be low at low phosphorus availabilities and that it should increase in response to added phosphorus. This hypothesis was supported by Koide and Li (1990), and Abbott, et al. (1984) and is consistent with the results from the present study. When phosphorus availability is exceptionally low there may be little that the additional absorptive surface area provided by VAM hyphae can do to promote phosphate uptake. Thus, the host plant will limit the extent of infection, even if phosphorus availability limits plant growth, because VAM infection cannot substantially improve the phosphorus status of the host plant (Koide and Li, 1990).

The phosphorus:copper ratio for the street soils ranged from 0.30 to 14.7, while the ratio for the nursery soils ranged from 23.4 to 33.9. The lack of high ratio values for the street soils is due to a lack of high phosphorus and a lack of low copper levels in the street soils. There were only six soils with more than 100 ppm phosphorus and five soils with less than 10 ppm copper. The nursery soils, on the other hand, had a minimum of 138 ppm phosphorus and a maximum of 6 ppm copper. It is not known what the effect would be if the phosphorus:copper ratio in the street soils was as high as the nursery soils. However, when previous research is considered, it is doubtful that VAM infection rates would continue to increase if the phosphorus:copper ratio increased to levels found in the nursery.

Studies have reported that, at low copper concentrations, VAM infection is not affected (Li, et al., 1991; Timmer and Leyden, 1990; Gildon and Tinker, 1983b). Moreover, Mosse (1978) hypothesized that after the initial increase in VAM infection in response to added phosphorus, VAM infection will begin to decline as phosphorus availability is increased still further. Other studies have supported this hypothesis (Son and Smith, 1988; Bogiano, et al., 1983; Schwab, et al., 1983; Graham, et al., 1982).

4.2.3 Potassium

The regulating role of soil potassium in VAM symbiosis is not clear. Potassium plays a crucial role in enzyme activation, charge balance and pH regulation, processes which occur at the host-endophyte interface of VAM and other symbioses (Smith and Smith, 1990). Zahka, et al. (1995) reported a positive correlation between foliar potassium and VAM infection. In a legume-*Rhizobium* symbiosis, an inadequate supply of potassium resulted in a reduced photosynthate supply to root nodules and reduced N_2 fixation (Collins and Duke, 1981; Mengel, et al., 1974).

Potassium, as is the case with phosphorus, promotes root branching in woody species (Vogt and Bloomfield, 1991). The increased root branching may possibly reduce VAM infection, since trees will be able to obtain nutrients without the need of VAM. Cooke, et al. (1993) found that the rate of VAM infection decreased with increasing rates of cations; however, calcium, magnesium and potassium were applied together and the effects of the three nutrients was not differentiated. Ouimet, et al. (1995) found a negative correlation between forest floor potassium saturation and VAM infection. It was suggested that the negative correlation may depend on forest floor pH, magnesium saturation and cation exchange capacity. Further research is needed to understand the role of potassium and other cations in VAM symbioses.

4.2.4 Tree health

The data suggest that VAM infection may be correlated with tree location. Trees growing on streets with unhealthy conditions had higher infection rates, while trees growing on streets with healthier conditions had lower infection rates. Colonization is regulated by the host-plant. Although the mechanisms are not clear yet, it seems that trees growing in stressed environments invest more in the symbiosis which acts as a buffer. This is true for phosphorus stress, and also water stress, to a certain extent (Chantal Hamel, pers. comm., December, 1997).

This interpretation of the relationship between VAM infection and tree health is based on circumstantial evidence and assumptions, and is not supported by other studies. Ouimet, et al. (1995) found that sugar maple decline was not associated with lower colonization levels of VAM fungi. Duckmanton and Widden (1994) found that VAM infection rates remained unchanged in sugar maple seedlings with increasing stress caused by ozone applications. Contrary to the present results, Cooke, et al. (1993) found that the rate of VAM infection decreased along with the health of sugar maple seedlings. Spitko, et al. (1978) and Guttay (1976) also found VAM infection rates to be lower in declining urban sugar maple trees.

4.2.5 Further issues

Before the discussion on VAM infection and tree health can be completed, two remaining topics need to be communicated . The first deals with whether or not VAM are beneficial in situations where trees are in poor health. The high VAM infection rates found in declining urban silver maples could be contributing to the higher dieback in these trees by draining the carbon supply. Ouimet, et al. (1995) suggested that VAM fungi may be contributing to the decline of sugar maple in the Beauce region; however, their results did not confirm nor invalidate this theory. Koide (1984) and Buwalda and Goh (1982) demonstrated that VAM colonization caused growth depressions in ryegrass and sunflower due to the competition for photosynthate between the fungi and the host plant. However these results were found in high phosphorus conditions which is rarely the case in downtown Montreal.

A study that determines the amount of photosynthate allocated to roots of healthy and unhealthy trees is needed to evaluate the hypothesis that VAM could be deleterious to declining urban silver maple. The benefits of VAM may also be evaluated by a long-term study. That is, if young trees that are highly colonized survive beyond the average lifespan for Montreal trees, then it could be suggested that VAM are providing benefits to street trees. On the other hand, if young trees that are colonized at a low rate survive beyond the average age, then this may provide evidence in favour of the hypothesis that VAM are deleterious.

VAM morphological changes in trees showing symptoms of decline is the final subject matter. It is important to distinguish between presence or abundance of VAM and the activity or actual benefit of VAM to the host plant. It is currently theorized that arbuscules are the site of nutrient exchange, while vesicles are either resting spores or storage sites. Hence, if the effects of VAM on tree health are to be estimated, it may be useful to define VAM infection in terms of the ratio of arbuscules and vesicles rather than as the total infection. Duckmanton and Widden (1994) showed that total VAM infection rates remained unchanged with decreasing plant health; however, the frequency of vesicles and hyphal coils increased while that of arbuscules decreased. It was suggested that VAM were responding to stress in the sugar maple seedlings by increasing the production of less energy demanding and less efficient organs for exchange of nutrients (hyphal coils) and by increasing the resources allocated to storage and future growth (vesicles). Cooke, et al. (1993) and Cooke (1992) also observed a change in VAM morphology in sugar maple seedlings and trees, respectively. Sugar maple seedlings and trees in poor health had more vesicles and fewer arbuscules as compared to seedlings and trees in good health.

Although declining urban silver maple trees were found to have higher VAM infection rates, it is possible that these trees had the same amounts of arbuscules as healthy trees. If this is the case, then it could be suggested that VAM are supplying equal benefits to declining and healthy trees. Silver maple roots produce large amounts of brown phenolic material which made it difficult to clear the roots used in the present study; as a result, it was difficult to distinguish between VAM structures. In addition, the maximum magnification of the microscope that was used in this study was 40x. This added to the difficulty of distinguishing between VAM structures, consequently I was constrained to use total VAM infection.

PREFACE TO CHAPTER 3

The previous study was conducted to examine the status of VAM in downtown Montreal street trees. It was suggested that many factors determine infection rates, such as potassium, phosphorus:copper ratio, size of root systems, water stress, and tree health. However, all of these factors vary concurrently, which made it problematic to generate solid conclusions on the specific effects of each factor on VAM infection. The following experiment was set up to separate the soil factors from all other factors by growing silver maple seedlings in a controlled environment. In this way the actual infectivity of typical urban soils could be determined.

CHAPTER 3

VAM INFECTION IN SILVER MAPLE SEEDLINGS IN SIX URBAN SOILS

1. Introduction

It is known that copper, zinc and sodium, at concentrations typically found in downtown Montreal soils, can inhibit VAM infection in crop and other annual plants (Weissenhorn and Leyval, 1995; Koomen, et al., 1990; McGee, 1987; Kim and Weber,1985). Although potassium and the phosphorus:copper ratio were found to be significantly correlated with VAM infection in the previous experiment, the coefficients of correlation (r) were very low (-0.217 for potassium and 0.226 for phosphorus:copper). My objective in conducting this study with silver maple seedlings in a controlled environment was to determine the full contribution of these soil parameters on VAM colonization.

The results of this research could have direct applications to the Montreal municipal nursery project to inoculate trees that will eventually be transplanted in downtown Montreal. If this study can establish that downtown Montreal soils can inhibit VAM development, the benefits that trees can derive from VAM fungi will be diminished unless VAM species tolerant to the unfavourable conditions are discovered and used in the inoculations.

2. Materials and Methods

2.1 Soil

Soils (0-10 cm deep) from seven silver maple trees from the study area described previously were collected. The soils were chosen to have a wide range of pH and nutrient concentrations. Soil was also collected from the municipal nursery in Terrebonne. Table 4 shows the nutrient concentrations of the eight soils.

2.2 Seedling establishment

Silver maple seeds from a single maple tree were collected in the spring of 1996. A total of 80 seeds were planted individually in 30 cm^3 plastic plugs and watered each day to maintain moisture levels. Seedlings were allowed to grow for five weeks after germination. It was decided beforehand that six seedlings from each soil type would be chosen at random to quantify VAM infection. For each type of soil 10 seeds were planted to maximize the chances of having at least six seedlings per soil type.

Seeds did not germinate in soils 2 and 5. All soils collected from downtown Montreal were very compactible, which may have prevented seeds from germinating in these two soils. The high sodium concentration of soil 2 (675 ppm) may also have inhibited germination. However, at least six seeds did germinate in the other six soils.

2.3 Staining and quantification of VAM

Maple feeder roots identified by their characteristic beaded appearance were washed from the soil samples and then cleared by autoclaving for 30 minutes in a 10% potassium hydroxide solution. Root samples were then rinsed three times with distilled water, bleached in 35% hydrogen peroxide for 1 h, acidified in 1% hydrogen chloride, and stained using a 0.01% solution of acid fuchsin (Kormanik and McGraw, 1982). The samples were left in the stain for 24 h and stored in a solution of equal volumes of lactic acid and glycerin. The quantification of VAM infection was performed using a Wild M3C dissecting microscope with a magnification of 40 x. The percent of infection for each sample was estimated using the grid-line intersect method (Giovannetti and Mosse, 1980), by evaluating 100 intersects for each sample. The thickness of the grid-lines was approximately 0.5 mm. The number of intersects where either vesicles, arbuscules, or internal mycelium were found was defined as total infection.

2.4 Statistical analysis

Descriptive statistics were obtained using the Microsoft Corporation Excel computer program, version 5.0 (Microsoft Corp., 1994). ANOVA was performed using the Excel program to examine differences between soil types for % VAM infections of seedlings and street trees ($P=0.05$). Scheffé post-hoc comparisons ($P=0.05$) were used for comparison of means. Multiple regression analyses were performed using the SAS System for Windows computer program, version 6.10 (SAS, 1990) to examine the relationship between % VAM infection and soil variables ($P=0.05$). It was decided beforehand that the phosphorus:copper ratio, potassium, sodium, and zinc (soil parameters with the highest r values from the previous experiment) would be used in the analysis.

In contrast with the first experiment, multiple regression analyses were used in this one instead of simple correlations. Multiple regression analyses were not performed in the first experiment since there were too many variables to take into consideration and which would decrease the effectiveness of the interpretation of the results of the analyses. Several conditions were controlled in the present experiment which allowed for the effective use of multiple regression analysis.

3. Results

The VAM infection levels of seedlings growing in different soils was found to be significantly different (Table 5). Seedlings in soil 3 had the highest VAM infection, those in soils 5 and 7 had lower levels, while those in the nursery soil, and soils 1 and 6 had the lowest VAM infection ($P<0.05$).

A preliminary plotting of the data showed that the relationship between VAM colonization and potassium, sodium and zinc could be best described by a linear function, while the phosphorus:copper ratio could be best described by an inverse (i.e. $f(x)=x^{-1}$) function. Hence, the phosphorus:copper ratio was transformed before a multiple regression analysis was performed. Zinc, sodium, potassium, and $(\text{phosphorus/copper})^{-1}$ explained 60.9% of the total variability in VAM infection (Table 6). However, when phosphorus and copper were used separately along with the other variables in a multiple regression analysis, 81.5% of the total variability was explained (Table 7). Copper explained the most variability at 36.7%, followed by phosphorus at 31.1%, potassium at 5.2%, zinc at 4.9%, while sodium explained the least at 3.7%. All variables were found to have a significant effect on VAM infection ($P<0.05$) (Table 7). The coefficients from the multiple regression analysis show that copper, phosphorus, and zinc were negatively affecting VAM infection, while sodium and potassium were positively affecting VAM infection.

Two significant differences were found between VAM infection of seedlings and that of trees growing in the same soil (Table 5). Seedlings growing in soil type 6, which was collected from a tree growing on René-Lévesque, had a significantly lower average % VAM infection rate (25%) than the street tree growing in the same soil (65%), while soil type 5, which was collected from a tree growing on Bleury, was significantly higher in % VAM (39.8%) than the street tree growing in the same soil (28.0%) ($P<0.05$) (Table 5).

Soil Type	Phosphorus (mg/kg)	Copper (mg/kg)	Zinc (mg/kg)	Sodium (mg/kg)	Potassium (mg/kg)
1	145.5	18.4	43	305	121
2	123.3	8.3	19	675	147
3	38.9	12.8	480	85	144
4	12.9	21.9	25	75	202
5	54.2	68.0	21	195	180
6	27.4	91.2	215	120	146
7	61.3	62.3	113	205	382
Nursery	159.3	5.6	12.7	73	266

Table 4: Nutrient concentrations of the eight soils used in seedling experiment

Soil Type	Seedling % VAM	Field % VAM
1	29.8 (2.0) c	35.5
2	n/a	78.0
3	58.0 (2.4) a	60.0
4	n/a	25.5
5	39.8 (2.8) b*	28.0 *
6	25.0 (1.3) c*	65.0 *
7	43.0 (2.5) b	44.0
Nursery	30.2 (2.7) c	36.1

Table 5: VAM infection rates of silver maple seedlings grown in controlled conditions and trees growing in the field in seven urban soils and one nursery soil

Means and standard errors (in parenthesis) are shown (n=6 for each soil type for seedlings; n/a= no seeds germinated).

Seedling % VAM values with different letters are significantly different according to a Scheffé post-hoc comparison test ($P<0.05$).

Rows with asterisks are significantly different according to a Scheffé post-hoc comparison test ($P<0.05$).

	df	**SS**	**MS**	**F-ratio**	**Coefficient**	**r^2**
Total	35	5342				
Regression	4	3253.117	813.279	12.0694*		0.6090
Zinc	1	2179.002	2179.002	32.3376*	-0.0593	0.4079
$(P:Cu)^{-1}$	1	652.096	652.096	9.6775*	-4.0350	0.1221
Potassium	1	347.230	347.230	5.1531*	0.0382	0.0650
Sodium	1	74.788	74.788	1.1099	0.0216	0.0140
Residual	31	2088.883	67.383			

Table 6: Sums of squares, coefficients and r^2 values from the multiple regression analysis with the phosphorus:copper ratio

*=$P<0.05$.

	df	**SS**	**MS**	**F-ratio**	**Coefficient**	r^2
Total	35	5342				
Regression	5	4352.333	870.467	26.3866*		0.8147
Copper	1	1959.446	1959.446	59.3971*	-0.6613	0.3668
Phosphorus	1	1659.225	1659.225	50.2965*	-0.47805	0.3106
Potassium	1	276.181	276.181	8.3719*	0.03281	0.0517
Zinc	1	259.087	259.087	7.8538*	-0.04581	0.0485
Sodium	1	198.188	198.188	6.0077*	0.03281	0.0371
Residual	30	989.667	32.9889			

TABLE 7: Sums of squares, coefficients and r^2 values from the multiple regression analysis without the phosphorus:copper ratio

*=$P<0.05$.

4. Discussion

The negative relationship between phosphorus, zinc and copper, and % VAM infection in silver maple seedlings found in this study are consistent with other studies that have used crop or annual plants (Leyval, et al. 1995; Abbott and Robson, 1991; Morita and Konishi, 1989; Gildon and Tinker, 1983a), and have implications for the inoculations being conducted by the municipal nursery. These results suggest that VAM species that are tolerant of the high zinc and copper concentrations may need to be used.

A copper tolerant VAM fungus has not yet been discovered; however some researchers have shown some fungal strains are zinc tolerant. Dehn and Schuepp (1989) showed that *Glomus fasciculatum*, G. *etunicatum* and G. *mosseae* increased the zinc resistance of lettuce seedlings. Gildon and Tinker (1983a) determined that a G. *mosseae* strain isolated from a site heavily contaminated with zinc was more efficient in reducing zinc uptake by onions than a strain from an uncontaminated site.

Yet, inoculations involving heavy metal tolerant VAM strains may not be necessary. The main purpose of the inoculations is to reduce the transplantation shock of newly planted trees. VAM would be necessary to increase the supply of water or phosphorus during the critical first two or three years when the trees are trying to establish themselves. The results from the soil survey implied that zinc and copper accumulate in soils. It is not known how quickly they can accumulate, but it is reasonable to suggest that the high concentrations that adversely affect VAM infection may be only attained after the critical two or three years, when high VAM colonization are not required as much.

Kim and Weber (1985) and Gildon and Tinker (1983) concluded that sodium could reduce or inhibit VAM germination. Sodium concentrations for these studies were as high as 10,000 ppm. This amount of sodium rarely occurs in street tree soils and was not tested in the present study. In addition, trees transplanted in downtown Montreal are already mycorrhizal and, therefore, their mycorrhizal development does not depend on spore germination. Kim and Weber (1985) found that soils with sodium concentrations of 153 ppm were colonized at a rate of 34.2%, which is similar to the amount of infection found in the present study for soils with similar sodium concentrations.

It is interesting to note that the significant negative effect of potassium on VAM colonization that was found in the first study was not observed in the present experiment. In fact, a slight positive relationship was detected by the multiple regression analysis. Zahka, et al. (1995) also found a positive relationship between this nutrient and colonization levels. However, no reasons were presented for this observation due to the lack of information on the regulating role of soil potassium in VAM symbioses. A thorough examination of the effect of soil potassium on VAM development is needed to determine whether there are positive or negative interactions and how they occur.

It was suggested that the negative correlation between potassium and VAM infection in the first study was due to competition between sodium and potassium. The seedlings in this study were only allowed to grow for five weeks. It is possible that this length of time was not long enough for the competition between sodium and potassium to occur. It is necessary to conduct a longer term study to determine whether this competition can occur in seedlings grown in controlled conditions.

By growing the seedlings in controlled conditions several factors that affected VAM colonization in the street trees, such as reduced light levels, or water stress, were removed from the present study. The significant differences found between VAM infection of the seedlings and the street trees growing in soil type 5 and 6 suggests that soil parameters were likely more important for VAM development in the seedlings than for the street trees.

The present study has filled some gaps in our knowledge of VAM colonization by examining how the chemistry of some typical urban soils affects VAM infection rates. Although the effects of each of the soil variables were not separated, in a large number of cases it is most useful to determine the combined effects of the various soil parameters. Knowledge of the specific effect of a soil parameter on VAM development is not necessarily required by researchers conducting inoculations at the Montreal municipal nursery. On the other hand, "real world" information of the combined effects of various factors is needed, since inoculated trees will not be transplanted in theoretical situations, but rather in "real" soil.

CHAPTER 4

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

This thesis has reported on a preliminary examination of VAM and silver maple tree health in downtown Montreal. The data show that trees from downtown Montreal grow in soils with lower concentrations of phosphorus and magnesium, higher concentrations of copper, zinc and sodium, and higher values of pH and bulk density than nursery soils. Street tree health, in terms of % dieback, was found to be positively correlated with soil phosphorus, potassium, calcium, and the phosphorus:copper ratio, and negatively correlated with soil copper, zinc and bulk density. It was suggested that the high sodium levels may be involved in the relationship between potassium and calcium, and tree health.

The data suggest that tree location is an important factor in determining the survival of street trees. Type 3 streets seem to provide the best conditions as these streets had the oldest and healthiest trees, while type 4 streets provided the least favourable conditions. The conditions that seem to be related to tree location include light levels, wind and probably most importantly soil volumes that are available to tree roots.

This thesis has also provided information regarding the status of VAM colonization levels of street trees. Downtown trees had significantly higher colonization levels (44.9%) than nursery trees (36.1%). The colonization levels of street trees was positively correlated with the phosphorus:copper ratio and negatively correlated with soil potassium. The negative correlation between colonization and soil potassium could not be fully explained due to the lack of information regarding the effect of potassium on

VAM development.

Colonization levels were also found to be positively correlated with tree age, which in turn is related to % dieback and tree location. Hence, I speculate that stressed trees invest more in the symbiosis, since the symbiosis acts as a buffer against certain stresses, such as low phosphorus or water availability.

Since inconclusive results were obtained in terms of the effect of typical street soils on VAM development, research was conducted under controlled conditions, using seven different soils collected from downtown Montreal. The effect of representative soil nutrient concentrations on VAM development was determined. VAM development was negatively affected by zinc, phosphorus and copper positively affected by sodium and potassium.

Although this research has answered many of the questions regarding the health of downtown Montreal silver maples and the role of VAM in this environment, the following indicates research required to further understand this symbiosis and increase the survival rates of urban trees:

1. What are the main environmental factors affecting urban tree health? Are there tree species that are more resistant to these stresses and can they be used for street tree plantings? Can the negative soil factors be removed by cultural practices, such as fertilization or irrigation?

2 What are the specific effects of typical urban soil parameters on VAM development? What are the impacts of other factors, such as light levels, on VAM?

3. What are the effects of VAM associations on urban tree health, nutrient and water uptake? Do VAM fungi provide a resistance to various urban environmental

stresses? Can VAM inoculations improve the survival rates of street trees?

4. Which VAM species exist in urban soils and what are their relative abundances in street tree roots? What is the morphology (arbuscules:vesicles) of these associations? Which species should be used to effectively inoculate urban trees?

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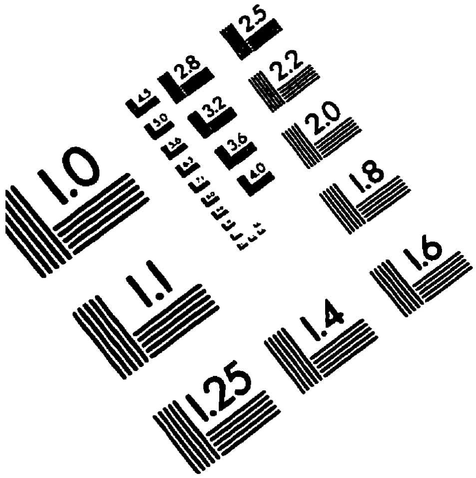
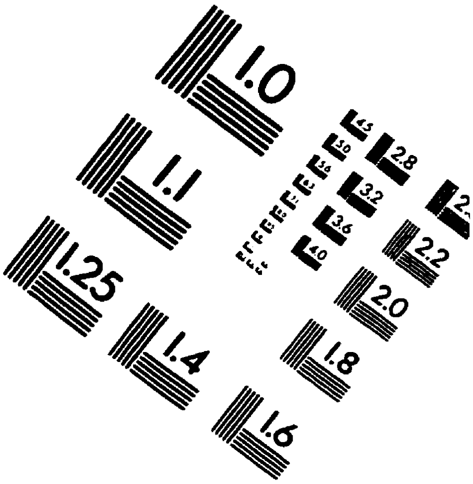
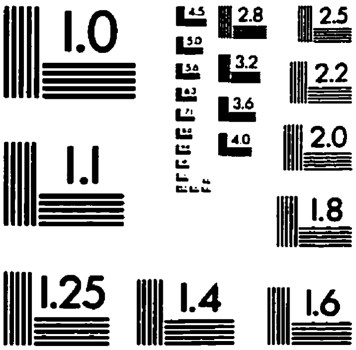
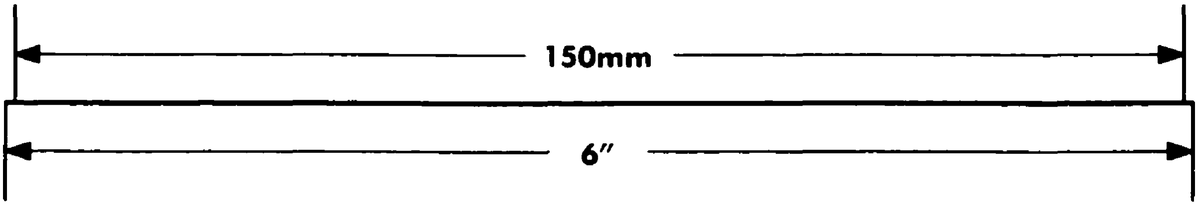
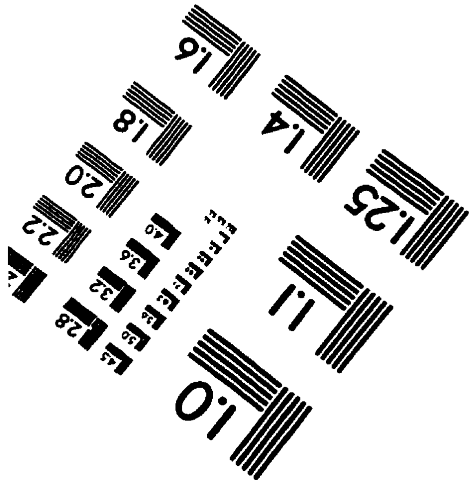
IMAGE EVALUATION
TEST TARGET (QA-3)

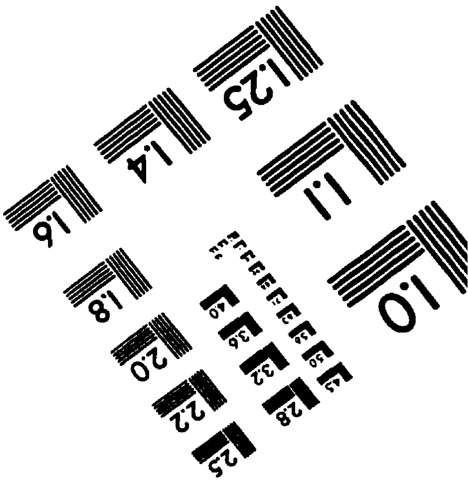












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